ACTIVITY AND ROOST SELECTION OF BATS IN MONTANE FORESTS ON NORTHERN VANCOUVER ISLAND

by

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Abstract

I examined species of bats and their distribution in mid and high elevation temperate rainforests of coastal British Columbia during 1997 and 1998. *Myotis volans, M. californicus, M. lucifugus, M. yumanensis, M. evotis/keenii,* and *Lasionycteris noctivagans* were caught in mist nets. Four of these species (*M. volans, M. californicus, M. lucifugus, M. evotis/keenii*) were likely reproducing in montane forests. Diets of bats varied among species, and flexibility in diet may enable bats to exploit harsh environments.

I monitored activity of bats at ponds and forest edges across 3 elevation classes to determine how and when bats use montane forests. Abundance and activity of bats, particularly of big bats, decreased with increasing elevation. Nevertheless, bats were present at high elevation sites from May, when sampling began, until October. Swarming activity occurred at several high elevation ponds in September.

Most bats that were captured and radio-tagged at mid and high elevations roosted in old growth forests at mid and high elevations. Of 50 roosts, 47 were beneath loose bark or in cracks in the bole of trees, and 3 roosts were in rock crevices. All visually confirmed roosts were south facing. Typical roost trees were large diameter and in intermediate stages of decay. Roost sites had less canopy cover than did random sites. Within the brief period of observation (1-18 days), bats switched roosts frequently, using from 1 to 8 roosts in roost areas up to at least 78 ha.

In spite of cool, damp weather in coastal mountains, montane forests are used for foraging and roosting by bats. Protection or provision of habitat for bats in montane forests should include retention of old growth forest in patches that contain various age

classes of trees and snags. Special consideration should be given to current and future supply of roost structures. Forest management plans that ensure habitat for other old growth- and snag-dependent wildlife will generally also meet the habitat needs of bats.

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General introduction

Bats (Chiroptera) are a diverse Order of mammals (approximately 900 species, Altringham 1996), second only to the Rodentia in species richness. They occur worldwide, including in many cold climates. Although species richness declines with increasing latitude, bats inhabit north temperate rainforests of coastal Alaska (Parker et al. 1996) and boreal forests, ranging north to the tree-line (Altringham 1996, de Jong 1994).

In cold climates, bats are faced with numerous energetic stresses. Because all northern bats hibernate or migrate for the winter, they only have a few months to accumulate fat reserves. All northern bats are insectivorous, but cool nightly temperatures reduce insect activity (Kunz 1982a, Hayes 1997) and probably make it difficult for bats, and particularly pregnant or lactating females, to meet their daily energy requirements. Cool temperatures during the day have serious consequences as well. To conserve energy, bats, under some environmental regimes, become torpid during the day. Torpor delays the development and birth of young, leaving juveniles with less time to grow and gain weight before the fall (Nagorsen and Brigham 1993). Females, in particular, should therefore try and reduce their use of torpor (Hamilton and Barclay 1994).

In British Columbia, there are up to 10 species of bats in the temperate coastal rainforest: *Myotis lucifugus, M. yumanensis, M. volans, M. californicus, M. keenii, M. evotis, Eptesicus fuscus, Lasionycteris noctivagans, Lasiurus cinereus,* and *Plecotus townsendii* (Nagorsen and Brigham 1993). The geographical distributions of these forest bats are poorly known and are based on few observations. Even less is known about the altitudinal limits of their distribution.

Montane forests, defined as montane Coastal Western Hemlock and subalpine Mountain Hemlock forest types, are widespread at mid and high elevations of coastal B.C., comprising up to 30% of the land base on Vancouver Island (Arnott and Beese 1997). These coastal montane forests are characterised by cool temperatures, frequent rainstorms throughout the year, and a deep and persistent snowpack. Bats occur in these forests, but their habitat requirements are unknown. In this energetically challenging environment, roost choice could be important in maintaining energy balance. Roosting requirements of bats in montane forests are inferred from studies conducted in low elevation forests (e. g., Stevens 1995). One coastal forest bat species (*Myotis volans*) roosts in large diameter dead or dying trees, which are typical of old growth stands (Ormsbee and McComb 1998). Other characteristics of roosts must be inferred from studies of interior populations (e. g., Campbell et al. 1996, Vonhof and Barclay 1996, Brigham et al. 1997, Vonhof and Barclay 1997).

Because of the history of logging in coastal British Columbia, most remaining old growth forest is at high elevations. Although these forests have become a focus for harvesting operations, current forest management and silvicultural practices are based primarily on knowledge of productive low elevation ecosystems. One notable exception is information from the Montane Alternative Silvicultural Systems project (Arnott and Beese 1997), which addresses primarily silvicultural but not wildlife issues.

Timber harvesting and its alteration of habitat structure may affect bats by the loss of roost trees, the increase of commuting distances between roost and foraging sites, and the creation of unsuitable habitat types. At the landscape level, these changes could result in loss of habitat, fragmentation of the remaining suitable habitat, and potentially

diminish biodiversity in managed landscapes. The lack of basic knowledge about coastal bats means that there is little ecological information to contribute to the management of montane forests.

My objectives are to examine the use of montane forests by bats and to identify habitat components needed by bat populations in these forests. In Chapter 1, I present information on species presence and diet. Knowledge of diet provides insight into factors that limit the distribution of bats. In Chapter 2, I investigate the influence of elevation on activity of bats, and the timing of use of montane forests. In Chapter 3, I describe day roosts used by bats. In Chapter 4, I summarize my research and relate my conclusions to management of montane forests. By examining activity across elevations and the roosts of bats captured at montane sites, I will determine when bats occupy these forests and infer what resources they exploit. Information on both foraging and roosting are needed to understand the use of montane forests by bats, and to provide appropriate recommendations for maintaining habitat for bats.

Study area

The study area is located on northern Vancouver Island (50° 12' N, 126° 20' W), approximately 90 km south of Port McNeill, British Columbia. The area includes Mt. Cain and Mt. Maquilla, and the surrounding watersheds of the Tsitika and Davie Rivers. The region is mountainous, steep, heavily forested, and contains numerous water bodies, varying from small wetlands to large lakes.

There are 2 forested biogeoclimatic zones in the area. The Coastal Western Hemlock zone (CWH) covers the lower slopes of mountains, and grades into the Mountain Hemlock (MH) zone above (Meidinger and Pojar 1991). Due to the large elevational gradient and influence of mountains, there are many biogeoclimatic subzone variants in the area (Table 1).

My study focussed on mid and high elevation ecosystems. I used the term 'montane ' to describe all forests above 600 m, which include primarily montane CWH (the vm2 variant) and subalpine MH (the mm1 variant) forests. When investigating the effects of elevation, I further subdivided montane forests into mid elevation sites (600 - 825 m), in predominantly montane CWH forest, and high elevation sites (850 - 1200 m), in predominantly subalpine MH forest.

Forests in the CWHvm2 variant have short summers, cool winters, and heavy snowfall. Climatic conditions are even more extreme in the MHmm1 variant, which has longer, wetter winters, cooler summers, and more snow (Table 2) (Green and Klinka 1994), often with a snowpack of greater than 4 m (Klinka et al. 1991). There were significant differences in weather during the 2 years of my study, presumably due to the drying effects of the 1998 El Niño phenomenon. Precipitation during May to October

Table 1. Biogeoclimatic variants present around Mt. Cain, Vancouver Island, B.C.

