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Roost-site Selection and Roosting Ecology of Forest-Dwelling
Bats in Southern British Columbia

by

Maarten J. Vonhof

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled "Roost-site Selection and Roosting Ecology of Forest-Dwelling Bats in Southern British Columbia" submitted by Maarten J. Vonhof in partial fulfillment of the requirements for the degree of Master of Science.



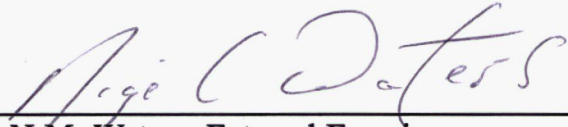
Dr. R.M.R. Barclay, Supervisor
Department of Biological Sciences



Dr. R. Longair
Department of Biological Sciences



Dr. E.A. Johnson
Department of Biological Sciences



Dr. N.M. Waters, External Examiner
Department of Geography

ABSTRACT

I examined the roosting ecology and roost-site preferences of forest-dwelling bats in southern British Columbia during the summers of 1993-94. Tree-roosting bats showed a strong preference for tall trees associated with low percent canopy closure and a small distance to the nearest available tree, and preferred western white pine trees in intermediate stages of decay. Tree roosting bats exhibited fidelity to a group of trees in a relatively small area, and switched roosts frequently.

Stump-roosting bats selected clearcuts providing large numbers of uncluttered stumps containing deep cavities, relative to clearcuts in which I found no bats roosting. Within clearcuts bats selected large diameter stumps with deep cavities that were relatively unobstructed by surrounding herbaceous vegetation. By roosting in stumps of this type, bats roosting in clearcuts gain significant thermoregulatory benefits, but at the same time are exposed to an increased risk of predation.

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To my parents,

Tina and Albert

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CHAPTER 1. INTRODUCTION

An animal's optimal habitat is that in which it experiences the highest reproductive success. Thus, natural selection favours those individuals in a population that select optimal habitats from the choices available. However, the factors influencing animals' decisions to use particular habitats are often poorly understood. Both predation (Martin 1993) and competition (e.g., Murie 1971, Jenssen 1973, Grant 1975) may play important roles in determining habitat use, and when these constraints are absent organisms may choose very different habitats than those in which they are typically found. Various other factors may also influence an organism's habitat use, such as the abundance and availability of shelter, the distribution and abundance of food resources, and the animal's social organization (Kunz 1982). The habitat selected by an organism is a reflection of the constraints acting on it, and is a function of some or all of these factors in combination.

Bats spend over half their lives subject to the selective pressures of their roost environment (Kunz 1982). Roosts provide sites for mating, rearing young, and hibernation. They also promote social interactions and offer protection from the ambient environment and from predators. Thus, the selection of roost-sites has important consequences in terms of survival and fitness.

Bats roost in a variety of structures, including caves, man-made structures, rock crevices, tree foliage, and tree cavities (Barbour and Davis 1969, Kunz 1982). Although the habits of bats roosting in caves, man-made structures and rock crevices are relatively well known (Kunz 1982), very few studies have specifically investigated the roost-site characteristics of forest-dwelling bats. This is because roosts in trees are relatively inaccessible to humans and difficult to find compared to roosts in other structures.

Individuals of many species of bats cluster into roosting colonies ranging in size from several to millions of individuals. Tree cavities generally cannot support as many bats as other types of roosts, but may house colonies of 10's or 100's of bats. Bats benefit by clustering in these colonies through reduced thermoregulatory costs, which are a major determinant of roost-site selection (Kunz 1982, Kurta 1986). Tightly clustered bats generally have more stable body temperatures, and experience lower metabolic costs for thermoregulation than do solitary bats (Kurta 1985, 1986, Kurta and Kunz 1988, Roverud and Chappell 1991, Genoud 1993). Clustering is often associated with higher body temperatures (Howell 1976, Kurta 1986), and this may be particularly important for pregnant females, as low temperatures slow fetal and juvenile development (Racey 1973, Racey and Swift 1981, McNab 1982). The exact thermal benefits experienced by a cluster of bats also depend on the insulation of the roost from the ambient environment, and in tree cavities this is influenced by wall thickness and state of decay (Moore 1945, Kurta 1985). Furthermore, the placement of a roost on a particular tree and the position of that tree within the forest canopy, will influence the amount of sunlight reaching the roost, and the degree to which the roost will be heated.

Roost selection by bats may differ between males and females, and among females in different stages of reproduction. Female bats should maintain a high body temperature during pregnancy and lactation to avoid delays in fetal or juvenile growth (Racey 1973, McNab 1982) and evidence supports this prediction (Audet and Fenton 1988, Hamilton and Barclay 1994). Males may be free to enter torpor more frequently as they do not have the reproductive burden of pregnancy and lactation (Williams and Findley 1979, Keen and Hitchcock 1980, Hitchcock *et al.* 1984). Males tend to roost singly or in small clusters (Menaker 1969, Kurta and Kunz 1988), and enter torpor on a regular basis (Hamilton and Barclay 1994, Grinevitch *et al.* 1995; but see Kurta and Kunz 1988). The different behaviours of males and females should result in differences in roost selection.

Another factor influencing roost selection by bats is predation. Bats returning to roosts often make a number of short, circling flights around the entrance before landing and crawling into the roost (e.g., Medway and Marshall 1972, Voute *et al.* 1974, Vaughan and O'Shea 1976, Barclay *et al.* 1982). This may increase the susceptibility of bats to aerial predators, such as owls, hawks, and falcons (Twente 1954, Downing and Baldwin 1961, Baker 1962, Barclay *et al.* 1982, Rodriguez-Duran and Lewis 1985, Fenton *et al.* 1994). The ease with which bats enter and leave their roost will determine the length of time they are exposed to predation, and thus bats may select tall, open trees which provide easy access.

Bats are also vulnerable to predation within their roosts, and may be relatively helpless if they have entered torpor. A variety of predators prey on bats and cavity nesting birds in their roosts, including weasels and other mustelids (Mumford 1969, Erskine and McLaren 1972, Dunn 1977), snakes (Dennis 1971, McIntosh and Gregory 1976, Lemke 1978), flying squirrels (*Glaucomys volans*; Loeb 1993), raccoons (*Procyon lotor*; Rendell and Robertson 1989), voles (*Microtus ochrogaster*; Martin 1961), chipmunks (R. Holt pers. comm., V. Campbell pers. comm.), red squirrels (*Tamiasciurus hudsonicus*; Erskine and McLaren 1972, Nilsson 1984a), and even bears (Erskine and McLaren 1972). Nilsson (1984a) and Rendell and Robertson (1989) found that nest predation rates on cavity nesting birds were significantly higher for roosts closer to the ground, and Rendell and Robertson (1989) found that nest sites where young fledged were significantly higher than those which were preyed upon. Thus, bats may select roosts high in tall trees to minimize exposure to ground predators.

Tall roost trees emerging from the surrounding canopy may also function as landmarks. Tinbergen (1951) found that when digger wasps left their burrow they hovered above the burrow entrance and used objects around the entrance as landmarks. Similarly, the circling flights characteristic of emerging bats immediately outside their

roost may serve to orient the bats as to the position of their roost tree within a forest stand. Bats that learn the spatial cues in the environment around and including the roost tree may significantly reduce time and energy spent searching for the roost-site.

Different tree species decay in different ways at different rates (e.g., Cline *et al.* 1980). As trees decay, they provide a varying number of suitable cavities for roosting bats. The roost-site preferences of bats roosting beneath loose bark, in particular, will be subject to the varying ways and stages of decay at which the bark of different tree species splits off from the trunk. On the other hand, the preferences of cavity roosting bats will be closely linked to the dynamics of natural cavity formation, or to the preferences of primary cavity excavating birds, on which bats may depend for cavities. Thus, the tree species and decay state preferences of tree roosting bats will be closely linked.

Tree-roosting bats switch roost trees relatively frequently (Medway and Marshall 1972, Fenton 1983, Fenton and Rautenbach 1986, Brigham 1991, Fenton *et al.* 1993), possibly due to predation risk (Bradbury and Emmons 1974, Morrison 1980, Fenton 1983, Fenton *et al.* 1994), parasite load (Wilkinson 1985, Lewis 1992), changing environmental temperatures (Humphrey *et al.* 1977), or to the ephemeral nature of roost-sites on dead trees (Kurta *et al.* 1993b). If suitable roost sites are not limited, individuals may have the option of selecting several sites between which they move regularly (Brigham 1991). Bats selecting particular areas for roosting (e.g. close to foraging sites) should switch roosts within those areas, and the distance between roost trees should be relatively short compared to distances travelled when foraging (Brigham 1991). The use of a number of roost trees within a limited area has been observed (e.g., Lunney *et al.* 1988, Taylor and Savva 1988, Brigham 1991, Fenton *et al.* 1993, Kurta *et al.* 1993a,b).

The roosting ecology of forest-dwelling bats is poorly understood. The purpose of my research was thus to examine the characteristics of roost trees used by bats, and

to determine whether bats are selecting trees at random or are selecting roost trees with certain characteristics and in certain forest types. I tested the following specific predictions:

HYPOTHESIS 1: Bats are selective in their choice of roost-sites.

PREDICTION 1: Bats select trees with greater than average height, and greater height than other trees in the immediate vicinity. By selecting trees of this kind bats may reduce search time associated with returning to the roost, reduce the time spent approaching and entering the roost, and minimize the flight distance to clear the canopy. By selecting tall trees bats will also benefit from increased exposure of the roost tree to sunlight.

PREDICTION 2: Bats select roosts with entrances at or near the top of the canopy, providing protection from ground predators, and reducing the time spent approaching and entering the roost.

PREDICTION 3: Bats select roosts with low percent canopy closure in the area immediately surrounding the tree. This would increase the exposure of the roost tree to sunlight, and minimize potential costs associated with approaching and leaving the roost tree.

PREDICTION 4: Bats roosting inside cavities select trees with large diameters. Larger cavities generally allow for larger colony sizes, which, along with the greater thermal inertia and thickness of insulation associated with larger diameter trees, will provide more suitable roost microclimates.

PREDICTION 5: Bats do not roost at random with respect to the availability of species of wildlife trees. Different species of trees provide different physical characteristics, influencing microclimate, and different numbers and kinds of roosting opportunities.

PREDICTION 6: Bats do not roost at random with respect to the availability of decay stages of wildlife trees. Trees in different stages of decay provide different physical characteristics, influencing roosting opportunities.

HYPOTHESIS 2: Bats exhibit fidelity to a particular group of trees or area of a forest.

PREDICTION 7: The distance between subsequent roost trees will be short, reducing search times and flight distances, and minimizing the time the bats are exposed to aerial predators.

CHAPTER 2. ROOST-SITE PREFERENCES OF TREE-ROOSTING BATS

INTRODUCTION

In summer, temperature zone bats spend over half of each day in a roost site. Because of this, roosts play a vital role in the lives of bats, and the selection and function of roosts has received much attention (Kunz 1982). 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 (Kurta 1985, Kurta and Kunz 1988, Roverud and Chappell 1991). 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 centered 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 used by bats are simply descriptions of small numbers of roost trees (e.g., Barclay and Cash 1985, Parsons *et al.* 1986, Kurta *et al.* 1993a, b; see references in Kunz 1982), or anecdotal accounts of bats found in hollows or crevices in trees (e.g., references in Barbour and Davis 1969, Nagorsen and Brigham 1993). 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.

Many bat species reside in forests and are considered to be dependent on trees for their roosting sites (Barbour and Davis 1969, Kunz 1982, Lunney *et al.* 1988, Nagorsen and Brigham 1993). The lack of research into the roosting requirements of these forest-dwelling bat species has left a large gap in our knowledge of the ecology and behaviour of bats. Understanding the factors influencing diurnal roost-site selection by bats is important not only for the conservation and maintenance of forest-dwelling bat species, but also for understanding the general principles underlying habitat selection.

The purpose of this study was to determine whether bats select trees for certain characteristics, or whether they simply select trees at random based on their availability. In this study I set out to find and characterize tree roosts used by bats in southern British Columbia. By comparing roost trees with randomly selected trees, I could then examine the specific tree and site characteristics selected by bats.

METHODS AND MATERIALS

Study Areas

I conducted the study during the summers of 1993 and 1994 in the West Arm Demonstration Forest (WADF), located 20km east of Nelson, B.C. along Kootenay Lake (117°05'W, 49°38'N; Fig. 1). The WADF is approximately 14,800ha in size and encompasses four complete watersheds. My study concentrated on the two western-most watersheds, Kokanee Creek and Redfish Creek, as these had road access. The WADF extends from an elevation of 650m (just above lake level) well into the subalpine region, to an elevation of 1800m. Over this elevation range the WADF encompasses a wide range of forest types and stand ages. At lower elevations a mixed coniferous forest with 12 major tree species predominates. At middle elevations the forest is primarily composed of western red cedar (*Thuja plicata*) and western hemlock

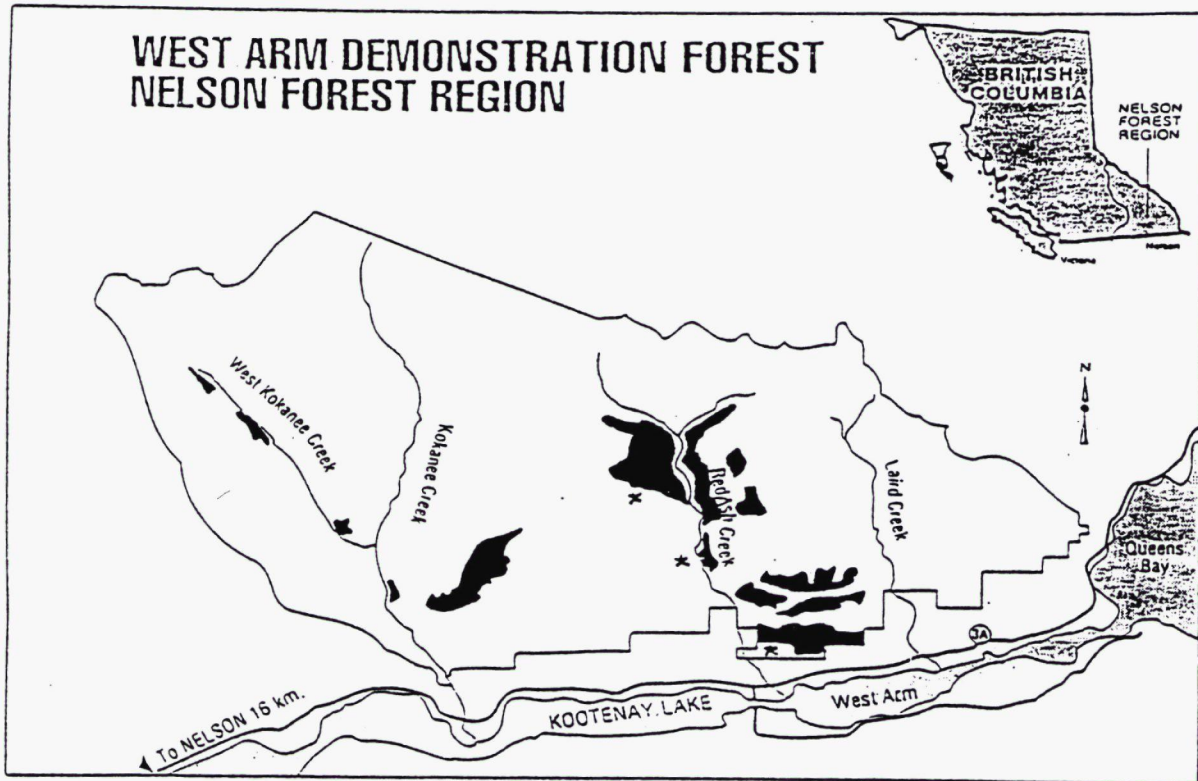


Figure 1. The West Arm Demonstration Forest.

(Tsuga heterophylla). At high elevations the forest is largely Engelmann spruce (Picea engelmannii) and subalpine fir (Abies lasiocarpa).

I conducted additional work during July 1994 in the Pend d'Oreille Valley (POV), situated directly north of the United States border in southern B.C. (117°27'W, 49°02'N). The river is dammed in several places, such that several large reservoirs take up much of the valley. The forests in the valley are dominated by Douglas-fir (Pseudotsuga menziesii) and to a lesser extent trembling aspen (Populus tremuloides), and extend from elevations of 550m (at reservoir level) up to a maximum of 1500m.

Bat Captures

Bats were captured in mistnets set over slow-moving or still water, along clear-cut edges, and across roads at various locations and elevations throughout the Kokanee Creek and Redfish Creek watersheds. Individuals 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 1988) for all captured individuals.

Roosting Sites

Roost sites were located using two methods. The first involved watching trees at dusk for emerging bats. Trees were arbitrarily selected at various locations in the WADF and watched from 10min before to 30min after local sunset. The presence of emerging bats was noted and emerging bats were classified as either small bats (Myotis spp.) or big bats (Eptesicus fuscus, Lasionycteris noctivagans), but exact species identifications could not be made.

The second method was radio-tracking. I attached small (0.6 - 0.8g; Model BD2, Holohil Systems Ltd., 3387 Stonecrest Road, Woodlawn, Ontario, Canada, K0A 3M0) radio-transmitters to female and male L. noctivagans, Myotis evotis, and M. volans, and to female E. fuscus. 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 (Merlin 12, Custom Electronics, 2009 Silver Court West, Urbana, IL 61801) and five-element yagi antennae. All roosts found by radio-tracking were verified by watching the tree at dusk for emerging bats. This also provided data on colony sizes, entrance heights, and entrance aspects.

Radio-transmitters remained attached to bats for up to four weeks. I tracked bats on successive days, for as long as the radio-transmitter remained functional, to determine how long individual bats remained in a particular roost site (residence time). Residence times are conservative estimates, as the residence time for a particular roost only included known dates; I did not know how long colonies or individuals had been using particular roost trees before I found them. I also measured the horizontal distance and elevation change between subsequent roost trees used by the same individual. Climatic data were obtained from meteorological stations placed throughout the WADF. I counted days of rain only if at least 2 mm of rain fell at any time during a particular day, and evenings of rain if at least 2mm of rain was deposited from 1800h to sunset.

Once roosting sites had been located, I measured a range of tree and site 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. To measure entrance aspect I faced the entrance, took a bearing which bisected the entrance using a compass, and recorded the opposite bearing. Data were corrected to true north. Two observers independently estimated the percent bark remaining on the tree and the mean was taken. Elevation was determined using a Casio digital altimeter, or taken from topographic maps. Stand ages were obtained from B.C. Ministry of Forests forest cover maps. I also measured the height of two downslope trees, defined

as the two nearest trees to the roost tree in a 90° arc directly downslope from the roost tree.

I classified each roost tree into one of nine decay stages (Table 1) based on characteristics of the tree such as the percent 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 2-7, as by definition decay stage 1 trees and decay stage 8-9 trees provide no suitable roosting opportunities for bats.

I established a 17.8m radius (0.1ha) circular plot around each roost tree. I measured all other available trees, defined as trees in decay stages 2-7 not known to contain bats, in the same manner as the roost trees. The percent 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 2-6) within the canopy using a clinometer and took the mean to estimate canopy height within the plot.

I measured the thickness of the bark on 10-15 randomly selected trees of varying diameters for each of the 13 major tree species found in the WADF. These data were analyzed to give a predictive equation for determining bark thickness at the height of the roost for each tree species, using simple regression analysis on log-transformed data. I estimated the tree diameter at the height of the roost from the ground, or directly measured it when possible.

To facilitate testing of the hypothesis that bats select certain characteristics of trees, I measured a sample of available trees to compare with roost trees. I selected a random point between 100-300m 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. Stands were delineated using air photos. I selected a

Table 1. Decay stage classification system applied to roost and available trees. All trees were coniferous. Modified from Cline *et al.* (1980) and Backhouse and Lousier (1991).

Stage	Description
1	Live, healthy; no decay; no obvious defects
2	Live, usually unhealthy; obvious defects such as broken top, cracks, or hollows present
3	Recently dead; dead needles still present, very little decay; heartwood hard
4	Dead; no needles/few twigs present; top often broken; <50% of branches lost; bark loose; heartwood hard; sapwood spongy
5	Dead; most branches and bark lost; top broken; heartwood spongy; sapwood soft
6	Dead; no branches or bark; broken off along mid-trunk; sapwood sloughing from upper bole; heartwood soft
7	Dead; stubs >3m in height; heartwood soft; extensive internal decay; outer shell may be hard
8	Dead; stubs <3m in height; heartwood soft; extensive internal decay; outer shell soft
9	Debris; downed stubs or stumps; extensive decay

minimum distance of 100m so that the available tree would lie outside the mean distance between subsequent roost trees used by individual bats (see Results), and a maximum distance of 300m to increase the probability that I remained within the same stand. I established a 17.8m radius (0.1ha) plot around the focal tree and measured all available trees within the plot in the same fashion as for roost trees.

To determine whether bats select roost trees for certain characteristics, I performed a stepwise discriminant function analysis including the variables outlined in Appendix 1 on the two groups of trees: roost trees and available trees. The sample of available trees consisted only of focal trees, to avoid large imbalances in sample size between the two groups. All roost trees were considered together in all analyses regardless of which bat species used them, because sample sizes did not permit separate analyses for single bat species. Trees from the WADF and the POV were grouped in all analyses. 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. The TSSCC's indicate the position of each discriminating variable along the discriminant axis. 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. Because tree species, decay stage, and top condition are categorical and could not be included in the discriminant function analyses, I analyzed them separately using randomization and likelihood ratio tests, comparing roost and available trees.

Because of the circular nature of directional data, I used circular statistics outlined in Zar (1984) to analyse directional data in most cases. I used V-tests with an expected angle of 180° to test whether entrances were uniformly distributed around roost trees, and Watson-Williams test for two samples to test for differences in the

entrance aspects used by bark and cavity roosting bats. To include directional data in the stepwise discriminant function analyses, I transformed directions by taking the absolute value of their deviation from 180°, thereby converting them to a more meaningful form for these analyses.

I analyzed residence time in each roost using multiple factor ANOVA's, and performed separate analyses for roost type (within L. noctivagans) and bat species (bark roosts only). Variables included in the model were individual bat, sex, number of days of rain during roosting period, number of evenings rained during roosting period, and either roost type or bat species, depending on the analysis.

RESULTS

Eight species of bats were captured during the study in the WADF and the POV (Table 2). A total of 23 bats (19 females and 4 males) of five species (E. fuscus, L. noctivagans, M. evotis, M. volans, and M. yumanensis) were outfitted with radio-transmitters. I watched a total of 73 randomly selected trees for 105 hrs during the summer of 1993.

Roost Trees

The combination of the two location methods led me to 21 roost trees over the two summers. I found sixteen trees by radio-telemetry and five by watching trees. Fifteen of the roosts were beneath loose bark and six were in abandoned woodpecker hollows (Appendix 2). I found eight roost trees used by L. noctivagans, five by M. volans, three by M. evotis, three by Myotis spp., and two by E. fuscus. Colony sizes were generally small (1-7 individuals; Appendix 2), and I commonly found bats roosting alone (13 of 19 cases; Appendix 2). Three radio-tagged female E. fuscus roosted in the attics of two houses at lower elevations, and the colonies contained 20 and 28 bats, respectively. All three bats were initially caught feeding along the edges

Table 2. Bats species captured and the number of bats radio-tagged in the WADF and the POV during the summers of 1993-94.

Bat Species	Number of Bats Radio-Tagged			
	WADF		POV	
	Females	Males	Females	Males
<u>Eptesicus fuscus</u>	4	0	0	0
<u>Lasionycteris noctivagans</u>	5	1	4	1
<u>Lasiurus cinereus</u>	0	0	0	0
<u>Myotis californicus</u>	0	0	0	0
<u>M. evotis</u>	3	1	0	0
<u>M. lucifugus</u>	0	0	0	0
<u>M. volans</u>	2	1	0	0
<u>M. yumanensis</u>	1	0	0	0

of clearcuts at higher elevations.

Four of the 21 roost trees were contained maternity colonies of L. noctivagans with between 5 and 21 individuals. The maternity colonies were all situated in abandoned woodpecker cavities. In one case, the radio-tagged female used three bark roosts in succession (for between 1 and 10 days each), both alone and with four other bats, and then switched to an abandoned woodpecker hollow with four other individuals and remained there for at least 13 days.

The roost, tree, and site characteristics of all roost trees, and the summary statistics, are outlined in Appendices 2, 3, and 4, respectively. Of the 22 variables initially entered into the stepwise discriminant function analysis (Appendix 1), only three variables significantly discriminated between roost trees and available trees (Table 3). Tree height was the first variable entered into the discriminant function, and accounted for 49.6% of the variation between roost and available trees (Table 3). Horizontal distance to the nearest available tree and percent canopy closure also significantly discriminated between the two groups of trees, and the two variables each explained just over 10% of the variation between them (Table 3).

Based on the canonical discriminant function analysis, 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 for tree height was positive and large, whereas the TSSCC's for both horizontal distance to the nearest available tree and percent canopy closure were considerably smaller and negative (Table 3). These results indicate that roost trees tend to be taller, are closer to other available trees, and have lower percent canopy closure than available trees do. Furthermore, tree height is a stronger discriminator between roost and available trees than either horizontal distance to the nearest available tree or percent canopy closure. The classification error rates (cross-validation) for roost trees and available trees were low, at 9.5% and 12.5%, respectively, and the overall classification error rate was 11%.

Table 3. Summary of the stepwise discriminant function analysis on tree and site characteristics of roost and available trees found in the WADF and the POV. The magnitude and sign of the total-sample standardized canonical coefficient (TSSCC) for each variable gives its position along the discriminant axis. The centroids for roost trees and available trees lie at the positive and negative ends of the discriminant axis, respectively.

Variable	Order Included	<i>F</i>	<i>P</i>	Partial <i>R</i> ²	TSSCC
Tree Height	1	53.06	0.0001	0.496	1.385
Horizontal Distance to Nearest Available Tree	2	7.22	0.0096	0.120	-0.467
Percent Canopy Closure	3	6.42	0.0144	0.110	-0.419

I found significant positive correlations between tree height and DBH; tree height and tree height relative to canopy height; DBH and tree height relative to canopy height; and DBH and the horizontal distance to the nearest neighbouring tree (Table 4). Significant negative correlations were found between percent canopy closure and horizontal distance to nearest neighbouring tree; elevation above valley bottom and tree height relative to canopy height; tree height and percent bark remaining; horizontal distance to nearest neighbouring tree and available tree density; and tree height relative to canopy height and percent bark remaining (Table 4).

Roost Entrances

Entrance heights ranged considerably, from 8 - 29.8m (mean = 18.4m; Appendix 2), and no significant differences were found between the entrance heights used by *L. noctivagans*, *M. evotis* and *M. volans* (Kruskal-Wallis; $\chi^2=6.79$, d.f. = 4, $P>0.10$) or by bats in bark versus cavity roosts (Kruskal-Wallis; $\chi^2=0.035$, d.f. = 1, $P>0.85$). Entrance height and tree height were positively correlated (Pearson correlation; $r=0.57$, $N=18$, $P<0.05$), but entrance height and canopy height were not ($r=-0.02$, $N=18$, $P>0.9$). Entrances tended to be considerably lower than the top of the tree (mean $\pm$ SD: 9.6 ± 6.85 m), and were significantly lower than canopy heights (paired t -test; $t_{17}=-4.52$, $P<0.001$). Entrance aspects also varied considerably, from 70° to 336° , with an overall mean of 186° . Entrance aspects were not uniformly distributed around roost trees (V -test; $\chi^2=1.84$, $P<0.05$) when bark and cavity roosts were combined. The mean entrance aspect for bark roosts ($N=12$) and cavity roosts ($N=6$) was 220° and 102° , respectively, and there was a significant difference between the entrance aspects of bats roosting in bark and cavity roosts (Fig. 2; Watson-Williams test for two samples; $F_{1,16}=10.29$, $P<0.01$). Entrance aspects for bark roosts were not distributed uniformly around roost trees (V -test; $\chi^2=1.95$, $P<0.05$), but entrance

Table 4. Correlation matrix of selected variables included in the discriminant functions analysis of tree and site characteristics, including roost and available tree data. Bracketed numbers refer to: (1) Diameter at breast height; (2) Tree height; (3) Tree height relative to canopy height; (4) Horizontal distance to the nearest available tree; (5) Percent canopy closure; (6) Horizontal distance to the nearest neighbouring tree; (7) Elevation above the valley floor; (8) Available tree density; (9) Percent bark remaining.

	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)
(1)	0.608 ***	0.321 *	-0.009	-0.200	0.321 *	-0.056	-0.162	-0.143
(2)		0.817 ***	-0.025	-0.178	0.204	0.123	-0.133	-0.355 **
(3)			-0.040	-0.254 *	-0.007	0.146	-0.026	-0.330 **
(4)				-0.018	-0.007	0.244	-0.276 *	0.170
(5)					-0.321 *	-0.302 *	-0.145	0.141
(6)						0.118	-0.098	-0.117
(7)							0.070	-0.044
(8)								0.048

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

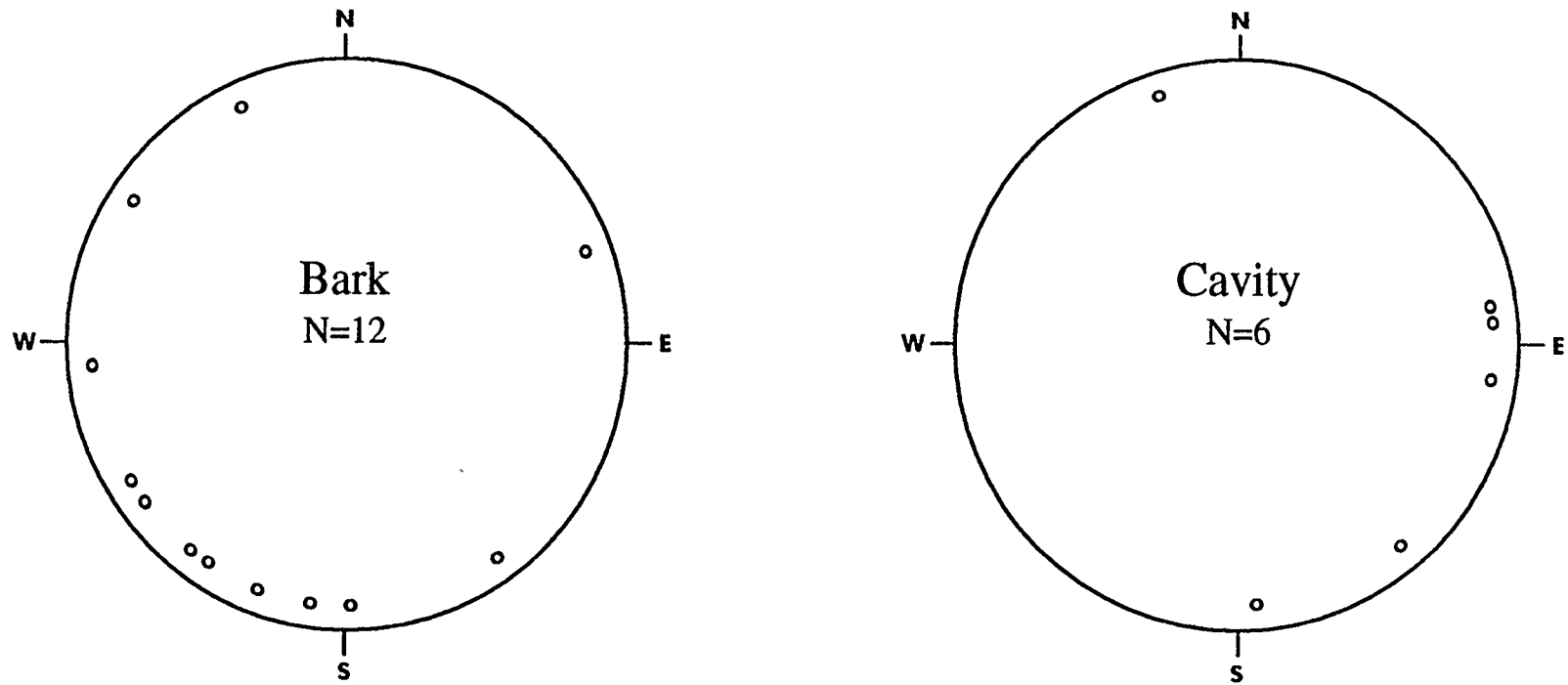


Figure 2. The distribution of compass bearings of entrance aspects for bark roosts and cavity roosts found in the WADF and the PDV.

aspects of cavity roosts were ($\chi^2=0.415$, $P>0.25$).

Tree Species and Decay Characteristics

Bats did not roost at random with respect to the availability of different tree species (Randomization test; $\chi^2=28.39$, $P<0.01$; Fig. 3). Instead, bats showed a clear preference for western white pine (*Pinus monticola*), and to a smaller extent western larch (*Larix occidentalis*) and ponderosa pine (*P. ponderosa*). Bats roosted less frequently than expected in Douglas-fir (*Pseudotsuga menziesii*), lodgepole pine (*P. contorta*), western hemlock (*T. heterophylla*), and western red cedar (*T. plicata*), based on their availability. Bats did not roost in any grand fir (*Abies grandis*), subalpine fir (*A. lasiocarpa*), or trembling aspen (*Populus tremuloides*). Twelve of the fourteen bark roosts were located in western white pine trees, and the other two were found in a lodgepole pine snag and a western hemlock snag. Cavity roosts were located in western hemlock, Douglas-fir (2), western white pine, western red cedar, western larch, and ponderosa pine.

Bats also did not roost at random with respect to the availability of different decay stages (Randomization test; $\chi^2=29.80$, $P<0.001$; Fig. 4). Bats only roosted in trees of decay stages 2, 4, and 5, and roosted more frequently than expected in decay stages 4 and 5, based on their availability. All bark roosts were found in either decay stage 4 or 5 (seven in each), and cavity roosts were located in all three decay stages (one in stage 2, two in stage 4, and four in stage 5). No preference was exhibited by bats for trees with broken or unbroken tops (Likelihood Ratio Test; $\chi^2=0.017$, $P>0.85$).

Roost Fidelity

The mean ($\pm$ SD) residence time in a roost for all individual bats combined was 11 ± 5.9 days (Table 5). With maternity colonies excluded, the mean residence time for individuals was 6 ± 3.7 days. No significant difference in residence time was

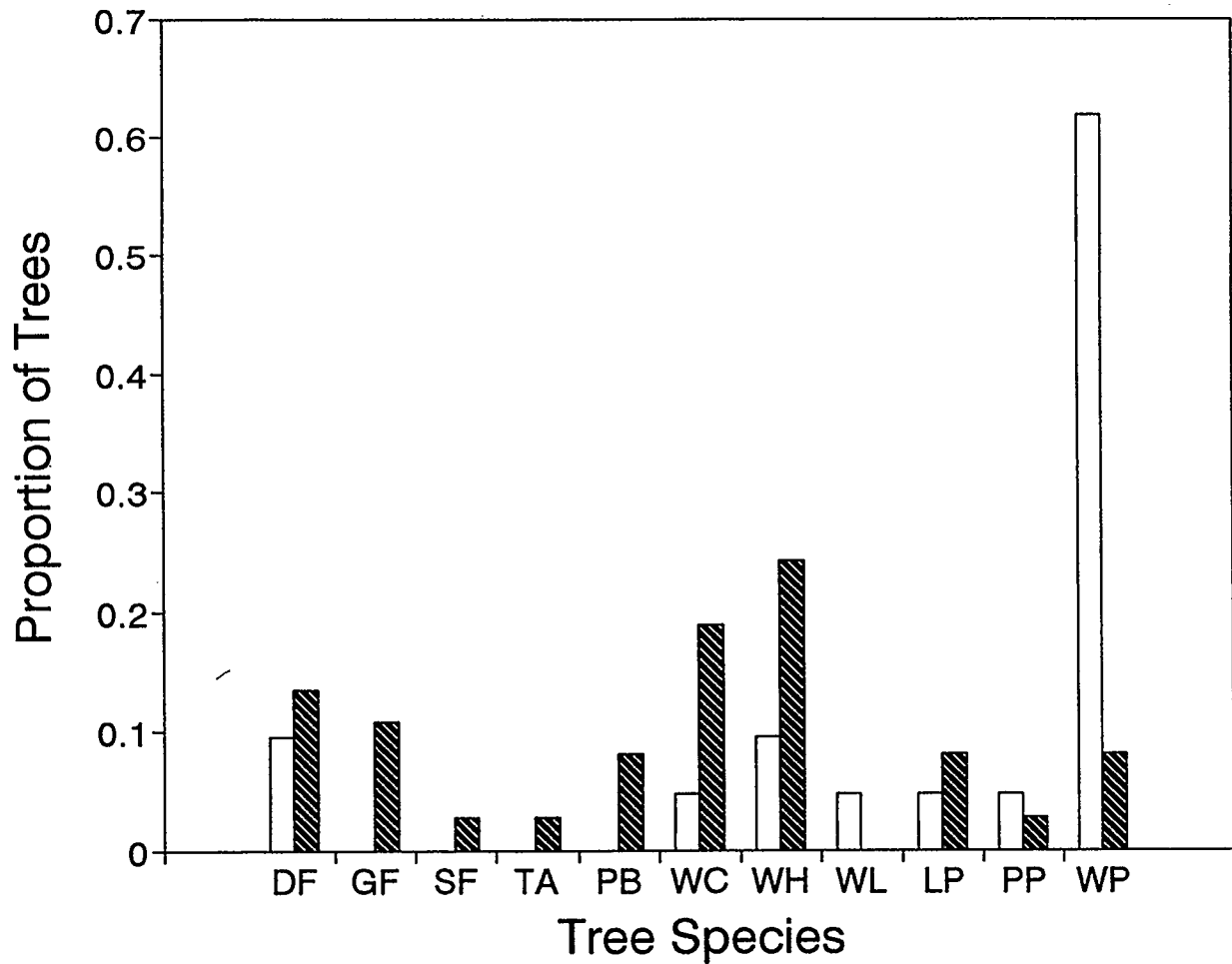


Figure 3. The proportion of roost and available trees in the 11 major tree species found in the WADF and POV. Roost trees are denoted by clear bars, and available trees by filled bars. Tree species notation is as follows: DF=Douglas-fir, GF=grand fir, SF=subalpine fir, TA=trembling aspen, PB=paper birch, WC=western red cedar, WH=western hemlock, WL=western larch, LP=lodgepole pine, PP=ponderosa pine, WP=western white pine.