Zone, subzone, and variant	Abbreviation	Elevation (m)
CWH xeric maritime	CWHxm2	< 500
CWH submontane very wet maritime	CWHvm1	500-700
CWH montane very wet maritime	CWHvm2	600-900
MH windward moist maritime	MHmm1	800-1200
MH moist maritime parkland	MHmmp	> 1100

From: Green and Klinka 1994

Table 2. Temperatures at sunset (a) and monthly nightly minimum temperatures (b) for low, middle, and high elevations at Mt. Cain, 1997-1998. Elevation ranges are for sites where temperature, bat, and insect data were collected for this study.

a) Temperatures at sunset (°C)

Month	Low elevation (300 – 450 m)				Mid elevation (650 – 800 m)				High elevation (850 – 1200 m)			
	Mean	Min.	Max.	# nights	Mean	Min.	Max.	# nights	Mean	Min.	Max.	# nights
Jun.	11.5	9.0	14.4	8	9.5	6.2	13.3	11	7.7	2.8	12.1	13
Jul.	14.2	10.9	16.7	10	11.1	7.8	13.7	9	9.0	5.8	12.9	12
Aug.	14.3	10.9	17.8	10	11.6	8.6	16.3	11	10.7	7.0	14.4	12
Sep.	11.8	9.0	14.1	10	9.4	5.8	14.4	13	8.3	3.7	10.9	11
Oct.	9.2	4.5	13.3	5	6.2	5.8	6.6	3	5.7	1.1	8.6	5

b) Nightly minimum temperatures (°C)

Month	Mean	Min.	Max.	# nights	Mean	Min.	Max.	# nights	Mean	Min.	Max.	# nights
Jun.	8.0	4.5	10.6	9	6.8	4.5	11.3	11	5.9	2.4	10.2	13
Jul.	9.7	3.7	12.5	10	5.8	2.0	9.8	9	6.1	2.0	10.2	12
Aug.	10.1	7.4	15.6	10	7.6	4.5	11.7	11	7.4	3.7	10.6	12
Sep.	7.8	4.9	10.9	10	4.8	1.1	8.6	13	4.3	1.6	8.6	11
Oct.	5.7	-1.4	9.4	5	4.4	3.7	5.8	3	4.6	-0.6	8.2	5

1998 was approximately half of that during the same period in 1997 (Table 3). At Mt.

Cain, there was a reduced snowpack and earlier snowmelt in spring 1998 relative to in

1997 (personal observation).

The dominant tree species in CWH forests are western hemlock (*Tsuga*

heterophylla (Raf.) Sarg.), western redcedar (*Thuja plicata* Donn *ex* D. Don), and

amabilis fir (*Abies amabilis* (Dougl. *ex* Laud.) Dougl. *ex* Forbes). In MH forests, western

hemlock and western redcedar are replaced by mountain hemlock (*Tsuga mertensiana*

(Bong.) Carr.) and yellow-cedar (*Chamaecyparis nootkatensis* (D. Don) Spach). In both

forest types, western white pine (*Pinus monticola* Dougl. *ex* D. Don) occurs sporadically,

and there is a well-developed shrub layer of *Vaccinium* species and small trees. Montane

forests generally have multi-storied canopies, and many small gaps created by the death

of a few trees (Lertzman and Krebs 1991) or by wetlands. Large-scale natural

disturbances are rare in high elevation coastal forests, and 800-year-old yellow-cedar

trees have been found at Mt. Cain (Laroque and Smith 1999).

The study area is in TFL 37, held by Canadian Forest Products, Ltd. There is a

long history of forest harvesting using clear-cut techniques, and an extensive network of

logging roads. To date, most of the harvesting on Vancouver Island has been in low

elevation forests, but future plans include increased harvesting from CWHvm2 and

MHmm1 forests (Arnott et al. 1995).

Table 3. Total precipitation and number of days with measurable precipitation in May –
October 1997 and 1998, measured at Port Hardy, Vancouver Island.

Month	1997		1998	
	Total precipitation (mm)	# days with measurable precipitation	Total precipitation (mm)	# days with measurable precipitation
May	122.4	15	44.8	15
Jun.	115.8	22	59.8	12
Jul.	74.6	12	56.0	11
Aug.	99.7	12	53.8	10
Sep.	157.0	20	61.2	13
Oct.	405.0	25	212.6	25
Total	974.5	106	488.2	86

Source: Environment Canada

Chapter 1. Natural history of bats on Mt. Cain: species presence, behaviour, and diet

Introduction

There has been a recent surge in research on bats in the temperate rainforests of northern and coastal Vancouver Island (Bradshaw 1997, Davis et al. 1998, Grindal 1998, van den Driessche et al. 1999). Seven species of bats have been captured and identified: *Myotis lucifugus*, *M. yumanensis*, *M. volans*, *M. californicus*, *M. evotis*, *M. keenii*, and *Eptesicus fuscus* (Bradshaw 1997, Davis et al. 1998, Grindal 1998). Other species have been identified solely on the basis of echolocation calls: *Lasionycteris noctivagans*, *Lasiurus cinereus* (Bradshaw 1997, Grindal 1998), and *Plecotus townsendii* (Grindal 1998). However, these studies were based primarily in valley bottoms.

The only information on species in montane forests comes from 1 site in Clayoquot Sound (van den Driessche et al. 1999) and the Weymer Cave study (Davis et al. 1998). At Clayoquot Sound, *M. lucifugus/yumanensis* and reproductively active *M. californicus* and *M. evotis/keenii* were captured near a lake in the CWHvm2 subzone. At Weymer Cave, 4 species of *Myotis* (*M. volans*, *M. lucifugus*, *M. yumanensis*, and *M. keenii*) were captured swarming in the cave entrance at 900 m elevation (Davis et al. 1998). Use of high elevation forests for activities other than swarming and hibernating is unknown.

All species of bats on Vancouver Island, like those elsewhere in Canada, are insectivorous (Nagorsen and Brigham 1993). Differences in diet among these species may reflect different ways of foraging, such as aerial hawking versus gleaning (Rydell 1989), or different abilities to consume prey items. Differences may also be a

consequence of habitat selection, and opportunistic foraging in that habitat. Information

on diet may therefore provide insights about life histories of bats in montane forests.

In this chapter, I document species presence for bats in coastal montane forests. I

also describe the diets of bats captured at Mt. Cain, to identify their major prey and

variation in diet.

Methods

I surveyed bats from 13 May to 7 October 1997 and 20 May to 10 October 1998,

using bat detectors and mist-nets. I sampled a variety of elevations and habitat types

using a broadband bat detector, night-activated delay switch (Anabat system, Titley

Electronics, Australia), and a tape recorder housed in a waterproof box. Each unit was

placed less than 2 m above ground level, and aimed upwards at a 30° angle.

I set mist nets over water bodies or along forest edges to capture bats. Captured

bats were kept in cloth bags for 0.5 to 1 hour to collect faeces for analysis, then the bats

were weighed, measured, identified (Nagorsen and Brigham 1993), and released. I air-

dried the faecal samples and stored them for up to 2.5 years before analysis. Samples

contained from 1 to 16 pellets each. All the pellets from each bat were softened in ethanol

and observed through a dissecting microscope at 16 or 40 power. I examined 110 samples

from 6 species of bats; this included 96 samples from 1997/1998, and 14 samples from

August 1996. I identified the arthropod contents to Order (Borror et al. 1981), with the

exception of spiders which were identified as Arachnida, to obtain a list of items in each

sample (Whitaker 1988).