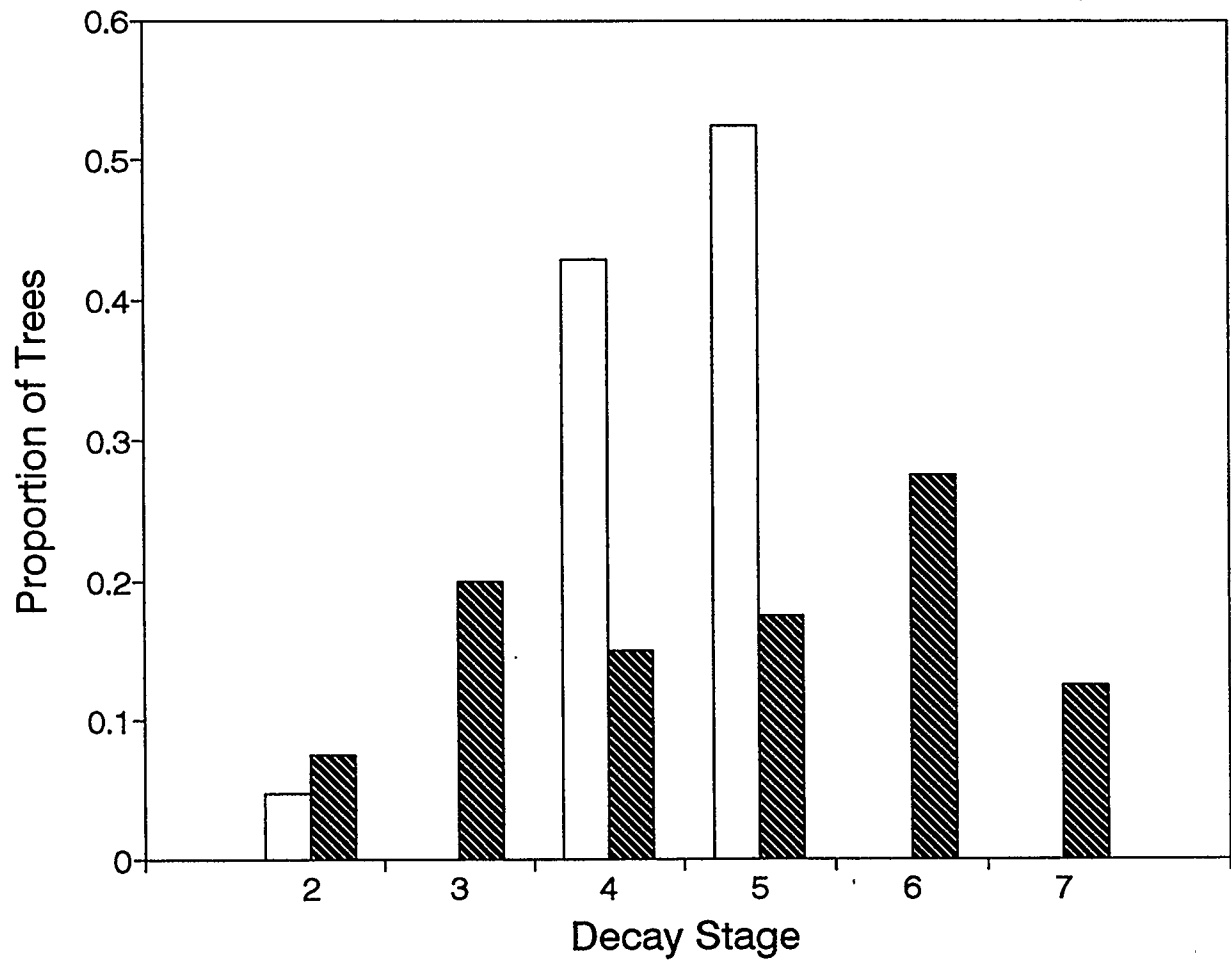


Figure 4. The proportion of roost and available trees falling in each of the six decay stages. Roost trees are denoted by clear bars, and available trees by filled bars.

found between bats of different species roosting under loose bark (ANOVA; $F_{2,6}=4.84$, $P>0.25$), or between different individuals ($F_{1,6}=0.74$, $P>0.40$). However, the number of days of rain during the roosting period significantly influenced the residence time of bark roosting bats ($F_{1,6}=43.13$, $P<0.001$), such that residence times increased with the number of days of rain. The estimated slope ($\pm$ SD) of the relation between the number of days of rain and residence time, 1.25 ± 0.190 , did not differ significantly from 1 (two-tailed single-sample t -test; $t_6=0.28$, $P>0.5$). For L. noctivagans, residence time in roosts was significantly different between bark (Mean $\pm$ SE: 6 ± 3.6 days; $n=3$) and cavity roosts (Mean $\pm$ SE: 14 ± 4.0 days; $n=5$) (Kruskal-Wallis; $\chi^2=3.94$, d.f.=1, $P<0.05$). In only one case did I observe an individual bat using the same roost tree (Tree #14) on different occasions. The bat switched from tree 14 to tree 15 and then back to tree 14.

The horizontal distance between subsequent roost trees used by the same bat varied over a relatively small range, from 28-206m, and the mean switching distance was 119 ± 88.2 m (Table 5). Roost switching distance did not differ significantly between L. noctivagans, M. evotis, and M. volans (ANOVA; $F_{2,5}=1.87$, $P>0.2$, based on inverse-log transformed data), but did differ between individuals ($F_{1,5}=10.18$, $P<.05$, based on inverse-log transformed data). Distances between capture site and roosting site (commuting distances) also ranged considerably, from 100m to over 4km (Table 5). Individual bats differed as to whether they flew uphill or downhill from their roost to feeding sites where they were captured (Table 5).

I found only one roost tree that was used as a roosting site in both summers (Tree #61). During the summer of 1993 the tree was used by both Myotis spp. bats and E. fuscus, whereas in 1994 the tree contained only Myotis spp. bats. During both summers, the bats remained in the tree for a considerable period of time (> 1.5 weeks, but exact residence times were not obtained) and may have been maternity groups. I also observed more than one species of bat emerge from another

Table 5. Mean residence times, mean horizontal distances between roosts, and the horizontal distance and elevation gain from the capture site for individual radio-tagged bats in the WADF. Blanks indicate missing values.

Bat Species	Bat Sex ^a	Bat Age ^b	Mean Residence Time (days) ^c	Mean Horizontal Distance Between Roosts (m) ^c	Horizontal Distance to Capture Site (m)	Elevation Gain from Capture Site (m)
<u>Lasionycteris noctivagans</u>	f ^d	a	8 ± 4.6 (4)	183 ± 159.6 (3)	750	180
<u>L. noctivagans</u>	f ^d	a	17 (1)		270	45
<u>L. noctivagans</u>	f ^d	a	17 (1)		270	45
<u>L. noctivagans</u>	f ^d	a	17 (1)		270	45
<u>L. noctivagans</u>	m ^d	j	8 (1)		4300	245
<u>Myotis evotis</u>	m	a	2 ± 1.4 (3)	61 ± 17.7 (2)	150	-45
<u>M. volans</u>	f	a	11 ± 4.9 (3)	28 ± 5.0 (2)	2950	-440
<u>M. volans</u>	m	a	5 ± 0 (2)	206 (1)	100	-10
OVERALL	Mean:		11	119	1130	8
	SD:		5.9	88.2	1593	204.8

a f=female, m=male

b a=adult, j=juvenile

c sample size in brackets

d includes one maternity colony

tree (tree #8) on the same night in 1994. My attention was focused on the entrance to a woodpecker hollow from which 21 *L. noctivagans* emerged, and I could not see from which of several possible cavities in the bottom 2m of the tree a single *Myotis* spp. bat emerged.

Competition With Other Species

In one case a potential takeover of a bat roost cavity by another cavity-dwelling species took place. At sunset on 12 August, 1994 I observed several (possibly 3) northern flying squirrels (*Glaucomys volans*) climbing up and jumping off the trunk of a roost tree (tree #7) housing a maternity colony of up to 21 *L. noctivagans*. I had located the maternity colony on 24 July. The flying squirrels repeated this behaviour several times before moving to other trees. On 15 August, when I returned to the roost, no bats emerged from the roost but two flying squirrels emerged from the same entrance hole that had previously been used by the bats. No direct interactions between the bats and flying squirrels were observed.

Provision of bark roosts

The three species of pines in the study area, and to a lesser extent western hemlock, were the only species I observed to consistently retain sheets of loose bark. Bark of the other tree species tended not to peel away from the bole in sheets large enough to be used as roosts by bats. The bark of lodgepole pine often adhered very closely to the tree bole, and the bark of ponderosa pine was often loose and prone to falling. Western white pine bark was intermediate between these two, and often large sheets of bark remained attached to the tree at the top of the sheet, providing ideal roosting sites for bats. These sheets were less prone to falling than the bark of ponderosa pine. I only found bark in this condition on trees of decay stages 4 and 5; trees in decay stages 2 and 3 had generally not decayed to the point where bark was

beginning to peel away from the trunk, and trees in decay stages 6 and 7 had, by definition, already lost all or most of their bark.

DISCUSSION

Tree and Site Preferences

Bats preferred tall trees close to other available trees, surrounded by a relatively open canopy. A preference for tall trees has been observed in a number of other tree-dwelling species, including a variety of woodpeckers (Raphael and White 1984,) and secondary cavity nesting birds (Cunningham *et al.* 1980, Nilsson 1984a, Raphael and White 1984, Rendell and Robertson 1989, Belthoff and Ritchison 1990). In contrast, previous studies on tree-roosting bats concluded that bats did not exhibit preferences for tall trees (Tidemann and Flavel 1987, Barclay *et al.* 1988, Taylor and Savva 1988). However, these studies either failed to compare the heights of roost trees to those of available trees (Tidemann and Flavel 1987, Taylor and Savva 1988), or the study was based on migrating bats, which are only in an area for a brief period and likely operate under different constraints (Barclay *et al.* 1988). Although I considered all roost trees together in all analyses regardless of which bat species used them, I do not believe this affected my conclusions. Minor differences in the characteristics preferred by different species may exist, but the selective pressures governing tree roosting bats in an area should be similar regardless of the species of bat.

There are several possible explanations as to why bats prefer tall trees associated with an open canopy. The first is protection from ground predators. A variety of predators prey on bats and cavity nesting birds in their roosts (see Chapter 1 for references). Entrance height and tree height were positively correlated, and presumably roosting high in tall trees reduces the risk of being preyed upon, either by increasing the difficulty for a predator climbing up to the roost, or by reducing the

chances of the roost being discovered by a predator on the ground. Nilsson (1984a) and Rendell and Robertson (1989) found that nest predation rates on cavity nesting birds were significantly higher for roosts closer to the ground, and Rendell and Robertson (1989) found that nest sites where young fledged were significantly higher than those which were preyed upon. Thus, the height of a roost may have a direct effect on fitness, and selecting roosts in tall trees may be adaptive.

A second hypothesis as to why bats prefer tall trees with an open canopy is that bats may gain significant energetic benefits by choosing trees that are exposed to sunlight. Low roost temperatures slow fetal and juvenile development in bats (Racey 1973, Racey and Swift 1981, McNab 1982), and seasonal low temperatures reduce the number of reproductive females and the number of young successfully fledged (Grindal *et al.* 1992, Lewis 1993). Early fledging juveniles have more time to learn to forage and accumulate fat before hibernation or migration, and thus should experience higher overwinter survival. If roosts become too warm, heat stress can occur (Licht and Leitner 1967, Vaughan and O'Shea 1976), and female bats must be obliged to compromise between these factors in their choice of roosts. Thus, reproductive female bats may benefit energetically by selecting roosts that are heated by the sun for at least part of the day. In contrast, adult male and non-reproductive female bats may select cooler roost sites that free them to enter torpor and minimize energy expenditure while roosting (Tuttle 1976, Keen and Hitchcock 1980, Hitchcock *et al.* 1984, Hamilton and Barclay 1994). Because low sample sizes forced me to group the sexes in my analysis, I could not address intersexual differences in tree-roost selection, but I would expect that thermal heating of the roost should be more important for reproductive females than for males and non-reproductive females.

Tall trees with open canopies are exposed to sunlight for a greater length of time than are trees with canopy cover. Indeed, nearly all of the roost trees I found, including all of the maternity colonies, were exposed to direct sunlight for most of the

day. Similarly, several studies have found that maternity colonies of the Indiana bat, *Myotis sodalis*, in the United States, are situated in locations where they are directly exposed to the sun (Humphrey *et al.* 1977, Kurta *et al.* 1993a,b).

If exposure to sunlight confers some benefit to tree-roosting bats, then bats should exhibit a preference for cavities with a specific orientation. I propose that cavity orientation will be more important for bark-roosting bats than for cavity roosting bats. 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. Bark roosts generally do not extend around the entire circumference of the tree, and therefore the orientation of the bark roost should have a stronger influence on the degree of thermal heating inside the roost that may occur if the tree is exposed to sunlight. I found a significant difference between the mean entrance aspects of bark and cavity roosts, and, while entrances to bark roosts were not uniformly distributed around roost trees, cavity entrances were. Although some studies on cavity nesting birds have provided evidence of preferred cavity entrance orientation, equal or greater numbers have not (see references in Rendell and Robertson 1994), and no studies have demonstrated that cavity-entrance orientation influences reproductive success. This suggests that cavity roosting bats may be more flexible in their choice of entrance-orientations than those roosting beneath loose bark, and that the orientation of bark roosts may influence the energetics and reproductive success of bark-roosting bats.

A third possible explanation as to why bats prefer tall trees with an open canopy is that trees of this type are easier to find than trees concealed by the canopy. When bats left their roosts, they made repeated circling flights in the immediate area of the roost tree, which may serve to orient the bats as to the position of their roost tree within the stand. A number of animal species use landmarks to remember the position of a nest-site or food source (e.g., Tinbergen 1951, Gould 1987), and it is likely that

tall trees in areas with an open canopy may stand out as landmarks to bats flying over the canopy surface, assisting in roost relocation.

A fourth explanation for the preference for tall trees with an open canopy is that such roosts provide easier access to and from the roost. Flight is costly (Thomas and Suthers 1972, Speakman and Racey 1991), and a clear flight path in front of the roost entrance may result in energetic savings. Furthermore, bats returning to roosts often make a number of short, circling flights around the entrance before leaving or landing and crawling into the roost (e.g., Medway and Marshall 1972, Vaughan and O'Shea 1976, Barclay *et al.* 1982). This may increase the susceptibility of bats to aerial predators, such as hawks, falcons, and owls (Twente 1954, Downing and Baldwin 1961, Baker 1962, Barclay *et al.* 1982, Rodriguez-Duran and Lewis 1985, Fenton *et al.* 1994). The ease with which bats enter and leave their roost will determine the length of time they are exposed to predation, and thus bats may select tall, open trees which provide easy access. On the other hand, ease of entry and exit to and from the roost for bats may translate into easier access by predators. A compromise must be achieved between minimizing time spent entering or leaving the roost and the degree of protection from aerial attacks. By selecting roost trees in areas with an open canopy, but choosing roost cavities situated beneath the canopy layer, as in this study, bats may achieve the necessary compromise. Only one instance of an owl preying on bats entering their roost has been documented in Canada (Barclay *et al.* 1982), making it difficult to generalize about the extent of aerial predation on bats in this study.

That absolute tree height was found to be a good discriminator between roost and available trees and the height of the tree relative to the canopy was not, suggests that bats may select tall trees to reduce the risk of predation by ground predators. The fact that entrance height was positively correlated with tree height but not with canopy height further supports this suggestion. The other three possible explanations all focus on the height of the tree relative to the canopy. However, selecting tall trees to avoid

predation does not explain the preference for more open canopies surrounding the roost tree. Unless more open canopies around a roost tree also lower the risk of predation, by limiting access to the roost from adjacent foliage-bearing trees, I must assume that bats are also selecting trees to take advantage of the potential energetic benefits associated with thermal heating, being able to use the tree as a landmark, or ease of access to and from the roost. However, these ideas need to be tested further.

Tree Diameter versus Tree Height

In other studies, tree-roosting bats preferred large diameter trees (e.g., Barclay *et al.* 1988, Lunney *et al.* 1988, Taylor and Savva 1988, Brigham 1991) rather than tall trees. Similarly, cavity nesting birds (Mannan *et al.* 1980, Bull 1983, Harestad and Keisker 1989, Lundquist and Mariani 1991) and red squirrels (Fancy 1980) prefer large diameter snags. For birds and squirrels, the tree must have a large enough diameter to accommodate a cavity with room for an adult and young, which may restrict the minimum diameter in which such animals can nest (e.g., Harestad and Keisker 1989). Indeed, several studies have found that, within cavity-nesting bird species, clutch size increases with increasing cavity size (Karlsson and Nilsson 1977, Nilsson 1984b, Rendell and Robertson 1989). The bats in my study have much smaller body sizes than most cavity nesting birds and squirrels, and can roost singly in small cracks or cavities (e.g., Barclay *et al.* 1988), but 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, 1986, Roverud and Chappell 1991, Genoud 1993). In addition, the larger a tree is at the time of death the longer it will stand, and the greater the range of cavity sizes it can eventually provide (Keen 1929, Cline *et al.* 1980, Newton 1994).

It is very difficult to separate preference for tree diameter from preference for tree height in many studies because the effects of the two variables were examined separately. I found that tree height and DBH were significantly positively correlated, and thus the tree height variable in the discriminant function analysis also included information with respect to DBH. However, it was tree height that best discriminated between roost and available trees, not DBH. Other studies have not examined the relative influence of each variable.

Tree Species and Decay Characteristics

Bats exhibited strong preferences for roosts in trees of particular species and particular stages of decay. I expect that the tree species preferences of bats should differ between bark and cavity roosters, but in both cases be related to differences in decay characteristics between tree species. Thus the decay stage and tree species preferences of bats should be closely linked. With the exception of one roost in a lodgepole pine and another in a western hemlock, all bark roosts were on western white pine snags, and all bark roosts were on trees of decay stages 4 and 5. My observations suggest that these are the only trees which provide suitable bark roosts for bats, and thus bats are simply selecting trees which provide them with suitable bark roosts. Western white pine is relatively rare and only locally abundant in the forests of southern British Columbia and the northwestern United States (e.g., Lundquist and Mariani 1991), and populations of western white pine have been severely reduced by outbreaks of white pine blister rust, *Cronartium ribicola* (e.g., Unger and Stewart 1991, Stewart 1993) and by logging practices in the last century. Thus, the availability of trees which can provide suitable bark roosts is low, and bat species which are restricted to roosting beneath loose bark may be roost-site limited.

The tree species and decay stage preferences of cavity roosters are more closely tied to the dynamics of natural cavity formation and the preferences of primary cavity

excavating birds (PCE's). In the northwestern United States and in British Columbia, in areas with similar forest types to those in my study site, PCE's exhibit strong preferences for western larch, western white pine, western hemlock, and trembling aspen (McClelland *et al.* 1979, Zarnowitz and Manuwal 1985, Harestad and Keisker 1989, Lundquist and Mariani 1991). Furthermore, PCE's prefer trees with decayed heartwood but relatively hard sapwood, such that there is a hard outer shell surrounding a relatively soft tree core (Conner *et al.* 1976, McClelland *et al.* 1979, Harestad and Keisker 1989, Lundquist and Mariani 1991). Trees in this condition are relatively easy to excavate once the sapwood has been breached, but still provide insulation and protection from the elements and predators. 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). Other tree species, such as Douglas-fir, tend to decay from the outside in, so that decay softens the sapwood before it affects the heartwood (Wright and Harvey 1967, Cline *et al.* 1980), and avoidance of Douglas-fir by PCE's has been noted (Crockett and Hadow 1975, McClelland *et al.* 1979). Trees such as trembling aspen and western hemlock often harbor heart rot while they are still alive (Engelhardt 1957, Winternitz and Cahn 1983) but do not remain standing for long periods after they are dead, and are therefore only suitable as potential roosts while in decay stages 2 and 3. Other species, such as western red cedar, western larch, and western white pine, are also prone to fungal heart rots but are much more resistant to falling (Cline *et al.* 1980; see also McClelland *et al.* 1979, Lundquist and Mariani 1991), and provide suitable cavities for longer periods (into decay stages 4-6).

Thus, the preferred tree species for roosting bats may simply be the ones which provided the appropriate decay conditions for suitable cavity excavation by PCE's or natural cavity formation, and for the formation of suitable bark roosts. Bats, being secondary cavity users, must choose among available cavities (e.g., Tidemann

and Flavel 1987) and are therefore affected by the preferences of PCE's and the dynamics of natural cavity formation.

In areas where choices are limited, tree-dwelling organisms may be forced to use tree species that they would otherwise not use. For example, in forests dominated by Douglas-fir with few dead trees of other species, many PCE's used Douglas-fir in proportion to its availability (Mannan *et al.* 1980). Similarly, in my study, in the POV, where Douglas-fir dominated the forest, the two *L. noctivagans* roosts I found were both in abandoned woodpecker cavities in Douglas-fir snags. In contrast, no bats roosted in Douglas-fir in the WADF, even though it was relatively abundant, but many other choices were available. Thus the tree species used depends on which species are available in a particular area, and observed species preferences differ from region to region. The state of decay of the tree is likely more important than tree species per se, and the tree species selected will be a function of their decay characteristics.

Roost Fidelity

Bats in my study moved between roost sites frequently, switching roosts on average every 11 days, or every six days if maternity colonies are excluded. I found no significant difference in residence time between *L. noctivagans*, *M. evotis*, and *M. volans*, but did find a significant difference between the residence time for *L. noctivagans* in bark versus cavity roosts. This is most likely due to the fact that the cavity roosts contained maternity colonies, and thus the females were constrained to remain in the roost until their young fledged, whereas the females using the bark roosts did not have young and did not face the same constraint. Frequent switching between alternate roost sites by tree or foliage roosting bats has been observed for several temperate insectivorous bats species (Brigham 1991, Kurta *et al.* 1993a, b) and for other species (see references in Kunz 1982, Fenton 1983, Brigham 1991). Frequent

roost switching has been documented for bats in all reproductive stages, including lactation (Lewis 1995).

A number of explanations have been proposed to explain roost-switching behaviour (see Lewis 1995 for review). Bats may switch roosts in response to disturbance (Kunz 1982), to avoid predators (Fenton 1983, Wilkinson 1985, Fenton *et al.* 1994), to interrupt parasite life cycles and reduce parasite loads (Lewis 1992), to minimize commuting distance if bats change their foraging areas (Kunz 1982), or to take advantage of differing microclimate and structural conditions within different roost sites (Humphrey *et al.* 1977). However, the potential benefits of roost-switching must trade-off with the benefits of remaining site-faithful, such as familiarity with high quality roosts (Brigham and Fenton 1986) and maintaining social relationships within a colony (Bradbury 1977, Morrison 1980). In her review of roost fidelity among 43 species of bats, Lewis (1995) found that after controlling for phylogeny, bats occupying spatially abundant, less permanent roosts exhibit lower roost-site fidelity than bats using less abundant, more permanent roosts. The degree of roost-switching observed for bats in this study, therefore, may be related to the relative impermanence of tree roosts, and in particular bark roosts (e.g., Taylor and Savva 1988, Kurta *et al.* 1993b), and the relative abundance of roosts of this type.

The number of days a bat resided in a particular roost was significantly influenced by the number of days of rain during the roosting period, such that residence time increased as the number of days of rain increased. This suggests that even though tree-roosting bats may benefit by frequent roost switching, ambient environmental conditions limit the degree to which they can do so. When ambient conditions are cool and wet, bats often remain in torpor and do not emerge from their roost-site to forage, and therefore do not have the opportunity to move between roosts.

Not only do tree-roosting bats switch roosts frequently, but subsequent roosts tend to be nearby. Bats in this study moved from 28 to 206m between subsequent

roosts. Switching distances of other species of bats generally fall into this range (e.g., Morrison 1980, Lunney *et al.* 1988, Taylor and Savva 1988), but may extend to well over one kilometer (e.g. Taylor and Savva 1988). Thus bats exhibit fidelity towards a particular area or group of trees rather than to any one particular tree (e.g. Kunz 1982, Lunney *et al.* 1988, Taylor and Savva 1988, Brigham 1991). Several costs may be associated with switching to new roost sites, including time and energy to locate a suitable roost, increased exposure to predation while searching, and potential disruption of the social structure of a colony (Lewis 1995). Having several roost sites within a small area may minimize these costs, as search and travel times will be relatively low, and individuals need not explore unfamiliar areas.

Competition With Other Species

My observations of flying squirrels apparently taking over a cavity containing a maternity colony of *L. noctivagans* suggest that there may be competition for tree cavities between bats and flying squirrels or other species. Tree cavities are used by a wide range of birds and mammals, and documented cases in which one species takes over a cavity previously used by another are common (e.g., Dennis 1971, Kilham 1971, Mason *et al.* 1972, Van Balen *et al.* 1982, Rendell and Robertson 1989, 1991). Although different species of secondary cavity users may have different preferences and requirements, overlap is common and a variety of species may compete for sites with similar characteristics (e.g. Nilsson 1984a, Raphael and White 1984, Rendell and Robertson 1991). Evidence from studies on both natural cavities and nest boxes suggests that the breeding densities of many bird species are limited by the availability of suitable nesting sites (see references in Newton 1994), and the same may be true for bats.

I have shown that bats prefer trees with certain characteristics. Management practices that only provide the minimum number of trees with suitable cavities will not

be enough to maintain bat populations, as the effective number of available cavities may be considerably lower, due to the presence of competitors and due to other factors such as cavity turnover (e.g., Sedgwick and Knopf 1992). The use of bark roosts by bats may free them to a large extent from competition with other species, as few species use spaces beneath loose bark for roosting sites. However, use of bark roosts by some bats before entering abandoned woodpecker cavities to form maternity colonies may reflect a high degree of competition with other species for these cavities. Alternatively, roost-site preferences may change over the season or between reproductive stages, such that bats only use cavities when they are suitable. Regardless of whether they have to compete for cavities, bats roosting beneath loose bark may still be affected by other tree dwelling species, as woodpecker foraging can result in the loss of bark from tree trunks and may destroy bat roosting sites (e.g., Kurta *et al.* 1993b).

Species Information

Only two maternity colonies of L. noctivagans have ever been described in Canada, one in Ontario and one in Saskatchewan (Parsons *et al.* 1986), and both previously described roosts were in abandoned woodpecker cavities. The fact that the four maternity colonies described here were also in abandoned woodpecker cavities suggests that roosts of this type may be the norm for this species, at least for maternity colonies, as I also found individuals roosting singly and in groups beneath loose bark.

Both M. volans and M. evotis roost in a wide variety of structures, including abandoned buildings, cracks in the ground, caves, mines, rock crevices, beneath loose bark and in tree cavities (Barbour and Davis 1969, Warner and Czaplewski 1984, Manning and Knox Jones Jr. 1989, Nagorsen and Brigham 1993). Although tree roosting in these species has been documented, few roosts of this type have been found for either species, and the trees used have not been described in significant detail (e.g.,

Baker and Phillips 1965). In this study I found male M. evotis and both male and female M. volans using bark roosts (see also Chapter 3).

Conclusion

Understanding the roosting requirements and especially maternity roost requirements for any bat species is essential to the conservation and maintenance of these species in a changing forest landscape. I have shown that only three variables, tree height, percent canopy closure, and horizontal distance to the nearest available tree significantly discriminate between roost trees and available trees. Bats show a strong preference for tall trees associated with a low percent canopy closure and small distance to the nearest available tree. Furthermore, forest-dwelling bats exhibit a preference for trees of certain stages of decay, and this in turn may influence preferences for particular tree species. Further research into the roosting ecology of forest-dwelling bats should focus on testing the hypotheses as to why these bats prefer the trees they do, and why tree-roosting bats switch roosts so frequently.

CHAPTER 3. ROOST-SITE PREFERENCES OF STUMP-ROOSTING BATS

INTRODUCTION

Bats roost in a variety of structures, including buildings, caves, rock crevices, tree hollows, and beneath exfoliating bark on tree trunks (Barbour and Davis 1969, Kunz 1982). 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 (Kurta 1985, Kurta and Kunz 1988, Roverud and Chappell 1991). Roosts may also serve as sites for social interactions with conspecifics (Morrison 1980), and provide protection from predators (Fenton 1983, Tidemann and Flavel 1987). Choices made by bats with respect to the type and location of roost sites should therefore have a strong influence on the survival and fitness of individuals.

Many bat species reside in forests and are considered to be dependent on trees for their roosting sites (Barbour and Davis 1969, Kunz 1982, Lunney *et al.* 1988, Nagorsen and Brigham 1993). However, because of the difficult nature of studying bats in forest ecosystems, few studies have examined the roosting ecology and roost-site preferences of forest-dwelling bats. Most records of tree-roost sites used by bats are simply anecdotal accounts of small numbers of roost trees (e.g., Barclay and Cash 1985, Parsons *et al.* 1986, Kurta *et al.* 1993a, b; see references in Barbour and Davis 1969, Kunz 1982), or comparisons of limited numbers of characteristics between roost trees and 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). Although several recent studies have examined tree-roost selection by bats in a more comprehensive fashion, by examining a wider range of tree and site characteristics (e.g., this study, M. Kalcounis pers. comm.), no published studies to date have specifically examined the roost-site selection of bats living in forested ecosystems that

have been modified by forest harvesting practices.. This study is the first to document the widespread use of bark cavities on stumps in clearcuts as roosting sites by bats.

The use of stumps in clearcuts by wildlife is not commonly observed, and has only been documented for a small number of vertebrate species. A number of bird species, including both primary excavating and secondary cavity nesting species (Morrison *et al.* 1983, R. Holt pers. comm.) nest in high-cut stumps in clearcuts. However, most species nest in stumps or snags greater than 2m high, and only two species consistently use stumps less than 2m tall for nesting (Morrison *et al.* 1983): mountain chickadees (*Parus gambeli*), and white-headed woodpeckers (*Picoides albolarvatus*).

Clearcuts provide unique habitat characteristics that are not found in surrounding forested areas. Because there is no canopy vegetation to block sunlight in clearcuts, the amount of incident solar radiation reaching the ground is increased (e.g., McComb and Noble 1981), as is the amount of radiative heat from the ground and debris within the clearcut. Increased incident solar radiation within clearcuts may result in increased roost temperatures, and this may be favorable for roosting bats in terms of reducing thermoregulatory costs. This may be particularly important for reproductive females, as high temperatures increase the rate of fetal development (Racey 1973, Racey and Swift 1981, McNab 1982). Males and nonreproductive females, on the other hand, should be expected to select cooler roost sites that allow them to enter torpor and minimize energy expenditure while roosting (Tuttle 1976, Keen and Hitchcock 1980, Hitchcock *et al.* 1984, Hamilton and Barclay 1994). I therefore expected that males and nonreproductive females would select bark cavities on stumps with characteristics that provide relatively cool temperatures compared to the roosts selected by reproductive females. Clearcuts are often burned and the amount of heat generated within a clearcut due to radiation from burned materials is high. If roosts become too warm, heat stress can occur (Licht and Leitner 1967, Vaughan and

O'Shea 1976), and thus a balance must be achieved between increased energetic savings through heating of the roost site and the risk of overheating.

Bats roosting in stumps in clearcuts may be subject to at least one major cost: predation by terrestrial predators. Clearcuts generally support large numbers of small mammals and their predators (e.g., Hooven and Black 1976, Yahner 1992), many of which prey on bats or cavity nesting birds in their cavities (e.g., Martin 1961, Mumford 1969, Erskine and McLaren 1972, Nilsson 1984a, R. Holt pers. comm.). Furthermore, foraging bears often rip apart stumps while foraging for ants (Knight 1994), and have been observed ripping apart the cavities of cavity-nesting birds (e.g., Erskine and McLaren 1972). Bats roosting in clearcuts, therefore, may be subject to considerable predation risk, and this should be reflected in their choice of roost sites.

After observing a single female western long-eared bat (Myotis evotis) roosting beneath loose bark on stumps in 1993, I initiated a more comprehensive study during the summer of 1994 to examine the roost-site preferences of clearcut-dwelling M. evotis. By describing the stump and cavity characteristics of roosts used by M. evotis, I could determine whether the bats were selecting stumps with certain characteristics, and whether the characteristics of stump roosts were related to either the microclimates they provide or the degree of protection from ground predators. Furthermore, I could determine the extent to which bats roost in clearcuts, and whether clearcuts differ in their suitability for bats as roosting habitat. I specifically tested the following hypotheses with respect to bats roosting in stumps:

HYPOTHESIS 1: Bats are selective in their choice of roost-sites.

PREDICTION 1: Bats do not roost at random with respect to the availability of tree (stump) species. Different species of trees provide different physical characteristics, influencing microclimate, and different numbers and kinds of roosting opportunities.

PREDICTION 2: Bats select stumps with large diameters. Larger diameter stumps will have larger cavities, which, along with greater thermal inertia and thickness of insulation associated with larger diameter stumps, will provide more suitable roost microclimates.

PREDICTION 3: Bats select stumps with greater than average height. By selecting stumps of this kind, bats may reduce search time associated with returning to the roost, reduce the time spent approaching and entering the roost, and benefit from increased exposure of the roost stump to sunlight.

PREDICTION 4: Bats select uncluttered stumps, with little or no vegetation in the immediate vicinity of potential bark cavities. This would make the stump easier to find, minimize costs associated with approaching and leaving the roost cavity, and increase the exposure of the roost to sunlight.

HYPOTHESIS 2: Male and nonreproductive female bats select roost sites with different microclimates than those selected by reproductive females.

PREDICTION 5: Male and nonreproductive female bats select bark cavities on the north side of stumps, leading to cooler cavity temperatures, which facilitates the use of torpor.

PREDICTION 6: Reproductive females are only found at lower elevations where temperatures are warmer, whereas males and non-reproductive females select roosts at higher elevations.

METHODS AND MATERIALS

Study Site

I conducted the study during the summers of 1993-94 in the Redfish Creek watershed (RCW) in the West Arm Demonstration Forest, located 20 km east of Nelson, British Columbia, along Kootenay Lake (117°05'W, 49°38'N). Forests in the

RCW extend from an elevation of 650 m well into the subalpine region, to an elevation of 1800m. Over this elevation range the RCW encompasses a wide range of forest types and stand ages. At lower elevations a mixed coniferous forest with 12 major tree species predominates. At middle elevations the forest is primarily composed of western red cedar (*Thuja plicata*) and western hemlock (*Tsuga heterophylla*), with concentrations of lodgepole pine (*Pinus contorta*). At high elevations the forest is largely Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*). The RCW has been extensively logged in the last two decades, and contains at least 16 different clearcuts, ranging in size from 7 to 18ha.