I analyzed dietary data as the percent occurrence of prey groups. I defined percent occurrence as the number of samples containing a particular prey item divided by the total number of samples (Whitaker 1988). The limitations of occurrence include loss of information about relative numbers or volume of prey groups. However, I could not confidently estimate the percent volume of each prey group, because pellets were often comprised of an unrecognisable mass dotted with identifiable insect parts from various orders. Because pellets often contained more than 1 type of prey (range 1-6), I could not assume that the unrecognisable parts belong to any particular prey group.

I described vegetation and site characteristics at all detector and mist-net sites, following Resource Inventory Committee Standards (Garcia and Barclay 1997). Measurements included elevation, slope, aspect, and the percent cover of trees, shrubs, and herbs.

Results

Species presence

I caught 71 bats of 6 or 7 species (Table 4) during 541 net-nights in montane habitats, or 1 bat per 7.6 net-nights. During 30.5 net-nights at low elevation sites, I caught 25 bats of 4 or 5 species, or 1 bat per 1.2 net-nights. I am uncertain about the number of species captured because I could not distinguish *Myotis evotis* and *M. keenii* in the field. Recordings from Anabat detectors were identified as *Myotis* species, *Lasionycteris noctivagans/Eptesicus fuscus*, and *Lasiurus cinereus*. I pooled data for *L. noctivagans*, *E. fuscus*, and *L. cinereus*, and collectively called them 'big bats'. Several species caught at

Table 4. Capture summary and netting effort during May - October 1997 and 1998. All bats were captured in mist nets and identified in-hand, with the exception of *Lasiurus cinereus/Eptesicus fuscus* and *Lasionycteris noctivagans*, which were heard but not captured at low elevation.

Species	Total	Females	Males
Montane sampling (> 600 m elevation, 86 nights, 541 net-nights (6 x 2 m net equivalents))			
Myotis lucifugus	38	14	24
M. yumanensis	3	0	3
M. evotis/keenii [a]	6	3	3
M. californicus	15	6	9
M. volans	6	3	3
Lasionycteris noctivagans	3	0	3
All species	.71	26	45
Low elevation sampling (< 450 m elevation, 5 nights, 30.5 net-nights (6 x 2 m net equivalents))			
M. lucifugus	3	1	2
M. yumanensis	6	4	2
M. lucifugus/yumanensis [b]	2	1	1
M. evotis/keenii	2	2	0
M. californicus	12	10	2
L. noctivagans/Eptesicus fuscus	Detected		
Lasiurus cinereus	Detected		
All species	25	18	7

[a] *M. evotis* and *M. keenii* could not be distinguished in the field.

[b] I could not be sure of the identity of these bats. Other *M. lucifugus* and *M. yumanensis* were identified primarily on the basis of behaviour and coat appearance.

montane sites were reproductively active, as defined by the presence of pregnant or

lactating females or the presence of juveniles (Table 5).

Behaviour

Capture rates and detection rates differed among species of bats. There were

activity peaks for big bats at low elevation sites during May and August in 1997, and at

all elevations in June 1998. I also noticed a sharp decrease in the number of *M.*

californicus netted in 1998 as the summer progressed. Although *M. californicus* was the

second most common bat netted, all captures in 1998 (n=11) were in May or June. In

1997, 4 *M. californicus* were captured, 2 of which were caught in July and 2 in August.

I observed swarming behaviour by *M. lucifugus* at a high elevation pond (850 m)

on 19 September 1997 and 16 September 1998, and at another high elevation pond (1150

m) on 15 September 1998. On these occasions, I had unusually high capture success,

netting 5 to 14 bats (adults and juveniles) each night.

Bats were often detected at snow-covered high elevation ponds in mid-May when

surveying began, and continued to be detected and captured at high elevation sites until

late September or early October.

Diet

Prey groups found in the scats and their percent occurrence are listed in Table 6.

Pellets contained recognisable pieces from 1 to 6 prey groups. Different species of bats

had different diets, as measured by the percent occurrence of prey groups in their pellets

(Fig. 1, Cochran-Mantel-Haenszel chi-square, Q=21.338, P=0.001). *M. lucifugus*

Table 5. Species of bat, age or reproductive state, capture elevation, and date, for reproductive females and juveniles caught at Mt. Cain during May to October 1997 and 1998.

Species	Evidence of reproduction	Elevation (m)	Date
M. lucifugus	Pregnant	1150	22 Jun., 1998
			17 Jul., 1998
			23 Jul., 1998
M. evotis/keenii	Pregnant	650	10 Jul., 1998
M. californicus	Pregnant	950	2 Jul., 1998
M. volans	Post-lactating	950	15 Aug., 1997
M. californicus	Juvenile	950	15 Aug., 1997
M. evotis/keenii	Juvenile	1000	22 Aug., 1997

Table 6. Prey groups in scats of all bats captured at Mt. Cain.

Prey group	Percent occurrence in all samples (n=110)
Diptera	83
Lepidoptera	63
Neuroptera	52
Hymenoptera	41
Coleoptera	17
Arachnida	15
Trichoptera	10
Ephemeroptera	5
Homoptera	5
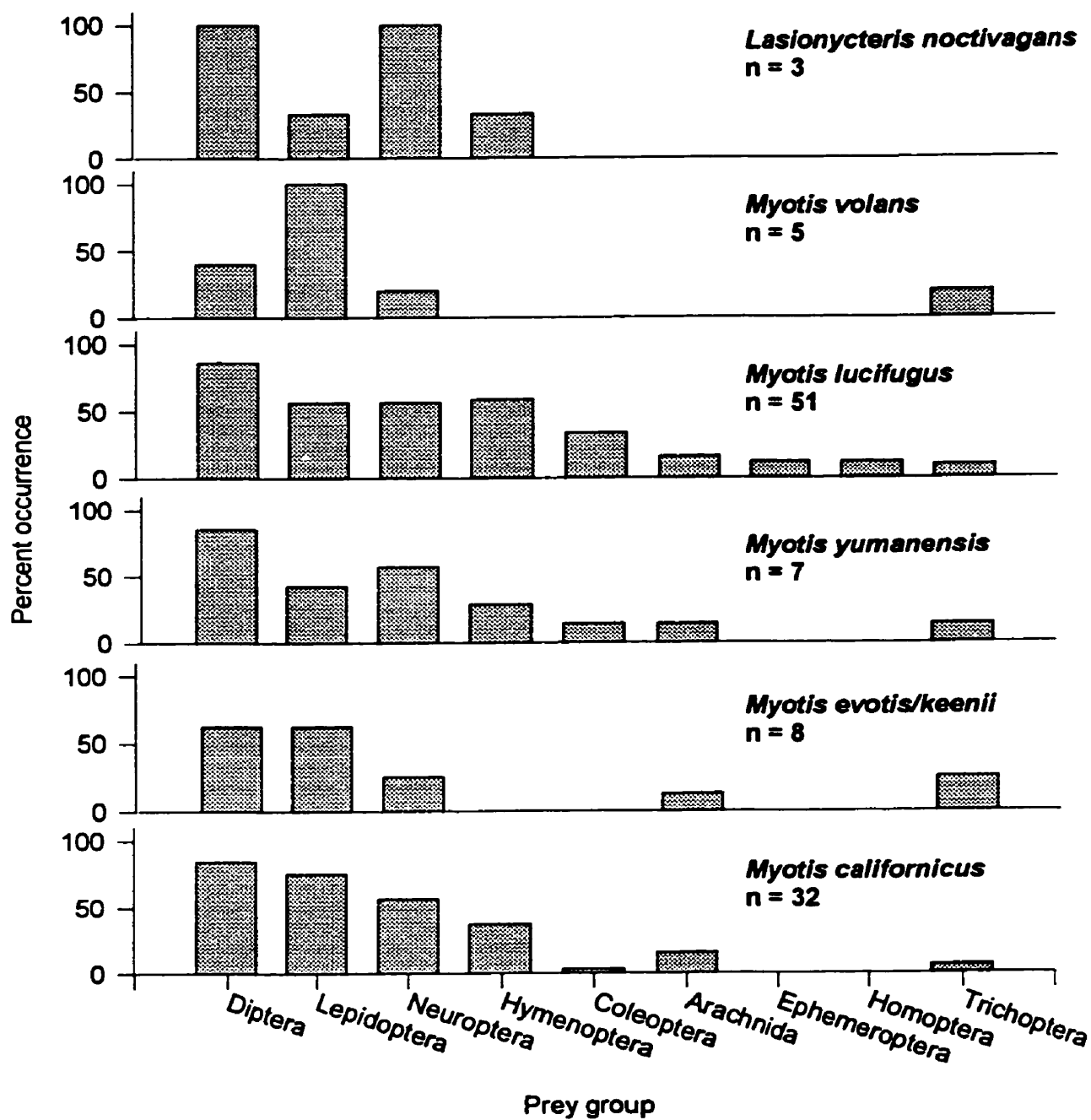
Figure 1. Percent occurrence of prey groups in 106 scats from 6 species of bats. Prey groups are listed by decreasing occurrence in the diet of *M. lucifugus*.