Location of Roost-Sites

I located stump roosts either by radio-tracking (1993) or by performing searches of stumps in 11 different clearcuts ranging in elevation from 780m to 1785m (1994). All clearcuts examined had a southerly aspect (SE to SW). Within each clearcut, I located roosts by systematically walking through portions of the clearcut and gently pulling back any pieces of loose bark on stumps which could have provided roosting sites for bats. A piece of loose bark was considered to provide a cavity if the space beneath it was at least 7.5cm deep, and if the entrance was at least 5mm wide. In cases where the bark was very loosely attached to the stump I gently probed the bark crevice with a piece of wire to avoid pulling the bark off the stump. The presence of bats within these bark crevices was determined visually or through agonistic calls emitted by the bats as the cavity was probed. I recorded the number of crevices examined, the time spent searching, and the number of stumps with obvious bear sign for all searches. Stumps with bear sign were those from which large sections of bark and/or wood had been torn or ripped off from the main body of the stump. The edges of the remains were generally ragged with numerous splinters, and occasionally claw marks were seen in the remaining wood. I also examined rock crevices for the presence of bats, and

found a total of five rock crevices housing bats during the two summers. Because rock crevices cannot be easily compared with stump roosts, and because the sample size was small, I excluded rock crevice roosts from all analyses. Each clearcut was examined on more than one occasion (range: 2-5 times).

Once the presence of a bat within a bark crevice was determined I captured the bat with minimal disturbance to the cavity itself. Individuals 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 1988) for all individuals captured.

Once stump roosts had been located, I measured a range of stump and cavity characteristics for all roosts (Appendix 5). I measured stump diameter with a standard DBH tape, and all distance and height measurements were made with a tape measure. I determined bark thickness by measuring the maximum and minimum thicknesses along the top edge of bark on a particular stump with dial calipers and taking the mean. Two observers independently estimated the percent bark remaining on the stump and the mean was taken. I determined crevice and entrance aspects by taking a bearing (with a compass) which bisected the crevice or entrance, and recorded the opposite bearing. All directions were corrected to true north. Two observers independently and subjectively classified stumps into one of four cover classes, ranging from uncovered to completely covered based on the degree to which each stump was surrounded by or covered with vegetation extending above the top of the stump and downed logs. Elevation was determined using a Casio digital altimeter, or taken from topographic maps.

I established a 17.8m radius (0.1ha) circular plot around each roost stump, and measured 20 randomly selected stumps within the plot in the same manner as for roost stumps. To estimate stump density I recorded the number of stumps within the plot. I

measured the height of approximately 5-6 herbs or shrubs falling within the upper most layer of vegetation to estimate "canopy" height.

I also established three 17.8m radius (0.1ha) circular plots in clearcuts in which I found no bats roosting, to determine whether stumps in these clearcuts differed from roost stumps. I randomly selected 15 stumps in two of these plots and measured them in the same fashion as for roost stumps, such that a total of 30 stumps were measured in each clearcut. I measured stump density and canopy height in all three plots. The age, time since burning, and time since planting, as well as average slopes (in percent) and midpoint elevations for each clearcut, were obtained from the B.C. Ministry of Forests.

To determine whether bats select roost stumps for certain characteristics within clearcuts, I performed a stepwise discriminant function analysis including the characteristics outlined in Appendix 6 on the two groups of stumps: roost stumps and random stumps within the 0.1ha plot around each roost stump. I then performed a similar stepwise discriminant function analysis on roost stumps and random stumps from clearcuts in which I found no bats roosting, to determine if bats select certain characteristics between clearcuts. In both cases I performed separate analyses on stump characteristics and cavity characteristics. Only two random stumps with cavities were included in the analyses to avoid large imbalances in sample size between the two groups. In cases where there was more than one cavity on a particular random stump, the characteristics of only one of the cavities were included.

I performed a third stepwise discriminant function analysis on clearcut characteristics (Appendix 7) using clearcuts used by bats and those in which I found no bats roosting as the categories. This allowed me to determine whether bats are choosing to roost in clearcuts with particular characteristics, or whether they simply choose clearcuts at random. Stumps falling into the partly covered, mostly covered, and totally covered cover classes were grouped into a single category, and the average

proportion of covered stumps was included as one of the variables in the analysis. All proportions were arcsin-square root transformed.

In all cases, after the stepwise discriminant function analysis was applied to a particular data set, a canonical discriminant function analysis was performed to determine the relative influence of each variable in discriminating between the two groups of stumps. This analysis provided the total sample standardized canonical coefficients (TSSCC) for each variable, and classification error rates based on cross-validation.

Because of the circular nature of directional data, I could not use standard statistical techniques on crevice and entrance aspects. Therefore, I used circular statistics (Zar 1984) to analyze directional data in most cases. I used χ^2 -tests with an expected angle of 180° to test whether cavities were uniformly distributed around roost stumps, and Watson-Williams tests for two samples to test for differences in the cavity aspect used by males and females. To include directional data in the stepwise discriminant function analyses, I transformed crevice and entrance aspects by taking the absolute value of their deviation from 180° , thereby converting them to a more meaningful form for these analyses.

Roost Temperatures

To determine whether bats selected stump roosts with certain thermal characteristics, I measured air temperatures within roost cavities. Sets of three temperature sensor - data logger units (Hobo-Temp, Onset Instruments, P.O. Box 3450, Pocasset, MA 02559) were placed in clearcuts for periods of at least two full days (range 2-5 days). One sensor was placed in a roost cavity, a second was placed in a randomly selected cavity within the 0.1ha plot around the roost stump, and the third was placed in the open between the two stumps, at a height of 0.5m, to measure ambient air temperature. The data-loggers recorded temperatures at 12 minute intervals

throughout the day and night, to the nearest 0.01°C . In four cases Campbell model 207 (Campbell Scientific Corp., 11564 149 St., Edmonton, Alberta) temperature sensors provided by the B.C. Ministry of Forest were used to obtain ambient air temperatures. These sensors were placed at a height of 0.4m in the open in the center of the clearcut. I ensured that temperature sensors within cavities did not touch the walls, and recorded the depth of the temperature sensor within the bark cavity.

To test whether bats select roost cavities with different temperatures than random cavities, I compared the mean, minimum, and maximum air temperatures within roost and random cavities using paired t -tests. Cavity temperatures were made relative to ambient by subtracting ambient temperatures from cavity temperatures. I also compared the mean, minimum, and maximum absolute air temperatures of roost and random cavities with ambient using paired t -tests. Only hourly temperatures between at least one hour after sunrise and one hour before sunset were included in all temperature analyses.

To test whether stump or cavity characteristics influenced air temperatures within cavities, I performed three separate multiple regression analyses with relative mean, minimum, and maximum cavity temperatures as the respective dependent variables. I included stump diameter, stump height, bark thickness, relative crevice aspect, entrance width, entrance length, entrance height, and crevice depth as the independent variables in all three analyses. All independent variables were log-transformed to ensure linear relations. Final model selection involved backward elimination of nonsignificant effects. Although the magnitude of partial regression coefficients can be affected by correlations between independent variables, for my results such correlations were too weak to affect my conclusions, based on variance inflation factors (Neter *et al.* 1990).

RESULTS

During the summers of 1993 and 1994 I found a total of 19 *M. evotis* roosts in bark cavities on 17 different stumps. In 1993 a single female *M. evotis* was radio-tracked to five roosts in four stumps, and the bat switched roosts every day. In 1994, I searched 1542 stumps for a total of 17h. These searches led me to 15 roosts in 14 different stumps (0.9% of stumps searched). Of the 1542 stumps searched, 115 (7.5%) had been damaged by the foraging behaviour of bears.

With one exception, the bats using stump roosts were *M. evotis*. The exception was a single male *M. yumanensis* roosting behind the loose bark of one stump. This stump was excluded from all analyses. Ten of the 19 *M. evotis* stump roosts were occupied by males, and the other nine by females. All bats were adult. Females using stump roosts were generally either nonreproductive or post-lactating, but a single pregnant female was also found. No lactating females were found roosting beneath loose bark on stumps. In all cases, bats in stumps roosted alone.

Roost stumps generally provided only a single bark cavity. However, two roost cavities were found on two of the stumps, and these cavities were used on different dates. The radio-tagged female in 1993 used the same stump twice, first roosting in the stump in question, and then roosting in two other stumps before returning to the first. The two cavities were on opposite sides of the stump. The second roost stump was used by different individuals on different dates, first by a male and then by a female. Both cavities were on the south side of the stump. Overall, 79% of random stumps with cavities ($n=77$) had only a single cavity, 10% had two cavities, and 11% provided three cavities.

Clearcut Characteristics

Stumps with roosting bats were only found in three of the 11 clearcuts that I searched for roosts. Two of the clearcuts were situated at a midpoint elevation of

780m and were situated next to one another, such that functionally they formed a single unit. These clearcuts were logged in 1985 and 1986, and both had been burned in 1986. The other clearcut used by bats was located at a midpoint elevation of 1250m, and was logged in 1991 and burned in 1992. Several other clearcuts in the RCW had been logged and burned in the past eight years, but were not used by bats. Twelve of the 19 roosts were found in the lower elevation clearcuts, and seven in the higher elevation clearcut. Both females ($n=9$) and males ($n=3$) were found roosting in the lower elevation clearcuts, whereas only males ($n=7$) were found roosting in the higher elevation clearcut. There was a significant difference in the sex ratio between the high and low elevation clearcuts (Randomization test; $G=12.791$, $P<0.001$).

Only one variable significantly discriminated between clearcuts used by bats and those in which I found no bats roosting: the proportion of covered stumps (arcsin-square root transformed data: $F_{1,7}=8.26$, $P<0.05$, Partial $R^2=0.54$). Based on the canonical discriminant function analysis, the centroid for clearcuts in which I found no bats roosting was at the positive end of the discriminant function, and the TSSCC for the arcsin(square root(proportion of covered stumps)) was 1.38. Thus, clearcuts in which I found no bats roosting tended to have a higher proportion of covered stumps. The classification error rates for clearcuts used by bats and those in which I found no bats roosting were 33.3% and 0%, respectively, with an overall classification error rate of 16.7%.

Stump and Cavity Characteristics

The stump and cavity characteristics of roost stumps are outlined in Appendices 8 and 9, respectively. No stump characteristics significantly discriminated between roost stumps and random stumps in clearcuts in which I found no bats roosting. However, cavity depth and distance to the nearest shrub discriminated between roost cavities and random cavities in clearcuts in which I found no bats roosting (Table 6).

Based on the canonical discriminant function analysis, the centroid for roost cavities was at the positive end of the discriminant function. The TSSCC's for both crevice depth and the distance to the nearest shrub were both positive (Table 6), indicating that roost cavities tended to be deeper and have a greater distance to the nearest shrub than did random cavities in clearcuts not used by bats. The classification error rates for roost cavities and random cavities were 33.3% and 19.2%, respectively, and the overall classification error rate was 26.3%.

To determine whether the discriminating variables were influenced by the effects of other independent variables, I tested for correlations between cavity depth and distance to the nearest shrub and the other independent variables included in the discriminant function analyses (Table 7). I found significant positive correlations between cavity depth and stump diameter, cavity depth and stump height, cavity depth and entrance height, distance to the nearest shrub and height of the nearest shrub, distance to the nearest shrub and relative crevice aspect, and distance to the nearest shrub and entrance length. I found further positive correlations between stump diameter and stump height, stump diameter and bark thickness, stump height and bark thickness, stump diameter and entrance height, stump height and entrance height, stump diameter and entrance length, stump height and entrance length, and bark thickness and entrance length (Table 7).

Within clearcuts used by bats, only stump diameter significantly discriminated between roost stumps and random stumps in the 0.1ha plot around each roost tree (Table 6). Although it was highly significant in the analysis, stump diameter only explained a small proportion of the variation between roost and random stumps (Table 6). For this and the following analysis, the canonical discriminant function analysis indicated that the centroid for roost stumps was at the positive end of the discriminant function. The TSSCC for stump diameter was relatively large and positive, suggesting that bats selected stumps with large diameters. The overall classification error rate was

Table 6. Summary of stepwise discriminant function analyses on stump and cavity characteristics of roost stumps found in the RCW. Analyses comparing roost stumps with random stumps in clearcuts in which I found no bats roosting (between), and comparing roost stumps with random stumps in the same clearcut within the 0.1ha plot around each roost stump (within) are included. The magnitude and sign of the total-sample standardized canonical coefficient (TSSCC) for each variable gives its position along the discriminant axis. The centroids for roost and random stumps lie at the positive and negative ends of the discriminant axis, respectively, for all analyses.

Variable	Order Included	<i>F</i>	<i>P</i>	Partial <i>R</i> ²	TSSCC
<u>Between, Cavity characteristics:</u>					
Cavity Depth	1	15.54	0.0003	0.290	0.928
Distance to the Nearest Shrub	2	5.53	0.0241	0.130	0.697
<u>Within, Stump characteristics:</u>					
Stump Diameter	1	8.89	0.0045	0.156	1.075
<u>Within, Cavity characteristics:</u>					
Crevice Depth	1	8.78	0.0049	0.163	0.871
Height of the Nearest Herb	2	4.42	0.0414	0.091	-0.647

Table 7. Correlation matrix of selected variables included in the discriminant functions analysis of stump and cavity characteristics, including data on roost stumps and random stumps in clearcuts in which I found no bats roosting. Bracketed numbers refer to: (1) Stump diameter; (2) Crevice depth; (3) Distance to the nearest shrub; (4) Average stump height; (5) Relative cavity aspect; (6) Average bark thickness; (7) Entrance length; (8) Entrance height.

	(2)	(3)	(4)	(5)	(6)	(7)	(8)
(1)	0.373 *	0.145	0.692 ***	-0.022	0.558 ***	0.555 ***	0.442 **
(2)		0.174	0.613 ***	-0.014	0.046	0.214	0.498 ***
(3)			0.068	-0.367 *	-0.080	0.390 **	0.167
(4)				-0.038	0.462 **	0.385 *	0.723 ***
(5)					0.136	-0.123	-0.076
(6)						0.390 **	0.222
(7)							0.223

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

relatively high, at 38.4%, and the error rate for random stumps (52.6%) was considerably higher than for roost stumps (24.2%).

Also within clearcuts used by bats, crevice depth and the height of the nearest herb significantly discriminated between roost cavities and random cavities within the 0.1ha plot around each roost stump (Table 6). The TSSCC's for crevice depth and the height of the nearest herb were positive and negative, respectively (Table 6). This indicates that roost cavities tended to be deeper, and the nearest herb shorter than for random cavities on stumps within the 0.1ha plot around each roost stump. Classification error rate estimates for the two variables were similar: 28.1% of roost cavities and 31.3% of random cavities were classified incorrectly. The overall classification error rate was 29.7%. No stump or cavity characteristics significantly discriminated between roost stumps used by males and females in the lower elevation clearcuts, but the sample size was small.

When I examined stump and cavity characteristics of roost stumps and random stumps within clearcuts used by bats, I found significant positive correlations between stump diameter and a number of variables, including stump height, bark thickness, crevice depth, entrance length, and entrance height (Table 8). Similarly, cavity depth was positively correlated with bark thickness, stump height, entrance length, entrance height, and relative cavity aspect (Table 8).

Almost all of the entrances to bark roosts faced directly upwards and were situated at the top of the piece of bark. Only three roosts had entrances that were vertical, such that the bat could only enter and exit the roost on the side of the piece of bark. Within the cavities, I generally found bats facing upwards, wedged into the bottom of the cavity. The bats were generally very active, and I found two stump roosts when the bat crawled out of the cavity during my approach to the stump. In one case, the bat actually flew away, flying approximately 10m, circling above another stump, and then flying directly into a bark cavity on another stump.

Table 8. Correlation matrix of selected variables included in the discriminant functions analysis of stump and cavity characteristics, including data on roost stumps and random stumps in the same clearcut within the 0.1ha plot around each roost stump. Bracketed numbers refer to: (1) Stump diameter; (2) Crevice depth; (3) Height of the nearest herb; (4) Average stump height; (5) Relative cavity aspect; (6) Average bark thickness; (7) Entrance width; (8) Entrance length; (9) Entrance height.

	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)
(1)	0.592 ***	-0.281	0.626 ***	0.154	0.738 ***	-0.152	0.535 ***	0.525 ***
(2)		-0.085	0.491 ***	0.302 *	0.311 *	0.261	0.325 *	0.413 **
(3)			-0.071	0.037	-0.161	-0.021	-0.316 *	-0.034
(4)				-0.061	0.542 ***	0.018	0.366 **	0.778 ***
(5)					-0.020	0.192	0.273	-0.016
(6)						-0.307 *	0.391 **	0.482 ***
(7)							-0.008	-0.038
(8)								0.181

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

Roost cavities tended to face S-SW, with a mean cavity aspect of $208 \pm 59.8^\circ$ ($\pm$ angular deviation; see Zar 1984), and cavities were not uniformly distributed around stumps (χ^2 -test; $\chi^2=2.48$, $P < 0.01$). The mean cavity aspects ($\pm$ angular dispersion) for males and females were $211 \pm 46.9^\circ$ and $198 \pm 71.3^\circ$, respectively (Fig. 5). Cavities used by males were not uniformly distributed around stumps (χ^2 -test; $\chi^2=2.56$, $P < 0.01$), whereas those used by females were ($\chi^2=0.91$, $P > 0.05$). I found no significant difference between cavity aspects used by males and those used by females (Watson-Williams test for two samples; $F_{1,17}=0.084$, $P > 0.5$).

Bats did not roost at random with respect to the availability of different tree species within clearcuts (Fig. 6; likelihood ratio test; $G=21.98$, $P < 0.01$). Bats preferred cavities on ponderosa pine (*Pinus ponderosa*) and lodgepole pine (*Pinus contorta*) stumps. Bats did not roost in any Douglas-fir (*Pseudotsuga menzeisii*), paper birch (*Betula papyrifera*), or western larch (*Larix occidentalis*) stumps at all. Bats roosted in grand fir (*Abies grandis*), western red cedar (*Thuja plicata*), and western white pine (*Pinus monticola*) stumps in proportion to their availability. Seven of the 12 roosts in the lower elevation clearcuts were in ponderosa pine, three in western red cedar, and two in grand fir. Of the seven roosts in the higher elevation clearcut, five were in lodgepole pine, one in western white pine, and one in western hemlock (*Tsuga heterophylla*).