had the most diverse diet, consuming 9 insect groups. Only *M. californicus* and *M. lucifugus* had sufficient sample sizes (n=32 and n=51, respectively) to investigate diet further by species. Males and females showed no difference in diet, whether analyzed for all bats (Q=0.528, df=1, P=0.468), or by species (*M. californicus*, Q=0.343, P=0.558; *M. lucifugus*, Q=0.482, P=0.487).

Percent occurrence of prey groups did not vary with time of year for *M. californicus* (Fig. 2, Q=1.403, df=2, P=0.236) but did vary seasonally for *M. lucifugus* (Q=6.111, df=2, P=0.047). The occurrence of Hymenoptera in particular increased significantly.

Samples were collected across a range of elevations (low, < 450 m; mid, 650-825 m; high, 850-1200 m). Overall diet did not change with elevation for *M. californicus* (Fig. 3, Q= 2.208, df=2, P=0.332), although occurrence of Hymenoptera decreased significantly at high elevations. Diet of *M. lucifugus* changed with elevation (Q=10.873, df=2, P=0.004). Neuroptera, Hymenoptera, and Coleoptera occurred significantly more often in samples from *M. lucifugus* at high elevation sites than at low or mid elevation sites.

Seasonal and elevational occurrence of prey groups are confounded. The month and elevation of samples were correlated (Spearman's rho = 0.401, n=109, P<0.001). As the summer progressed, I focussed sampling on high elevation sites to radio-tag bats using montane forests. Small sample sizes made it impossible to separate effects of month and elevation by testing subsets of the data.

On a nightly basis, there were no significant differences in overall diet as the time between sunset and capture of bats increased (Fig. 4; *M. californicus*, Q=4.879, df=2,
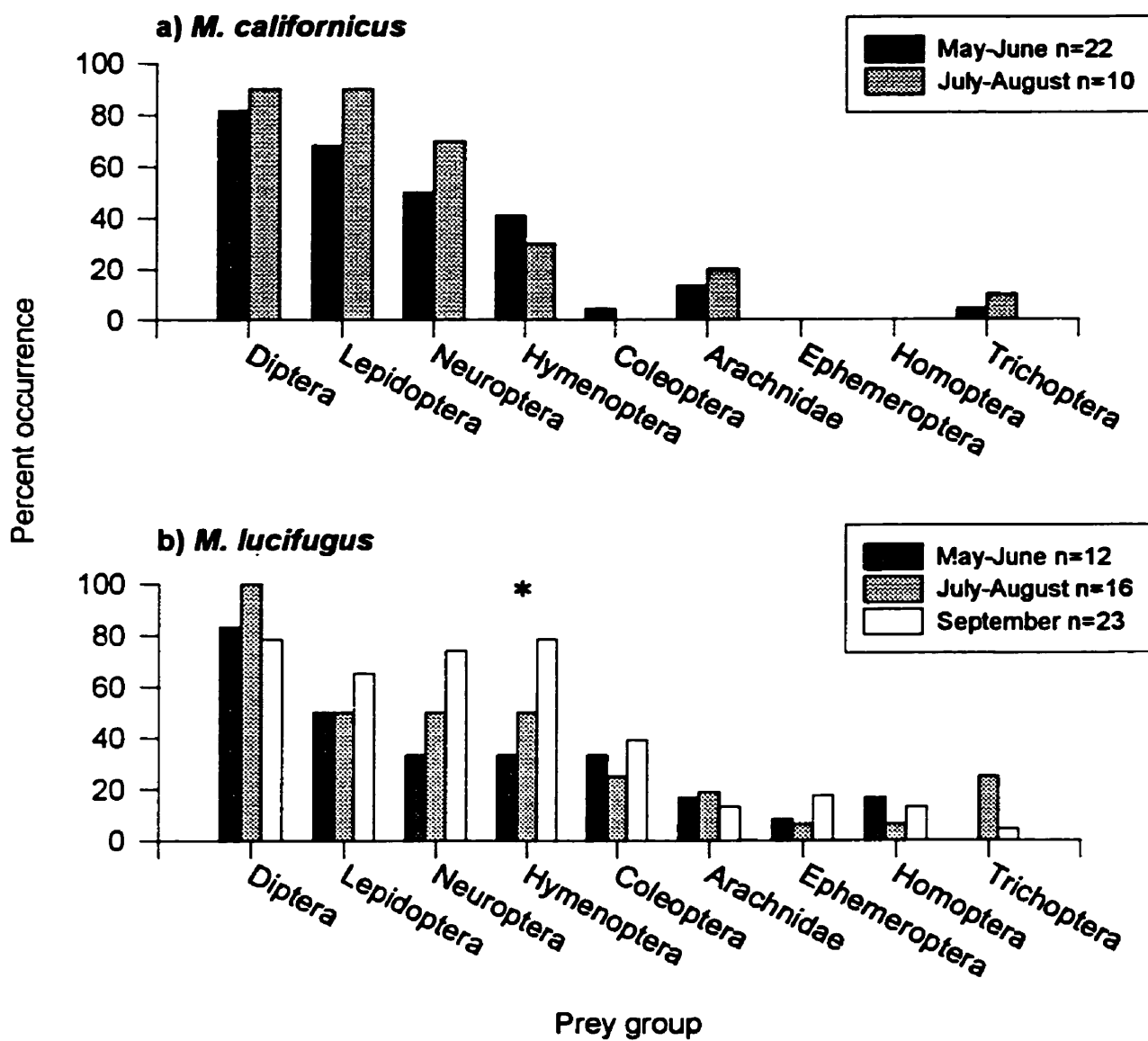
Figure 2. Diets of a) *M. californicus* in May-June and July-August, and b) *M. lucifugus* in May-June, July-August, and September. The asterisk indicates the prey group with a significant difference in percent occurrence in diet among periods.
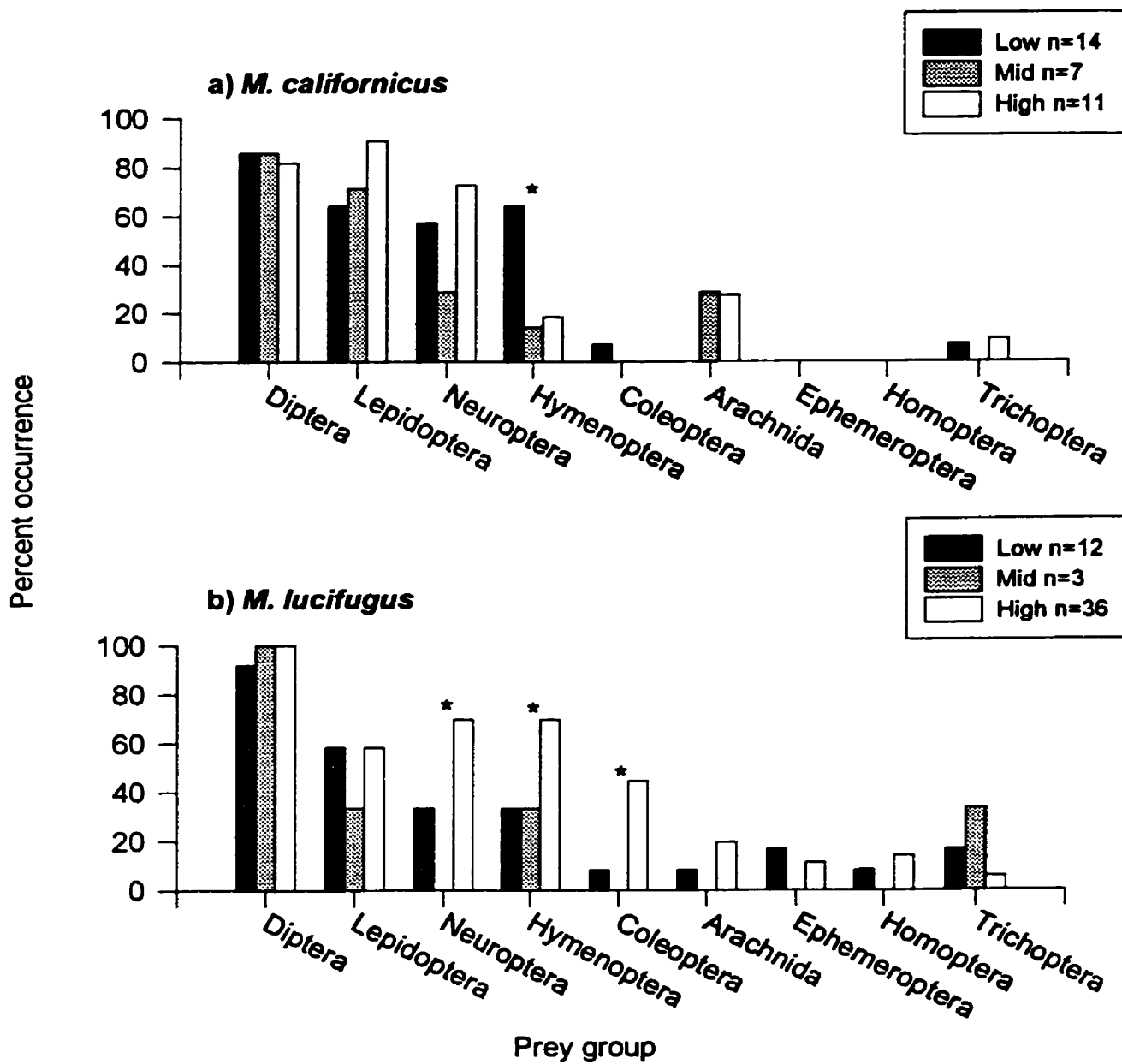
Figure 3. Diets of a) *M. californicus*, and b) *M. lucifugus*, by elevation. Asterisks indicate prey groups with significant differences in percent occurrence in diet among elevations.
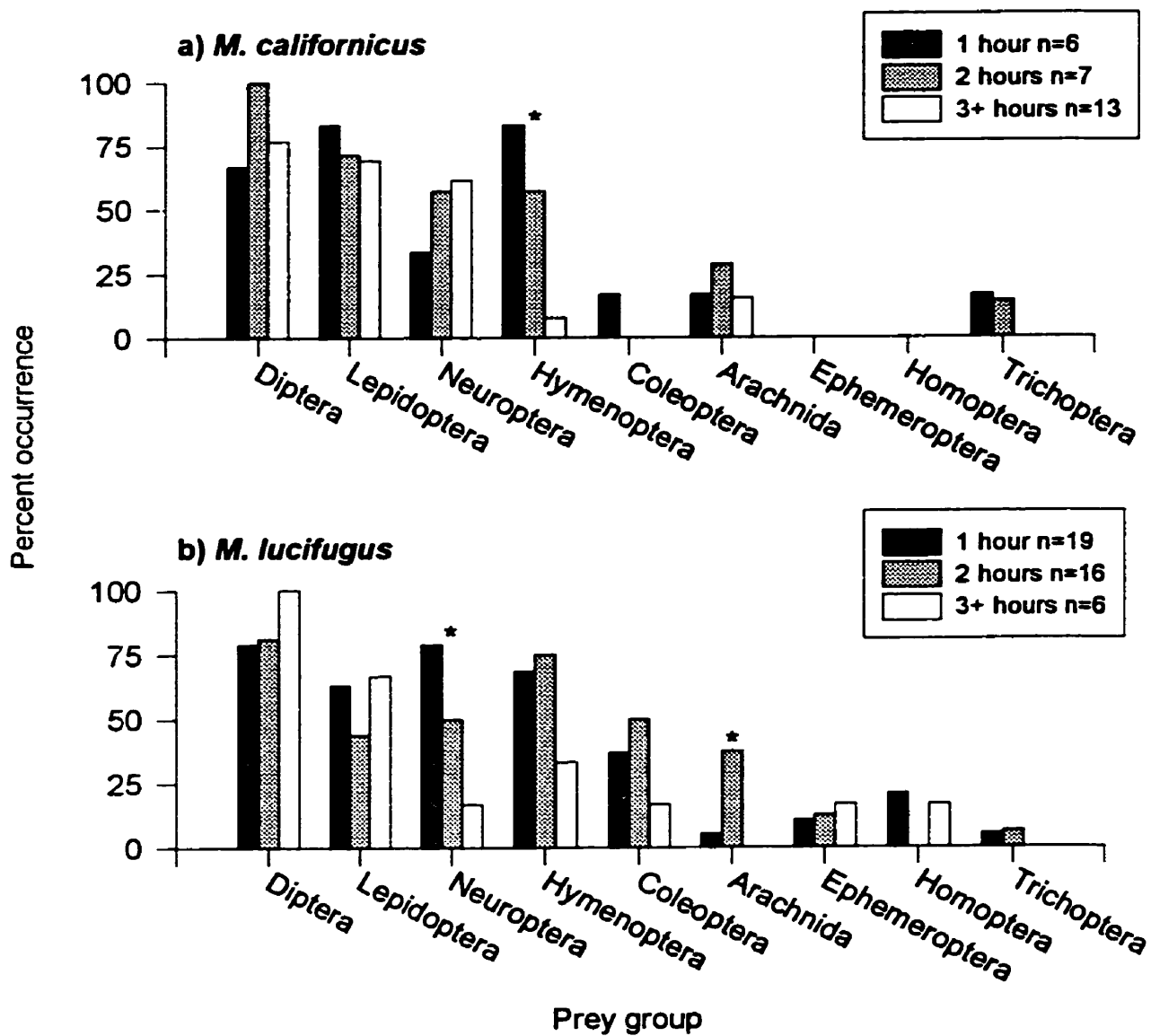
Figure 4. Diets of a) *M. californicus* and b) *M. lucifugus*, by time since sunset. Asterisks indicate prey groups with significant differences in percent occurrence in diet among periods.