Roost Temperatures

I found no significant difference in the mean (Paired t -test; $t_9=-0.268$, $P > 0.5$), minimum ($t_9=-0.511$, $P > 0.5$), or maximum ($t_9=-0.894$, $P > 0.25$) air temperatures between roost cavities and random cavities. I also found no significant difference in mean ($t_9=1.45$, $P > 0.1$) or maximum ($t_9=1.63$, $P > 0.1$) roost cavity and ambient air temperatures, or in mean ($t_9=2.07$, $P > 0.05$) or minimum ($t_9=1.70$, $P > 0.1$) random

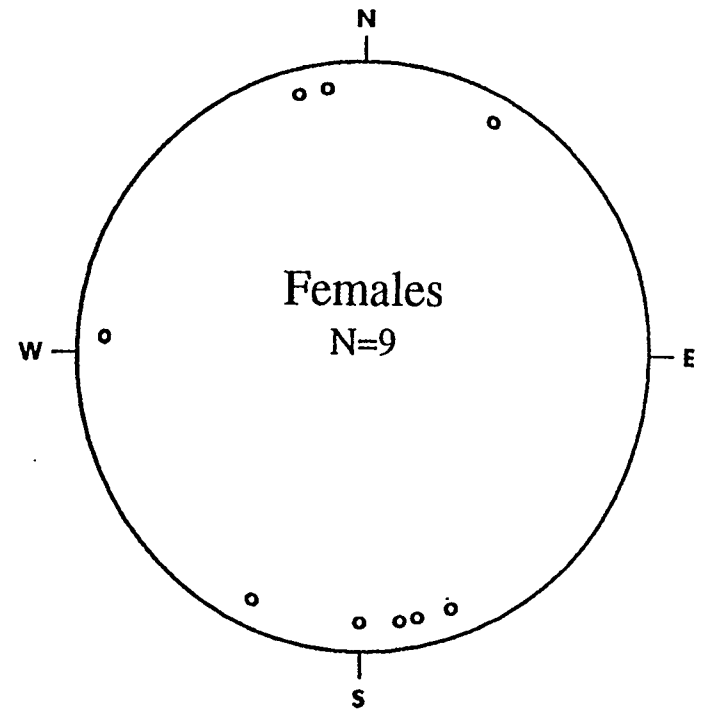
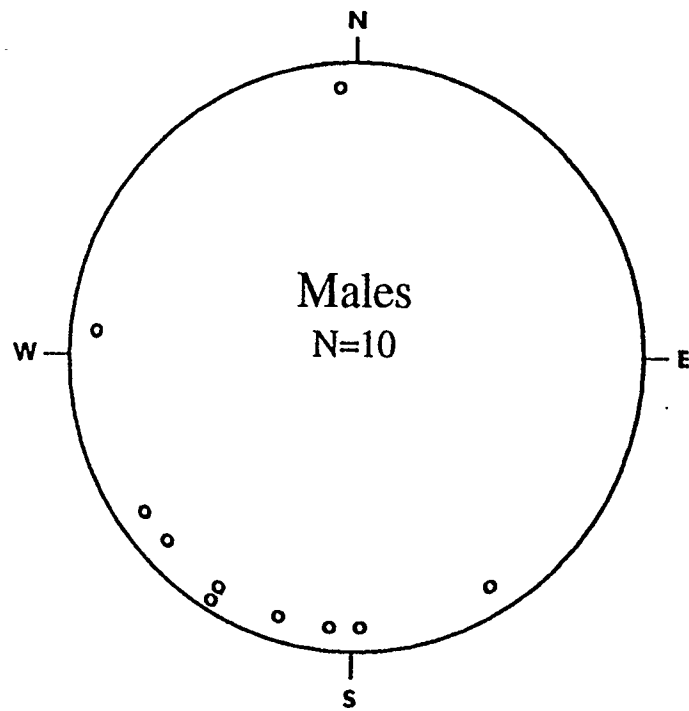


Figure 5. Distributions of the compass bearings of roost cavities used by male and female M. evotis found during the summers of 1993-94 in the RCW. Where two cavity aspects are the same, the points are arranged perpendicular to the edge of the circle.

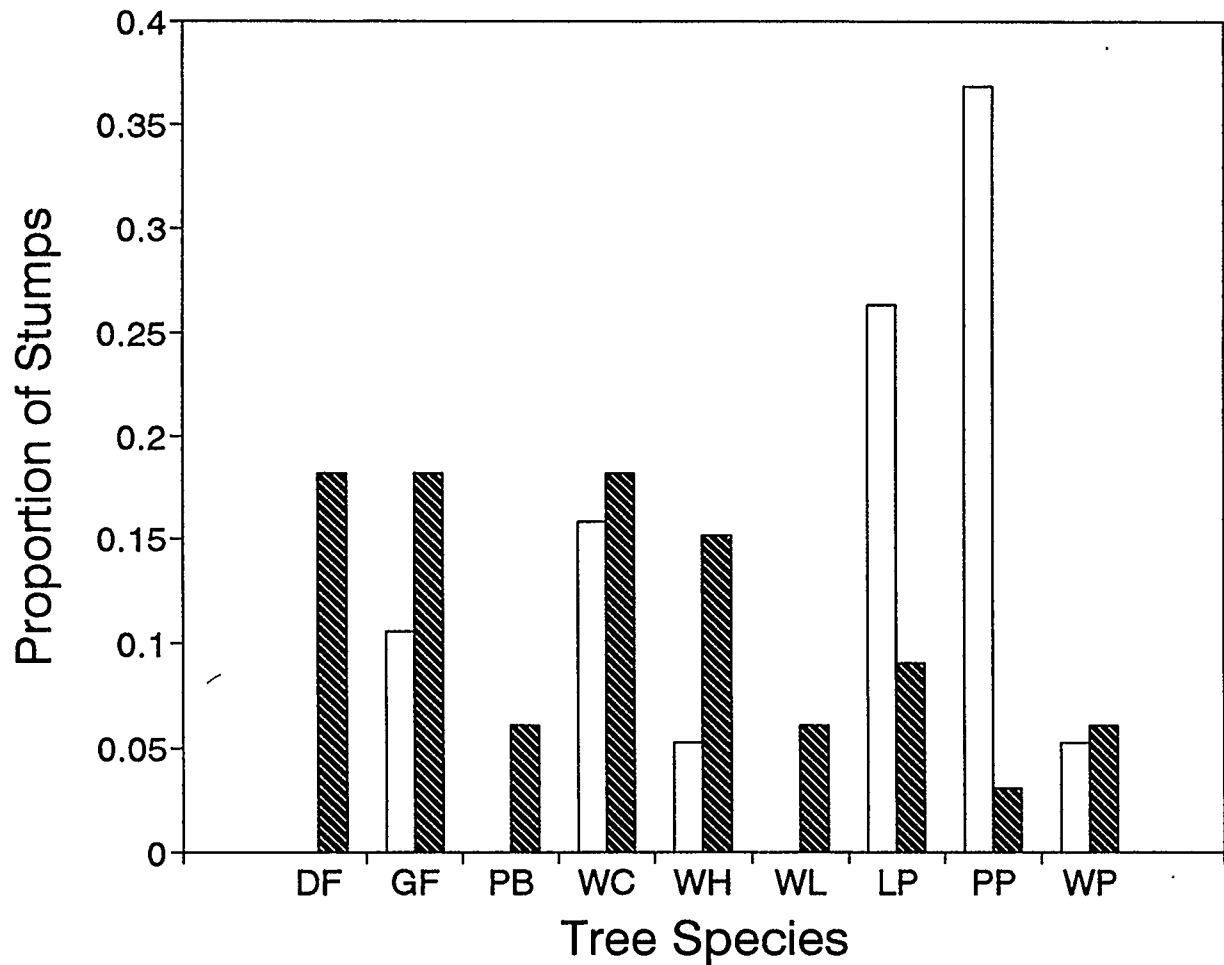
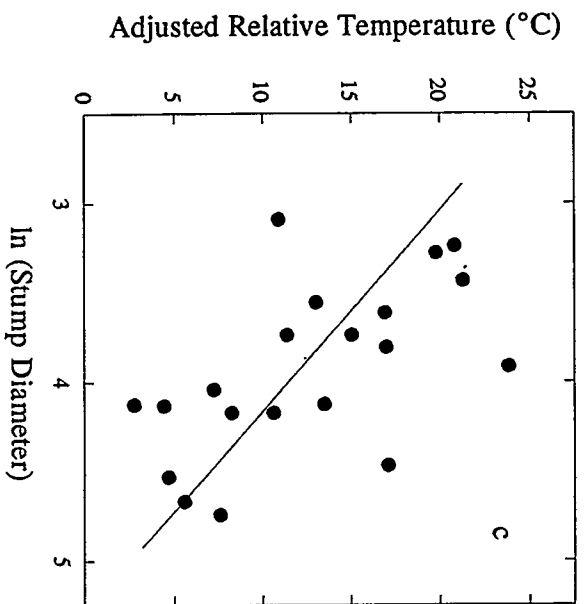
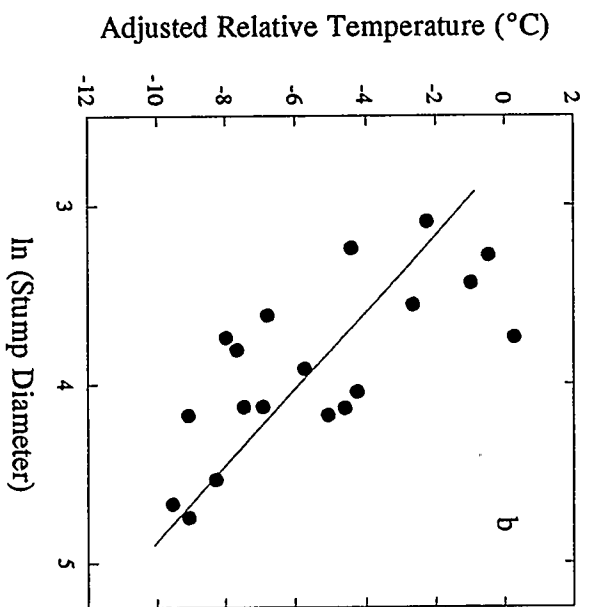
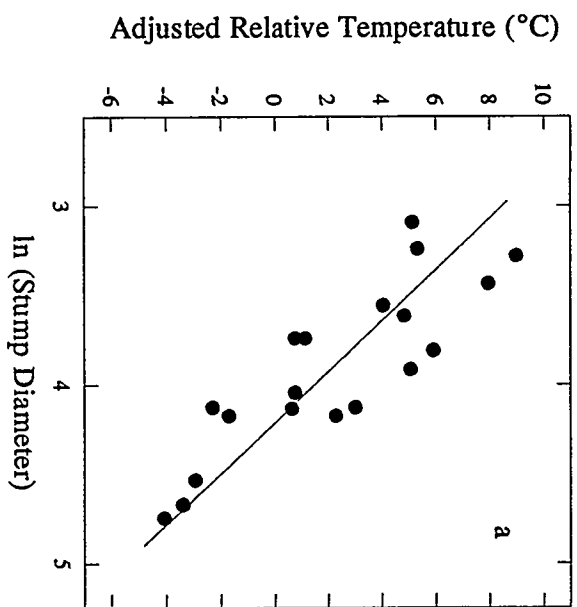


Figure 6. The proportion of roost and random stumps (from within the 0.1ha plot around each roost stump) in nine of the major tree species found in the RCW. Roost stumps are denoted by clear bars, and random stumps by filled bars. Tree species notation is as follows: DF=Douglas-fir, GF=grand fir, PB=paper birch, WC=western red cedar, WH=western hemlock, WL=western larch, LP=lodgepole pine, PP=ponderosa pine, WP=western white pine.

cavity and ambient air temperatures. However, I did find significant differences between minimum roost cavity and ambient air temperatures ($t_9=2.73$, $P<0.05$) and between maximum random cavity and ambient air temperatures ($t_9=4.52$, $P<0.01$). Minimum temperatures within roost cavities tended to be warmer than ambient, but temperatures within random cavities were not. Conversely, maximum temperatures within random cavities tended to be warmer than ambient, but roost cavity temperatures were not. Mean temperature in roost cavities was intermediate between those in random cavities and ambient temperatures.

Stump diameter and relative crevice aspect explained significant proportions of the variation in both mean (Fig. 7a; mean temperature= $-7.00\ln[\text{stump diameter}] - 1.39\ln[\text{relative crevice aspect}]$; $F_{2,16}=18.59$, $P<0.001$, $R^2=0.699$) and minimum air temperature within cavities (Fig. 7b; minimum temperature= $-4.67\ln[\text{stump diameter}] - 1.30\ln[\text{relative crevice aspect}]$; $F_{2,16}=8.53$, $P<0.01$, $R^2=0.516$), whereas only stump diameter explained a significant proportion of the variation in maximum air temperature within cavities (Fig. 7c; maximum temperature= $-8.90\ln[\text{stump diameter}]$; $F_{1,17}=13.25$, $P<0.01$, $R^2=0.438$). The depth of the temperature sensor in the cavity and the number of days since the stump was used as a roost did not significantly influence cavity temperature in any of the cases.

Figure 7. The relation between mean (a), minimum (b), and maximum (c) relative cavity temperature and the natural logarithm of stump diameter for roost and random cavities. The influence of $\ln(\text{cavity aspect})$ has been controlled for mean and minimum relative temperatures by calculating predicted values for each species for a constant (the mean for all cavities) cavity aspect, and adding the residual from the regression line.



DISCUSSION

Use of Clearcuts

The fact that I found significant numbers of both male and female M. evotis roosting beneath loose bark on stumps over a period of two summers suggests that this behaviour is widespread and well-established, at least in this species at this location. As already noted, the use of stumps by wildlife is relatively rare, and only two other species, the mountain chickadee and the white-headed woodpecker, have been reported to commonly use stumps shorter than 2m (Morrison et al. 1983). No other vertebrates have been shown to roost or nest beneath loose bark on stumps. Other bird species that use clearcuts, including both primary cavity excavators and secondary cavity nesters, tend to nest in high-cut stumps or snags within clearcuts (Morrison et al. 1983), rather than the relatively short stumps used by M. evotis in this study. However, at least one other bat species was found roosting beneath loose bark on a stump (M. yumanensis), and in other areas other species may exhibit this behaviour as well (Rasheed and Holroyd 1995).

Stump roosting bats did not roost in all of the clearcuts available to them. Instead, they selected clearcuts with significantly lower proportions of stumps that were at least partially obstructed by surrounding vegetation and downed material. I observed no preferences with respect to the age of the clearcut, whether the clearcut had been burned or brushed, the height of the dominant vegetation layer, or even the proportion of stumps in the clearcut with bark cavities. Furthermore, stumps in clearcuts in which I found no bats roosting tended to have shallower bark cavities and to be closer to surrounding shrubs than roost stumps. Thus, M. evotis selected clearcuts which provided them with deep cavities in which to roost, and with cavities that were open and easily accessible.

Flight is costly (Thomas and Suthers 1972, Speakman and Racey 1991), and bats will expend more energy maneuvering in and out of a cluttered roost entrance than an open one. Furthermore, bats often make a number of short circling flights around the roost entrance before leaving or landing and crawling into the roost (e.g., Medway and Marshall 1972, Vaughan and O'Shea 1976, Barclay *et al.* 1982). These circling flights leave bats more susceptible to aerial predation by hawks, owls, or falcons (Twente 1954, Downing and Baldwin 1961, Baker 1962, Barclay *et al.* 1982, Rodriguez-Duran and Lewis 1985, Fenton *et al.* 1994), and easy access to a roost will decrease the length of time bats are exposed to such predation. By selecting clearcuts with lower proportions of cluttered stumps, and with stumps that tend to be further away from surrounding shrubs, bats may minimize the energetic expenditures and predation risk associated with exit and entry into their roost site, and may be able to exit the roost more quickly if disturbed by a predator while roosting. Furthermore, relatively open stumps should be easier to locate via echolocation, and are therefore more likely to be used by bats as roosting sites than are cluttered stumps.

Thermal Characteristics of Clearcuts and Stumps

Bats roosting in clearcuts should experience higher temperatures than bats roosting in the forest. Because there is no or very little canopy vegetation to block sunlight in clearcuts, the amount of incident solar radiation reaching the ground is increased (e.g., McComb and Noble 1981). In addition, the majority of the clearcuts that I searched had previously been burned, thereby increasing the amount of heat absorbed by the ground and burned material, and increasing the amount of radiative heat generated within these clearcuts. Indeed, maximum ambient temperatures in the clearcuts used by *M. evotis* often exceeded 40°C in the afternoon on sunny days, and occasionally reached over 50°C. Increased heat within clearcuts will result in increased roost temperatures, as will solar heating of the burnt bark used as roost-sites by *M.*

evotis. Increased roost temperatures should result in energetic savings to bats through passive warming and decreased thermoregulatory costs, and a number of bat species select roosts in very warm locations (e.g., Licht and Leitner 1967). However, if roosts become too warm, heat stress can occur (Licht and Leitner 1967, Vaughan and O'Shea 1976), and thus a balance must be achieved between increased energy savings through heating of the roost site and the risk of overheating.

I contend that the decision by M. evotis to roost in clearcuts is based on the increased thermoregulatory and energetic benefits associated with the warmer temperatures provided in such habitats. Overall, bats tended to roost on the south side of stumps, and relative cavity aspect was negatively related to air temperature within the cavity, such that cavity temperature decreased as the deviation of the cavity from true south increased. Similarly, Schmid et al. (1991) found that bark temperatures on the north side of ponderosa pines were significantly cooler than those on the south side, at all hours of the day. By roosting beneath burnt bark in cavities on the south side of stumps, and by selecting cavities that are relatively unobstructed by adjacent vegetation, bats are increasing the extent to which roost cavities are exposed to sunlight during the day and the degree to which these cavities are directly heated by solar radiation. However, stump diameter significantly affected mean, minimum and maximum air temperature within cavities, and the partial regression coefficient for stump diameter was negative. This means that as stump diameter increases, air temperature within cavities decreases, and thus bats selecting large diameter stumps experience lower cavity temperatures relative to those choosing smaller diameter stumps. By selecting larger diameter stumps, bats minimize the possibility of overheating, as cavities on large diameter stumps provide cooler air temperatures relative to smaller diameter stumps. Therefore, I suggest that bats are roosting in clearcuts to take advantage of warmer ambient, and therefore warmer roost

temperatures, but within these clearcuts select large diameter stumps to minimize the risk of overheating.