P=0.087; *M. lucifugus*, Q=3.175, df=2, P=0.204). In *M. lucifugus* samples, the percent

occurrence of Neuroptera decreased during the night (Fisher's exact test, P=0.015), while

the percent occurrence of Arachnida peaked 2 hours after sunset (Fisher's exact test,

P=0.024). Both *M. lucifugus* and *M. californicus* had decreased percent occurrence of

Hymenoptera, although this decrease was only significant for *M. californicus* (Fisher's

exact test, P=0.002).

Discussion

Species presence

The montane forests of Mt. Cain have a diverse community of bats, with little

difference in species composition between low elevation and montane forests. *L. cinereus*

was the only species identified solely at low elevations. *M. volans* was not captured while

mist-netting at low elevations, but was documented in low elevation habitats near the

study area (Grindal 1998). I did not capture *E. fuscus*, but this species has been caught

south-west of the study area (Davis et al. 1998). Unfortunately, the calls of *E. fuscus* and

L. noctivagans are difficult to separate (Betts 1998). Because I captured only *L.*

noctivagans, I am uncertain about the presence of *E. fuscus* at Mt. Cain.

Sexual segregation and an absence of female bats at high elevation sites has been

found for *M. lucifugus* in the eastern Rockies (Barclay 1991) and for several species in

the western Cascades in Washington (Thomas 1988). This segregation has been attributed

to the higher energetic demands of reproductive female bats. The presence of

reproductively active females at high elevations on Mt. Cain indicates that several species

are not exhibiting sexual segregation, in spite of the low temperatures and short summer

season. The timing of reproduction is consistent with the timing reported by Nagorsen and Brigham (1993) for these species.

Much of the information on the winter distribution and behaviour of bats is based on information gathered during the summer. *L. noctivagans* is believed to migrate. The pulses of activity recorded for big bats at Mt. Cain are typical for this species, and are perhaps evidence for north- and southward migrations in the early and late summer (Nagorsen and Brigham 1993). Although no hibernacula are known for the study area, the swarming behaviour observed for *M. lucifugus* suggests that this species is probably hibernating in or near the study area.

Diet

There are several limitations imposed by using percent occurrence to examine diets. Percent occurrence does not account for different sizes of prey items. Also, the frequency of items with easily-identified parts, such as Lepidopteran scales, may be over-estimated. Soft-bodied items, such as Dipterans, may be under-estimated, due to the difficulty of recognizing disassociated body parts. These biases were found by Kunz and Whitaker (1983) and Belwood and Fenton (1976). Nevertheless, percent occurrence does provide a list of items consumed, and an index of their importance in the diet.

Species of bat was a main factor influencing the diets of bats at Mt. Cain. Prey groups consumed at Mt. Cain are consistent with the results from other diet studies, although the primary prey groups often differ. *M. volans* had lepidopteran scales in 100% of the samples, which is in accordance with its description as a Lepidoptera "specialist" (Whitaker et al. 1977). For other species, however, Diptera appeared more frequently

than is reported in other areas. *M. evotis* has been documented as eating primarily

Lepidoptera (Whitaker et al. 1977, Barclay 1991), but in the 5 samples from Mt. Cain, *M.*

evotis consumed Diptera as often as Lepidoptera. The diet of *L. noctivagans* was higher

in Dipterans than in Lepidoptera, contrary to the findings of Whitaker et al. (1977).

Unlike in the Okanagan (Nagorsen and Brigham 1993), *M. californicus* on Mt. Cain

rarely ate Trichoptera, feeding more frequently on Diptera, Lepidoptera, and Neuroptera.

Diets of bats have been observed to change seasonally, presumably as bats exploit

seasonal abundances of insects (Brigham et al. 1992). This flexibility may be important

to survival, as diversity of diet and foraging strategies have been suggested as factors

which influence the ability of bats to live in harsh environments (Belwood and Fenton

1976, Barclay 1991). At Mt. Cain, *M. lucifugus* consumed prey groups other than

Diptera, their primary prey, more frequently at high elevation sites and later in the year.

Flexibility in diet over time, and contrasts between diets described in this and in other

studies, suggests that bats on northern Vancouver Island may adapt their diets to enable

them to extend their range into montane forests and adjust to seasonal variations in food

supply.

Chapter 2. Elevation and activity of bats on northern Vancouver Island

Introduction

Climate can influence the community structure and activity of bats (Thomas 1988, Barclay 1991). Despite a large elevation gradient, with the associated changes in habitat, temperature, and length of summer, montane forests on Vancouver Island support similar bat species as low elevation forests (Chapter 1). Nightly activity of bats increases with increasing temperature (Audet 1990, Hayes 1997), presumably because warmer temperatures cause increased insect activity (Kunz 1982a, Hayes 1997). Hence, activity levels of bats in higher elevation forests should be depressed compared to those in lower elevations.

Mobile animals have the option of exploiting different habitats at different times. Bats, like many animals, can shift foraging areas across horizontally structured space, perhaps in response to changing insect abundance (de Jong 1994). The sharp relief of the mountains on northern Vancouver Island offers the potential for vertical movements by bats. Bats use low elevation coastal forests for roosting, foraging, and commuting between roost and foraging sites (Thomas 1988, Parker et al. 1996, Grindal 1998). High elevation forests provide roosting habitat for bats (Chapter 3), but the extent of other activities in these forests is unknown. Because bats are volant, they can travel long distances between roosting and foraging sites each night, potentially roosting in montane forests and foraging in more productive areas at lower elevations.

Bats may also shift between elevations on a longer time scale. Animals such as mountain goats (*Oreamnos americanus*), mule deer (*Odocoileus hemionus*), and white-

tailed ptarmigan (*Lagopus leucurus*), migrate seasonally between elevations. At the Weymer cave system on north-eastern Vancouver Island, use of upper elevation (400-900 m) cave sites by bats is seasonal. Activity of bats is restricted to swarming by males beginning in late July, and by females beginning in early September. As well, both males and females use the caves for hibernation over winter. In this same area, some use of high elevation 'surface' sites by bats occurred from spring to fall (Davis et al. 1998).

I monitored pond and upland habitats to investigate activity of bats in montane forests relative to those in lower elevation forests. My objectives are to compare the activity of bats across elevations and to understand how bats use montane forests. I expected activity to be seasonally constrained with increasing elevation, and activity to be associated with insect abundance.

Methods

Sampling design

I compared relative activity of bats by remote sampling with ultrasonic bat detectors. A bat detector and night-activated delay switch (Anabat5 system, Titley Electronics) were powered with a 12 v battery at each monitoring site. This apparatus and a tape recorder were housed in a waterproof box. Each unit was placed approximately 1 to 2 m above the ground, and aimed upwards at a 30° angle. Detectors were placed at the same location when re-sampling sites.

In 1997, I sampled 10 ponds at each of low, mid and high elevations. Low elevation sites were in at 300 to 450 m a.s.l., in CWHxm2 or vm1 variants. Mid elevation sites were mid-slope, from 650 to 825 m a.s.l., in CWHvm1 and vm2 variants. High

elevation sites were ponds on the upper slopes of mountains, from 850 to 1200 m a.s.l., in

CWHvm2, MHmm1, or MHmmp variants. Each site was sampled once a month from

May to October, with at least one site at each elevation being sampled on a given night

(elevational blocking). I sampled 7 to 10 sites each night, depending on the number of bat

detectors available. Sampling began in the middle of each month and continued until all

sites had been visited. I did not use data from nights in which I did not detect bats at any

site. These were usually exceedingly windy or wet nights.

I repeated the pond sampling in 1998, but added 7 to 10 forest edge sites at each

elevation, to: a) compare riparian and upland activity at each elevation; and b) record

non-*Myotis* species, which were not detected at high elevation ponds in 1997. Edges were

abrupt, man-made old growth-clearcut edges, and were chosen due to the high levels of

bat activity at edges relative to other upland habitats. At each detector site, I described the

site characteristics, tree species, and tree density according to standards of the B.C.

Ministry of Environment Resource Inventory Committee (Garcia and Barclay 1997) and

the vegetation and wildlife tree sampling protocol from the B.C. Ministry of Forests'

Coastal Montane Biodiversity Project.

Analysis of detector data

I listened to the tapes from detectors, and divided the recorded bat calls into two

groups: *Myotis* species and 'big bats' (*Lasionycteris noctivagans, Lasiurus cinereus*, and

possibly *Eptesicus fuscus*). These groups were created because of the difficulty in further

species identification. Calls of *Myotis* bats and big bats are easy to distinguish, and the

flight patterns and foraging strategies of the two groups are predicted to be quite different

due to differences in wing morphology and echolocation call structure (Fenton 1990).

The same groupings, called either *Myotis* and non-*Myotis*, or clutter- and open-adapted,

have been used in other studies (e. g., Erikson and West 1996, Grindal 1996, Hayes and

Adam 1996).

I separated bat activity into the number of "commuting passes" (passes) or

"foraging buzzes" (buzzes) at each site. A pass was defined as a sequence of 2 or more

discernable echolocation calls, as in the Resource Inventory Committee Standards

(Garcia and Barclay 1997). The Anabat system uses a time of 1 second between calls to

differentiate between successive sequences of passes. A buzz was the obvious increase in

rate of echolocation calls as a bat approached and attempted to capture an insect. I

defined foraging rate as the number of foraging buzzes as a percent of the total number of

calls (commuting passes and foraging buzzes).

At many of the busier sites, the cassette tapes filled quickly and further bat

activity could not be recorded. Hence, I restricted the analyses to data collected during

the first 2 hours of sampling each evening. Although activity occurred well past this time,

this approach increased my sample size and allowed inclusion of the busy sites, which

would be excluded if sites had to be monitored all night before being considered for

analyses. Data are presented as the total number of passes during this 2-hour period.

There was extremely high variation in the number of passes recorded per night at

different elevations and in different months. The range in variances necessitated the use

of non-parametric statistics. I used Kruskal-Wallis 1-way non-parametric ANOVAs to

investigate differences between activity across elevations, and Dunn's Q (Zar 1999, p.

224) for multiple comparisons to identify where differences occurred. I used P=0.05 as the level of significance for all tests.

I also compared occurrence of bats at different sites. I defined presence as the detection of at least 1 pass, recorded during the first 2 hours of sampling. Occurrence data were analyzed using Cochran-Mantel-Haenszel (CMH) chi-square tests (Stokes et al. 1995) and Fisher's exact tests (Zar 1999). The CMH chi-square was used to test for general association between elevation and presence, after adjusting for the stratifying variable, month. This test provided a means to investigate blocked occurrence data much as a randomized block ANOVA would be used to investigate blocked interval-scaled data. I examined 1997 and 1998 data separately because environmental conditions were different between the 2 years, with 1998 being much warmer and drier. Correspondingly, there was greater activity in 1998 at most mid and high elevation sites.

I compared nightly activity patterns at different elevations, using data from nights that I sampled completely until dawn. I pooled data across months and calculated the total number of passes, and the fraction of this total that was recorded in each 15-min period following sunset. For big bats, I pooled data across months and elevations, due to the few passes recorded at mid and high elevation sites.

Insect sampling

I estimated the abundance of flying insects at sites by sampling them with a ground malaise trap on the same night that I sampled bats with a bat detector. The malaise traps were set at ground level on one day and collected on the following day. Traps were open for a variable amount of time, but they were randomly set up and retrieved amongst sites and elevations. I did not obtain paired samples for all sites on all

survey nights because I had fewer malaise traps (6 traps) than bat detectors (7 to 9

detectors), and on some nights the bat detectors malfunctioned and did not record bats.

Captured insects were counted and identified to Order. Counts of insects were

square-root transformed, after adding 0.5, to stabilise variances (Zar 1999), and then

analyzed with parametric ANOVAs. Analyses were performed on all insects together and

on Diptera and Lepidoptera, because these 2 Orders were important prey items (Chapter

1).

Results

Myotis spp.

<u>Activity across elevations</u>

The presence of *Myotis* bats at ponds was associated with elevation in 1997 and

1998 (Figs. 5 and 6, Table 7). The percent of sites with bats present decreased with

increasing elevation. Nevertheless, *Myotis* were present at a majority of sites across all

elevations during May through September. Activity, measured as the number of passes

recorded in 2 hours, was extremely variable. There was a trend for the median activity to

decrease with increasing elevation, although high variance resulted in few statistical

differences (Table 8).

The presence of *Myotis* bats at edges was strongly associated with elevation (Fig.

7, Table 7), with bats detected more often at low elevation sites. However, bats occurred

at all elevations. Within each month, activity at edge habitats was less variable than at

ponds. Activity was low at edges at all elevations, with the exception of August, when

activity increased at low and mid elevation sites.

a) occurrence

b) activity

Figure 5. *Myotis* bats at ponds, 1997. Percentage of sites sampled that had at least 1 detection of a *Myotis* bat (a), and activity represented as median number of passes (b). 'n' is the number of sites sampled.

a) occurrence

b) activity

Figure 6. *Myotis* bats at ponds, 1998. Percentage of sites sampled that had at least 1 detection of a *Myotis* bat (a), and activity represented as median number of passes (b). 'n' is the number of sites sampled.