I obtained further evidence for the notion that *M. evotis* is striking a balance between increased thermal benefits and the risk of overheating by comparing roost and random cavity temperatures. There was no significant difference in mean or maximum air temperatures of roost cavities versus ambient, or in mean and minimum air temperatures of random cavities versus ambient. These results suggest that, to a large extent, cavity temperatures are determined by ambient conditions within the clearcut, a conclusion supported by my findings that mean, minimum, and maximum temperatures did not differ significantly between roost and random cavities. However, minimum roost cavity temperatures and maximum random cavity temperatures were significantly warmer than corresponding ambient temperatures. Thus, *M. evotis* selected roosts which stayed warmer during cool conditions and cooler during hot conditions than did random cavities, and were therefore more stable overall. By choosing roosts of this type, bats could avoid overheating in very hot conditions, while ensuring relatively warm temperatures during cooler periods.

All but one of the bats found roosting beneath loose bark on stumps were either males or non-reproductive females. Roost temperatures were so high, and the bats so active when discovered, that the use of torpor by any of these bats was highly unlikely. Furthermore, I found that males selected cavities on the south side of stumps, whereas roosts used by females were uniformly distributed around roost stumps. South-facing cavities provide the warmest temperatures, and thus males appeared to be selecting warmer roosts than did females. Although some females may have experienced slightly cooler temperatures than did males by roosting on the north side of the stumps, there was no significant difference between the aspects of cavities used by males and females. These results are contrary to the expectation from other studies (e.g., Hamilton and Barclay 1994) that thermal heating of the roost should be more important

for reproductive females than for males and non-reproductive females, as low roost temperatures result in slow fetal development in bats (Racey 1973, Racey and Swift 1981, McNab 1982), and seasonal low temperatures reduce the number of young successfully fledged and the number of reproductive females in a season (Grindal *et al.* 1992, Lewis 1993). In contrast, adult male and non-reproductive female bats should be expected to select cooler roost sites that free them to enter torpor and minimize energy expenditure while roosting (Tuttle 1976, Keen and Hitchcock 1980, Hitchcock *et al.* 1984, Hamilton and Barclay 1994). Roost temperatures were warm for all bats, and presumably much warmer than in bark roosts on trees in the forest. Roosting in stumps may be an alternative strategy used by males and non-reproductive females to achieve lower thermoregulatory and energetic costs through passive warming rather than the use of torpor in cooler roost sites. Rewarming is the most energetically costly phase of torpor (Prothero and Jurgens 1986), and the use of passive warming by bats may reduce this cost (Vaughan and O'Shea 1976). Clearly, for this behaviour to be maintained, the benefits of selecting warm roosts on stumps in clearcuts and maintaining a high body temperature at minimal cost must be equal to or outweigh the potential benefits associated with selecting cooler roost sites and entering torpor more frequently.

The Risk of Predation

Although bats roosting in stumps in clearcuts may gain significant thermal and energetic benefits, they may also be subject to at least one major cost: predation by terrestrial predators. A wide variety of predators prey on bats and cavity nesting birds in their roosts, including weasels and other mustelids (Mumford 1969, Erskine and McLaren 1972, Dunn 1977), snakes (Dennis 1971, McIntosh and Gregory 1976, Lemke 1978), raccoons (Procyon lotor; Rendell and Robertson 1989), voles (Microtus ochrogaster; Martin 1961), red squirrels (Tamiasciurus hudsonicus; Erskine and

McLaren 1972, Nilsson 1984a), mice (R. Holt pers. comm., V. Campbell pers. comm.), chipmunks (R. Holt pers. comm., V. Campbell pers. comm.), and even bears (Erskine and McLaren 1972). Clearcuts often support large numbers of small mammals (e.g., Hooven and Black 1976, Yahner 1992), and I commonly observed chipmunks (Eutamias amoenus), a major predator of western bluebirds (Sialia mexicana) nesting in clearcuts (R. Holt pers. comm.), feeding in close proximity to roost stumps. In addition, approximately 7.5% of all stumps that I searched for bat roosts had been damaged by the foraging activity of bears, including two of the roost stumps. Relative to other clearcuts, the greatest concentration of bear damaged stumps was in the lower elevation clearcuts used by M. evotis in this study. Thus, potential predators of stump-roosting M. evotis were present and active within the clearcuts in the RCW. Among cavity nesting birds, both Nilsson (1984a) and Rendell and Robertson (1989) found that nest predation rates were significantly higher for cavities closer to the ground, and Rendell and Robertson (1989) found that nest sites where young fledged were significantly higher than those which were preyed upon. Thus, the height of a roost may have a direct effect on fitness, and selecting roosts in short stumps may place bats at risk of predation. Bats roosting in clearcuts, therefore, may be subject to a trade-off between increased thermal and energetics benefits, and increased risk of predation by ground-dwelling predators. Furthermore, the increased risk of predation may explain the absence of lactating females found roosting in stumps, as non-volant young are extremely vulnerable to predation, relative to adults.

The preference of bats for deeper roost cavities may be a response to the increased risk of predation. Deeper cavities should provide a greater degree of protection to the bats, by reducing the chance of detection by a visually searching predator. Bats were most often found face-up, wedged into the bottom portion of the cavity, where the space between the bark and wood was narrowest, and were very well camouflaged to the naked eye. Furthermore, a predator trying to attack a bat in this

position would find it difficult to maneuver around the bat, and would be unable to avoid the bat's jaws during an attack. In addition, bats found roosting in stumps were active and not in torpor. Relatively high levels of activity may be required for stump-roosting bats, as bats using torpor will be more vulnerable to attacks by predators, and bats minimize the energetic costs associated with maintaining these levels of activity by selecting warm roosts. The frequent roost-switching behaviour observed for one of the radio-tagged individuals may also be a strategy to decrease the risk of predation (Bradbury and Emmons 1974, Morrison 1980, Fenton 1983, Fenton *et al.* 1994). Remaining in a particular roost for a short time should decrease the risk of a predator discovering the roost by repeated observation, and help to avoid the build up of a strong odor in the roost.

The preference for deeper cavities may also be associated with bats' preferences for roosts that minimize the risk of overheating. Because deeper cavities contain larger air masses, bats roosting within them will occupy proportionately less of the air volume than bats roosting in smaller cavities. Increased cavity size:body size ratios lead to greater convective heat losses (e.g., Moore 1945, Kurta 1985), and bats within larger cavities will experience cooler body temperatures. Thus, deep cavities may provide bats with the dual benefits of increased protection from predators, and a mechanism to minimize the risk of overheating.

Tree Species Preferences

The tree species preferences of stump roosting *M. evotis* should be related to differences in how the bark of different species reacts to being burned, and how the bark decays after being burned. Bats showed a clear preference for pines, using mainly ponderosa pine in the lower elevation clearcuts and lodgepole pine in the higher elevation clearcut. However, bats also used tree species such as western red cedar, grand fir, western white pine, and western hemlock in proportion to their availability in

the respective clearcuts. In general, pines are the only tree species which I observed to consistently retain sheets of loose bark along the bole of the tree after they die, and thus are the species which provide the greatest number of suitable cavities. The bark of other species, such as western hemlock and grand fir, often did not form large sheets around the bole of the stump, and therefore did not often form suitable cavities for roosting bats. Although it was the preferred tree species for tree roosting bats (see Chapter 2), I found that the bark of burnt western white pine stumps was often brittle and broke very easily, reducing its value as a potential roost site for bats.

The relatively low abundance of both ponderosa pine and lodgepole pine stumps in the study area, combined with the fact that two of the 19 stumps were reused during the course of the study, by the same individual in one case and separate individuals in the other, suggests that suitable stump roosts may be limited and that individuals may compete for stump roost-sites. Roost stumps will likely only remain suitable to bats for a relatively short period, as vegetation in clearcuts grows relatively rapidly, and bark cavities will be destroyed by natural decay processes or by the activity of bears.

Flexibility in Roosting Behaviour

In general, *M. evotis* is very flexible in its choice of roost sites, and commonly roosts in buildings, rock crevices, caves and mines, tree hollows, and behind loose bark on trees (Manning and Knox Jones, Jr. 1989). They have even been found roosting in crevices below ground (this study, Morrell *et al.* 1994, Rasheed and Holroyd 1995). This is in contrast to other species in my study area which are restricted to certain roost types (e.g., *L. noctivagans*). The inherent flexibility already present in the roosting behaviour of *M. evotis* may have allowed it to take advantage of roosting opportunities provided by stumps in clearcuts that are not available to other species because of behavioural restrictions. This may explain why, with only one exception, it was the only bat species found roosting beneath loose bark on stumps. Given this flexibility in

roosting behaviour, and additional flexibility in foraging behaviour (Manning and Knox Jones, Jr. 1989), it is surprising that M. evotis is not more abundant and widespread than it currently is.

Conclusion

The discovery of M. evotis roosting beneath loose bark on stumps in clearcuts adds yet another interesting facet to the roosting behaviour of this species. I have shown that individuals do not roost in all clearcuts, but instead prefer to roost in clearcuts with greater proportions of uncluttered stumps, and which provide stumps with deep cavities. Within clearcuts, M. evotis prefers to roost in large diameter stumps with deep cavities unobstructed by surrounding herbaceous vegetation. The preferred roost characteristics may be directly tied to the thermal conditions provided in these roosts, such that bats are selecting roosts which provide warm temperatures but minimize the risk of overheating. However, it should be noted that I examined only air temperature within cavities, which provided a measure of convective heat, and did not examine conductive heat transfer between the inner bark surface and bats roosting within the cavities, or between bats and the bole of the stump. Future research should focus on examining the thermoregulatory strategies employed by stump roosting bats, to determine whether these bats do use torpor or whether they simply rely on passive warming, and to determine if there are any intersexual differences. A more detailed examination of heat transfer within these roosts is required to fully elucidate the thermal conditions experienced by bats roosting in these cavities. Furthermore, common predators and levels of predation should be identified, to determine how widespread predation on these bats is, and whether these bats are indeed the subject of a trade-off between increased energetic benefits and increased predation risk.

CHAPTER 4. CONCLUSIONS

SUMMARY

Understanding the roosting requirements, and especially the maternity roost requirements, for any bat species is essential to the conservation and maintenance of the species in a changing forest landscape. In summer, bats spend over half their lives in a roost (Kunz 1982), and choices made with respect to the nature and characteristics of roost-sites will therefore have a strong influence on survival and fitness. Because roost-sites in the forest are relatively inaccessible to humans, the roosting requirements of forest-dwelling bats remain poorly understood. The goal of my study was to provide information on roost-site preferences and roosting ecology of forest-dwelling bats.

Tree-roosting bats showed a strong preference for tall trees associated with low percent canopy closure and a small distance to the nearest available tree. Potential reasons for selecting roost trees of this type include increased protection from ground predators, increased exposure of the roost to sunlight, greater ease of access to and from the roost, and the potential of the roost tree to act as a landmark. However, entrance height was positively correlated with tree height and absolute, not relative, tree height was the best discriminator between roost and available trees, suggesting that predation may be the primary reason for the observed preference for tree height. Cavity orientation is likely more important for bark-roosting bats than cavity-roosting bats, because bark roosts generally do not extend around the circumference of the tree, and the orientation of bark roosts will determine the amount of incident sunlight reaching the roost, whereas cavity roosts will be heated by the sun no matter what the entrance orientation. Bats did not select trees at random with respect to tree species or decay stage, but instead showed preferences for western white pine, and to a lesser extent ponderosa pine, in decay stages 4 and 5. Species and decay stage preferences are tightly linked, such that preferred tree species are those which provide the greatest

number of suitable cavities, particularly for bark roosting bats. The preferences of cavity roosting bats are tied to both the dynamics of natural cavity formation, and the preferences of primary cavity excavating birds.

Tree roosting bats switched roosts frequently, and the distance between roosts was relatively small compared to the distances covered each night while foraging. The short distance between subsequent roost trees suggests that bats exhibit fidelity to a particular group of trees or area of forest, and switch between roosts within this restricted area. Frequent roost switching may be a strategy to minimize the risk of predation (Fenton *et al.* 1994), by decreasing the chances of the roost-site being discovered by repeated observation or through the build up of a strong odor in the roost. Alternatively, bats may switch roosts frequently to minimize parasite loads by interrupting parasite life cycles (Lewis 1992), or to take advantage of different microclimates at different times of the year (Humphrey *et al.* 1977). Only through further testing of these hypotheses will we be able to determine the underlying mechanisms driving this behaviour. I found that the number of days of rain during the roosting period significantly influenced the number of days spent in a particular roost. Thus, ambient environmental conditions may restrict the frequency at which bats can switch roosts.

The kinds of roosts available to bats in forests and clearcuts are very different, and consequently the roost site preferences of bats roosting in clearcuts are quite distinct from those of bats roosting in forested areas. I only found one bat species, *M. evotis*, consistently roosting in stumps in clearcuts, even though seven other species were present in the same area. Bats did not roost in all clearcuts available, but instead selected clearcuts with high proportions of uncluttered stumps that were further away from neighbouring shrubs, and that provided relatively deep cavities. Within clearcuts, bats selected large diameter stumps with deep cavities that were relatively unobstructed by nearby herbaceous vegetation, and bats tended to roost in SW facing cavities. The

bark of all but two of the cavities were previously burned. I contend that the characteristics of stumps and cavities selected by bats are related to the microclimate conditions produced within these roosts. Ambient temperatures within clearcuts were generally warm, and often exceeded 40°C on sunny days. Mean and maximum temperatures of roost cavities were intermediate between, and did not differ significantly from those within randomly selected cavities, or from ambient temperatures. However, maximum temperatures within randomly-selected cavities and minimum temperatures within roost cavities were significantly warmer than ambient temperatures, suggesting that bats roost in cavities providing warm and relatively stable temperatures. This is mediated through selection of south-facing cavities by males and some females, which leads to higher cavity temperatures, while choosing large diameter stumps, which provide cooler temperatures relative to smaller diameter stumps. I thus conclude that bats chose to roost in clearcuts to gain significant thermal benefits through increased exposure to sunlight and reflective heat, but within these clearcuts chose stumps which provided relatively cooler temperatures, presumably to avoid heat stress. However, bats roosting in clearcuts may be subject to a trade-off between increased energetic savings and increased predation risk, as ground predators are abundant and active within clearcuts used by bats. Bats may gain a certain degree of protection from these ground predators by roosting in deep cavities, and by remaining relatively active rather than entering torpor.

Based on my results it appears that predation and the energetics of thermoregulation both strongly influence the roost-site preferences of both tree and stump roosting bats. By roosting in tall trees, tree-roosting bats may gain significant protection from ground predators, while at the same time benefiting energetically from increased exposure to sunlight, easier access to and from the roost, and using the tree as a landmark. Stump-roosting bats appear to have sacrificed protection from predators to take advantage of the relatively favorable thermal conditions provided in stump-

roosts situated in clearcuts. Predation on bats is poorly understood and few studies have quantified the predation risk experienced by bats inside and immediately outside their roosts (see Fenton *et al.* 1994). Future work on the roosting ecology of forest-dwelling bats should focus on determining the levels of predation on bats, so that we can determine its exact effects on roost-site preferences. Furthermore, the microclimates within roosts and thermoregulatory strategies used by bats in both tree and stump roosts need to be examined further, to determine the relative importance of energetics on roost-site preferences, and to determine whether there are any differences in the thermoregulatory strategies used by the two sexes or by females in different reproductive stages. Determining levels of predation and energetic strategies, as well as levels of ectoparasitism, will also be necessary to understand the reasons behind the frequent roost-switching behaviour observed for tree-roosting bats. The influence of other factors, such as social interactions within the roost (e.g., Morrison 1980) and the social structure of bat populations, also needs to be explored. Forest-dwelling bats provide an excellent opportunity to further our knowledge of the roosting ecology and roost-site preferences of a variety of bat species, as well as the principles underlying habitat selection in general.

MANAGEMENT IMPLICATIONS

Tree-Roosting Bats

Current forest-harvesting practices are unlikely to provide enough suitable habitat for tree-roosting bats to maintain bat populations at current levels. The practice common to my study area of putting in relatively large cutblocks separated by small strips of forest removes large proportions of the available roosting habitat, and because older aged stands are the ones most often targeted in forest-harvesting operations, the remaining forested areas are often deficient of suitable roosting habitat. Older aged stands contain a wider range of snags in different decay stages than do younger stands,

and the snags that are present have larger than average heights and diameters (Cline *et al.* 1980). Furthermore, the structural characteristics of older stands, such as greater tree spacing and large gaps in the canopy (Franklin *et al.* 1981), will provide more suitable roosting habitat for tree-roosting bats, given their preference for areas with low percent canopy closure. 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. Bats in my study generally roosted in tall trees in older aged stands, and the roost trees located in slightly younger stands were clearly remnant snags from previous 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 well within forest stands, rather than in the open or along edges. Tree-roosting bats switched roosts frequently, and subsequent roost trees were situated within a relatively small area in the same stand. 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.

The choice of areas to leave unharvested should take into account the strong preference of tree-roosting bats, particularly those roosting beneath loose bark, for western white pine, and to a lesser extent ponderosa pine, in decay stages 4 and 5.

Western white pine is relatively rare and only locally abundant in the forests of southern British Columbia and the northwestern United States (e.g., Lundquist and Mariani 1991), and populations of western white pine have been severely reduced by outbreaks of white pine blister rust, Cronartium ribicola (e.g., Unger and Stewart 1991, Stewart 1993) and by logging practices in the last century. Thus, the availability of trees which can provide suitable bark roosts is low, and bat species which are restricted to roosting beneath loose bark may be roost-site limited. Special attention needs to be focused on providing suitable roosting habitat for bark-roosting bats, as this group of animals has traditionally not been considered in forest management practices.

Bats roosting in cavities depend to a greater extent on the dynamics of cavity formation, and the preferences of Primary Cavity Excavators (PCE's), for roosting sites. Managing for PCE's has been suggested as a means to maintain secondary cavity user populations, the idea being that if the requirements of PCE's 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 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. Leaving large areas of unmanaged forest to develop naturally so as to promote natural cavity formation, and managing forests to sustain populations of PCE's will maintain the number of available cavities for tree-roosting bats.

Forest managers often find it difficult to maintain snags in some forests because of intensive timber management and firewood harvesting (Bull and Partridge 1986). Consequently, several methods have been developed to create wildlife trees, including tree-topping, tree-girdling, fungal inoculation, pheromone application, and herbicide application (Conner et al. 1981, Conner et al. 1983, Bull and Partridge 1986). Bull

and Partridge (1986) found that in terms of tree longevity, suitability for woodpeckers, and cost, tree-topping was by far the most efficient method. However, bats in my study strongly preferred tall trees, and therefore topping would not be an appropriate method for creating potential bat roost trees. Other methods such as tree girdling and fungal inoculation may be more suitable, but the effectiveness of these methods in providing wildlife habitat is still poorly understood, and has never been examined with respect to the requirement of tree-roosting bats. Again, from a biological perspective, providing large, intact areas of undisturbed forest is the best way to ensure a continual supply of suitable roosting habitat for tree-roosting bats.

Thus, to maintain bat populations, I recommend that undisturbed tracts of older-aged forest, with relatively large numbers of western white pine trees, be left untouched, or at the least minimally managed, to ensure the continued provision of suitable roosting habitat. Forest reserves should not be restricted to older-aged stands, if suitable trees (tall with open canopy) can be provided under different conditions, such as in second growth stands in which a significant component of tall trees were retained.

Stump-roosting bats

Although forest harvesting practices remove suitable roosting habitat for most forest-dwelling bats, at least one species of bat, *M. evotis*, has taken advantage of the different roosting opportunities available in clearcuts, in the form of stumps. My study is the first to report the widespread use of stumps in clearcuts as roosts by bats, and this behaviour must be examined in greater detail before any strict management guidelines are recommended. Extreme caution must be observed in making generalizations about the usefulness of creating roosting habitat for this species through clearcutting. Of the 11 clearcuts that I regularly searched for the presence of roosting bats, only three were actually used by bats. Not all clearcuts provide suitable roost-sites for bats.

Furthermore, I only examined south-facing clearcuts within a particular elevational range, and further studies of clearcuts with different site characteristics must be undertaken before we can be sure that this behaviour is not unique to the bats present in the WADF.

The clearcuts that were used by roosting bats were all relatively recent, had been burned and brushed in the recent past, and contained numerous small rock outcroppings or patches of bare ground. Stumps used as roosts in these clearcuts were very open and not closely surrounded by nearby vegetation. In addition, all but one of the roost stumps had been burned. The creation of suitable clearcuts will depend, therefore, on a combination of selecting sites with the potential to contain rock outcroppings or patches of bare ground after the trees are removed, and site preparations after harvesting, such as controlled fires and regular brushing, that modify the habitat within the clearcuts. Furthermore, potential sites must contain a large proportion of pines, as stump-roosting bats exhibited a strong preference for ponderosa pine and lodgepole pine stumps.

I contend that the clearcuts used by bats in my study will only remain suitable for bats for a relatively short period of time, as vegetation in clearcuts grows rapidly and within a period of several years stumps will be at least partially covered and almost totally surrounded by vegetation. Unless existing clearcuts used by bats are managed so that vegetation around stumps is kept to a minimum, they will quickly lose their value as roosting habitat for bats. Thus, relative to other bats roosting in trees, the negative impacts of forest harvesting on bats, in terms of loss of roosting habitat, may simply be delayed for M. evotis that have taken advantage of roosting opportunities in stumps.

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Appendix 1. Tree and site characteristics included in the stepwise discriminant function analysis on roost and available trees.

Tree Characteristics

Diameter at Breast Height (DBH)

Tree Height

Tree Height Relative To Canopy Height

Percent Bark Remaining

Number of Limbs

Site Characteristics

Slope

Elevation

Elevation Above Valley Floor

Percent Canopy Closure

Canopy Height

Number of Canopy Layers

Horizontal Distance to Nearest Edge

Horizontal Distance to Nearest Water

Horizontal Distance to Nearest Neighbouring Tree

Height of Nearest Neighbouring Tree

Horizontal Distance to Nearest Tree of Same Height or Taller

Height of Nearest Tree of Same Height or Taller

Horizontal Distance to Downslope Trees

Height of Downslope Trees

Height of Downslope Trees Relative to Roost Tree

Horizontal Distance to Nearest Available Tree

Available Tree Density

Appendix 2. Roost characteristics of bat roost trees found during the summers of 1993-94 in the WADF and the PDV. Blanks indicate missing values.

Bat Species	Tree #	Year Found	Type of Roost	Bat Sex ^a	# Bats Emerged	Entrance Height (m)	Entrance Aspect (°azi.)	Trunk Diameter at Entrance (cm)	Bark Thickness (mm)
<u>Eptesicus fuscus</u>	1	93	natural hollow		1	20.5	98	70	50
<u>E. fuscus</u> / <u>M. spp.</u>	2	93	natural hollow		7	15	85	180	22
<u>Lasionycteris noctivagans</u>	3	93	loose bark	f	1	18	70	75	24
<u>L. noctivagans</u>	4	93	loose bark	f	5	17.1	188	40	7
<u>L. noctivagans</u>	5	93	loose bark	f					
<u>L. noctivagans</u>	6	93	woodpecker hollow	f ^b	5	21.6	342	25	5
<u>L. noctivagans</u>	7	94	woodpecker hollow	f ^b	21	29.8	82	30	12
<u>L. noctivagans</u> / <u>M. spp.</u>	8	94	woodpecker hollow	f ^b	21	19	176	47	29
<u>L. noctivagans</u>	9	94	woodpecker hollow	f ^b					
<u>L. noctivagans</u>	10	94	woodpecker hollow	m	1	8	140	20	12
<u>Myotis evotis</u>	11	93	loose bark	m	1	20.6	233	19	5
<u>M. evotis</u>	12	93	loose bark	m	1	22.6	144	14	4
<u>M. evotis</u>	13	93	loose bark	m	1	24	238	30	6

cont. . . .

Appendix 2 cont. . . .

Bat Species	Tree #	Year Found	Type of Roost	Bat Sex ^a	# Bats Emerged	Entrance Height (m)	Entrance Aspect (°azi)	Trunk Diameter at Entrance (cm)	Bark Thickness (mm)
<u>M. volans</u>	14	94	loose bark	f	1	8.1	303	31.5	6
<u>M. volans</u>	15	94	loose bark	f	1	14.4	218	25	5
<u>M. volans</u>	16	94	loose bark	f	1	11.7	336	50	8
<u>M. volans</u>	17	94	loose bark	m	1				
<u>M. volans</u>	18	94	loose bark	m	1	18.7	200	30	6
<u>M. spp.</u>	19	93	loose bark		5	25.8	213	60	9
<u>M. spp.</u>	20	93	loose bark		1	15.7	265	55	8
<u>M. spp.</u>	21	93	loose bark		1	21.3	179	29	6
Mean:					3.9	18.4	186	46	12
SD:					6.14	5.73	67.4 ^c	37.8	11.8

a f = female, m = male

b maternity colony

c angular deviation

Appendix 3. Tree characteristics of bat roost trees found during the summers of 1993-94 in the WADF and the PDV.

Bat Species	Tree #	Tree Species ^a	Tree Height (m)	Tree Height Relative to Canopy Height (m)	DBH (cm)	Percent Bark Remaining	Decay Stage	No. of Limbs	Top Present
<u>Eptesicus fuscus</u>	1	pp	31.6	6.6	97	35	4	15	no
<u>E. fuscus</u> / <u>M. spp</u>	2	wc	21.8	-23.2	190	100	5	18	no
<u>Lasionycteris noctivagans</u>	3	wh	35.3	5.3	105.5	20	4	29	no
<u>L. noctivagans</u>	4	wp	20	-7.5	56	15	5	28	no
<u>L. noctivagans</u>	5	wp	25.9	3.4	70.5	5	5	13	no
<u>L. noctivagans</u>	6	wp	32.1	4.6	48	20	5	33	yes
<u>L. noctivagans</u>	7	wh	32.7	5.2	93	95	2	80	no
<u>L. noctivagans</u> / <u>M. spp.</u>	8	wl	39.3	21.8	61	0	5	3	yes
<u>L. noctivagans</u>	9	df	20.6	-9.4	43.5	100	4	67	no
<u>L. noctivagans</u>	10	df	8.3	-11.7	25	100	5	0	no
<u>Myotis evotis</u>	11	wp	25.5	-4.5	38	45	5	24	no
<u>M. evotis</u>	12	lp	26.5	1.5	33	65	4	20	no
<u>M. evotis</u>	13	wp	35	10	48.5	100	4	85	yes
<u>M. volans</u>	14	wp	35.1	5.1	39	30	4	125	yes

cont. . . .

Appendix 3 cont. . .

Bat Species	Tree #	Tree Species ^a	Tree Height (m)	Tree Height Relative to Canopy Height (m)	DBH (cm)	Percent Bark Remaining	Decay Stage	No. of Limbs	Top Present
<u>M. volans</u>	15	wp	26.3	-3.7	35	40	4	41	yes
<u>M. volans</u>	16	wp	13.7	-8.8	64	75	5	12	no
<u>M. volans</u>	17	wp	25.9	0.9	34.5	30	5	9	no
<u>M. volans</u>	18	wp	26.6	-3.4	35.5	50	4	50	yes
<u>M. spp.</u>	19	wp	35.4	10.4	72	20	5	4	no
<u>M. spp.</u>	20	wp	24.6	2.1	70.5	25	5	11	no
<u>M. spp.</u>	21	wp	34.3	4.3	47	75	4	45	yes
Mean:			27.5	0.4	62	50		34	
SD:			7.76	9.50	37.0	34.4		32.1	

^a df = Douglas fir, lp = lodgepole pine, pp = ponderosa pine, wc = western red cedar, wh = western hemlock, wl = western larch, wp = western white pine

Appendix 4. Site characteristics of bat roost trees found during the summers of 1993-94 in the WADF and the PDV. Blanks indicate missing values.

Bat Species	Tree #	Slope (°)	Elevation (m)	Elevation Above Valley (m)	Percent Canopy Closure	Nearest Available Tree (m)	Available Tree Density (# / ha)	Dist. to Nearest Tree (m)	Dist. to Nearest Edge (m)	Dist. to Nearest Water (m)	Approx. Stand Age (years)
<u>Eptesicus fuscus</u>	1	28	875	335	40	4.4	90	4.5	150	575	140-250
<u>E. fuscus</u> / <u>M. spp.</u>	2	25	1080	5	20	7.1	40	5.2	13	13	>250
<u>Lasionycteris noctivagans</u>	3	39	1260	225	60	2.2	50	2.2	0	10	80-100
<u>L. noctivagans</u>	4	38	1165	130	25	4.6	90	2.0	40	40	80-100
<u>L. noctivagans</u>	5	33	1230	195	10	2.5	140	1.5	45	50	80-100
<u>L. noctivagans</u>	6	33	1100	65	20	4.6	90	2.4	35	40	140-250
<u>L. noctivagans</u>	7	26	1120	45	10	4.1	30	1.4	160	200	40-60
<u>L. noctivagans</u> / <u>M. spp.</u>	8	27	1065	215	30	5.8	160	1.0	25	950	60-80
<u>L. noctivagans</u>	9	17	915	365	5	4.5	130	4.5	35	1400	
<u>L. noctivagans</u>	10	21.5	790	60	20	1.3	290	1.3	30	300	
<u>Myotis evotis</u>	11	28	885	50	85	1.4	30	1.4	98	98	140-250
<u>M. evotis</u>	12	19	900	110	60	2.6	280	0.5	60	60	140-250

cont. . . .

Appendix 4 cont. . .

Bat Species	Tree #	Slope (°)	Elevation (m)	Elevation Above Valley (m)	Percent Canopy Closure	Nearest Available Tree (m)	Available Tree Density (# / ha)	Dist. to Nearest Tree (m)	Dist. to Nearest Edge (m)	Dist. to Nearest Water (m)	Approx. Stand Age (years)
<u>M. evotis</u>	13	28	870	80	70	0.4	100	0.4	25	25	140-250
<u>M. volans</u>	14	0	540	0	20	2.2	50	1.2	50	90	80-100
<u>M. volans</u>	15	0	540	0	15	7.6	110	3.0	17	120	80-100
<u>M. volans</u>	16	0	540	0	30	7.7	40	2.5	55	80	80-100
<u>M. volans</u>	17	18	970	430	35	4.9	60	0.9	27	1400	80-100
<u>M. volans</u>	18	9	965	425	25	2.5	90	0.8	66	1375	80-100
<u>M. spp.</u>	19	33	1135	5	60	4.1	60	1.2	8	8	>250
<u>M. spp.</u>	20	33	1225	190	15	4.5	140	1.0	50	55	80-100
<u>M. spp.</u>	21	28	885	50	85	1.4	30	1.9	100	100	140-250
Mean:		23	955	142	35	3.8	100	1.9	52	333	
SD:		12	219.8	143.1	24.7	2.11	73.1	1.35	42.8	495.5	

Appendix 5. Slopes ($\pm$ SD) of the regression between log(tree diameter) and log(bark thickness) for the major tree species found in the WADF. Diameter was measured in centimetres and bark thickness in millimetres. Regression lines were forced through the origin. $P < 0.001$ in all cases.

Tree Species	Slope	<i>t</i>	R^2	<i>N</i>
Douglas-fir	0.833 ± 0.0169	49.46	0.996	12
Grand fir	0.621 ± 0.0284	21.87	0.978	12
Lodgepole pine	0.524 ± 0.0350	14.97	0.949	13
Ponderosa pine	0.920 ± 0.0228	40.27	0.994	11
Western red cedar	0.594 ± 0.0320	18.55	0.966	13
Western hemlock	0.735 ± 0.0171	43.05	0.993	14
Western larch	0.876 ± 0.0230	38.05	0.993	11
Western white pine (live)	0.526 ± 0.0300	17.51	0.956	15
Western white pine (dead)	0.564 ± 0.0281	20.06	0.981	9

Appendix 6. Stump and cavity characteristics included in the stepwise discriminant function analyses on roost and random stumps.

Stump Characteristics:

Stump Diameter

Average Stump Height

Percent Bark Remaining

Distance to the Nearest Stump

Cavity Characteristics:

Relative Cavity Aspect

Relative Entrance Aspect

Average Bark Thickness

Cavity Depth

Entrance Width

Entrance Length

Entrance Height

Distance to the Nearest Herb

Height of the Nearest Herb

Distance to the Nearest Shrub

Height of the Nearest Shrub

Appendix 7. Clearcut characteristics included in the discriminant function analysis of clearcut characteristics, comparing clearcuts used by bats and those in which I found no roosting bats.

Clearcut Area

Midpoint Elevation

Average Slope

Number of Years Since Cut

Number of Years Since Burned

Number of Years Since Planted

Canopy Height

Stump Density

Proportion of Stumps With Crevices

Proportion of Covered Stumps

Appendix 8. Stump and site characteristics of bat roosts found during the summers of 1993-94 in the RCW.

Stump #	Bat Sex ^a	Bat Reprod. Condition ^b	Tree Species ^c	Diameter (cm)	Average Height (cm)	% Bark Remaining	Elevation (m)	Slope (°)	Dist. to Nearest Edge (m)
1	f	nr	gf	44.5	58	60	790	11.5	125
2	f	nr	pp	101.5	68.5	75	785	9	140
3	f	nr	pp	104.5	82	40	790	30	122
4	f	nr	wc	46.5	63.75	85	785	21.5	133
5	f	p	pp	50.5	41.5	95	760	24	125
6	m		wp	62.5	41	85	1300	18	25
7	m		lp	57	36	50	1295	17.5	28
8	m		lp	37	29	80	1275	24	35
9	m		lp	25.5	38.5	70	1240	27	27
10	m		lp	44	37	80	1240	27	27
11	m		wh	45	47.5	90	1270	31.5	35
12	m		lp	26.5	31	60	1220	23	15
13	f	pl	pp	106.5	76	20	760	14	90
14	f	pl	pp	115	95.5	70	765	18	83
15	m / f	pl	pp	93	67.5	95	780	28.5	160

cont. . . .

Appendix 8 cont. . .

Stump #	Bat Sex ^a	Bat Reprod. Condition ^b	Tree Species ^c	Diameter (cm)	Average Height (cm)	% Bark Remaining	Elevation (m)	Slope (°)	Dist. to Nearest Edge (m)
16	m		wc	65	63	75	845	11	65
17	m		wc	40.5	42.5	50	875	21	125
Mean:				62.5	54	69		21	80
SD:				29.7	19.5	20.5		6.9	50.4

a f = female, m = male

b nr = non-reproductive, p = pregnant, pl = post-lactating

c gf = grand fir, lp = lodgepole pine, pp = ponderosa pine, wc = western red cedar, wh = western hemlock, wp = western white pine

Appendix 9. Cavity characteristics of bat roost stumps found during the summers of 1993-94 in the RCW. Blanks indicate missing values.

Stump #	Bark Thick. (mm)	Bark Burnt	Cavity Depth (cm)	Entrance Width (mm)	Entrance Length (cm)	Entrance Height (cm)	Crevice Aspect (° azi.)	Dist. to Nearest Shrub (cm)	Height of Nearest Shrub (cm)	Dist. to Nearest Herb (cm)	Height of Nearest Herb (cm)
1	7.8	yes					172	7	34	42	60
1	11.6	yes	32	22	12	53	29	30	16	11.5	17
2	37.88	no	18	19	53	42	168	82.5	2.5	81	19
3	19	yes	60	17	11	77.5	346	41	83	38	87
4	7.15	yes	30	30	7	66	160	4	24.5	20.5	94
5	17.8	yes	33.5	14	14	49.5	273	30	89	14	24
6	13.1	yes	29	15	38.5	50	196	208	198	46	18
7	6.2	yes	18	18	6	35	185	127	36	32	53
8	5.05	yes	38	47	3.5	42	210	77	46	>500	
9	8.2	yes	18.5	8	5	40.5	275	29	61	>500	
10	5.9	yes	30	15		44	211	101.5	37	35.5	56
11	5.4	yes	52	34	9	28	234	35	17	180	100
12	8.2	yes	25	19	8	18	226	21	30	147	53
13	58.9	yes	50	16	43	61	352	2.5	78	130	60

cont. . . .

Appendix 9 cont. . . .

Stump #	Average Bark Thick. (mm)	Bark Burnt	Cavity Depth (cm)	Entrance Width (mm)	Entrance Length (cm)	Entrance Height (cm)	Crevice Aspect (° azi)	Dist. to Nearest Shrub (cm)	Height of Nearest Shrub (cm)	Dist. to Nearest Herb (cm)	Height of Nearest Herb (cm)
14	39.15	yes	72	15	25	64	180	100	65	124	19
15	42.5	yes	31	15	12	45.5	148	53	46	98	38
15	40.7	yes	32	15	20	77	205	35	21	88	22
16	6.1	yes	52	45	10.5	61.5	178	18	75	23	58
17	5.6	yes	36	35	13	41	357	10	56	49	25
Mean:	18.2		34.5	21	15	47	208	53	53.5	68 ^b	42 ^b
SD:	16.70		16.8	12.0	14.7	19.2	59.8 ^a	52.2	42.9	51.5 ^b	30.1 ^b

a angular dispersion

b excluding stumps 8 and 9