Table 7. Results of Cochran-Mantel-Haenszel chi-square tests for general association between elevation and the presence of *Myotis* bats, blocked by month, and results of Fisher's exact tests for differences between the 3 elevations, within each month.

Habitat	Year	Month	CMH chi-square test (df=2)		Fisher's exact test
			χ^2	P	P
Ponds	1997		7.161	0.028 *	
		May			0.006 *
		Jun.			0.591
		Jul.			0.048 *
		Aug.			0.306
		Sep.			1.000
		Oct.			1.000
Ponds	1998		6.206	0.045 *	
		May			0.089
		Jun.			0.621
		Jul.			1.000
		Aug.			0.230
		Sep.			0.253
		Oct.			0.363
Edges	1998		10.71	0.005 *	
		May			0.050 *
		Jun.			1.000
		Jul.			0.758
		Aug.			1.000
		Sep.			0.091
		Oct.			0.066

Table 8. Results of one-way Kruskal-Wallis tests on the activity of *Myotis* bats across elevations, by month. Elevations with different letters were significantly different (Dunn's Q, P<0.050).

Habitat	Year	Month	Kruskal-Wallis (df=2) χ^2	P	Elevation in order of mean rank		
Ponds	1997	May	10.70	0.005 •	Low (a)	Mid (a,b)	High (b)
		Jun.	2.751	0.253			
		Jul.	7.747	0.021 *	Low (a)	High (a,b)	Mid (b)
		Aug.	4.480	0.106			
		Sep.	1.419	0.492			
		Oct.	1.333	0.513			
Ponds	1998	May	2.238	0.327			
		Jun.	2.477	0.290			
		Jul.	1.136	0.567			
		Aug.	8.107	0.017 *	Low (a)	High (a, b)	Mid (b)
		Sep.	3.476	0.176			
		Oct.	2.942	0.230			
Edges	1998	May	4.145	0.126			
		Jun.	1.772	0.412			
		Jul.	2.450	0.294			
		Aug.	7.814	0.020 •	Low (a)	Mid (a,b)	High (b)
		Sep.	1.041	0.594			
		Oct.	6.372	0.041 *	Low (a)	Mid (a)	High (a)

a) occurrence
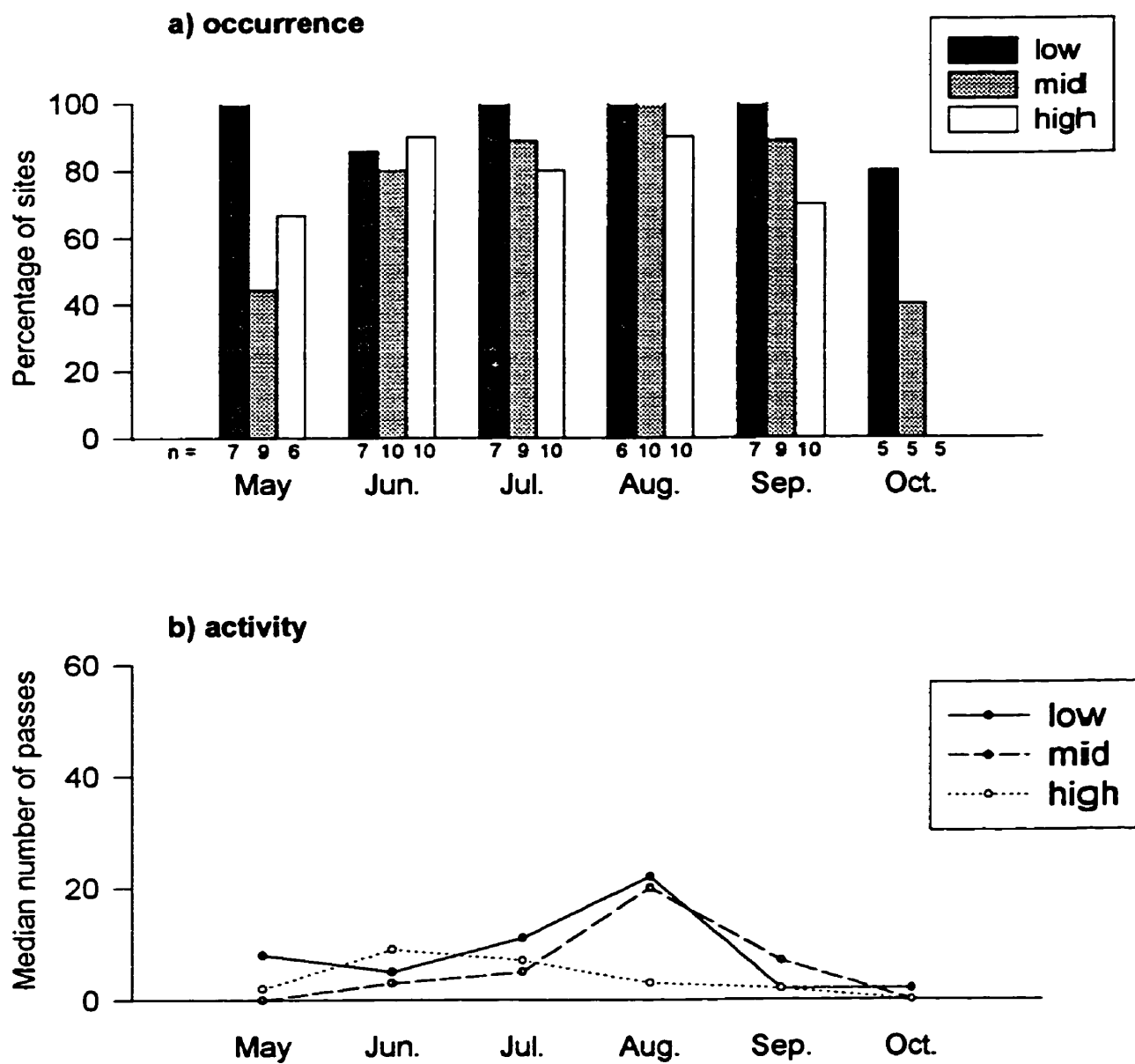
b) activity

Figure 7. *Myotis* bats at edges, 1998. Percentage of sites sampled that had at least 1 detection of a *Myotis* bat (a), and activity represented as median number of passes (b). 'n' is the number of sites sampled.

Seasonal activity

Myotis bats were present at ponds and edges at all elevations when sampling began in May. At ponds, presence and activity peaked in July or August at all elevations (Figs. 5 and 6). By September, bats were either much less active or fewer in number. Presence of Myotis bats remained high but median activity and the range in amount of activity decreased, with the exception of 2 high elevation sites where I think swarming was occurring. By October, most bats had left the study area or had begun hibernating, although there was minor activity at several high elevation ponds, at 1 low elevation pond, and at several low and mid elevation edges.

Comparison of activity at ponds and edges

Myotis bats were fairly ubiquitous throughout the study area during the summer. There was no difference in the percentages of edge and pond sites with bats present (CMH chi-square blocked by elevation and month; $Q=0.031$, $P=0.861$). As noted above, bats were present at high elevation ponds but not edges in October.

There was greater activity at ponds than at edges at low elevation sites. The difference was only significant for July, when ponds had greater activity (Mann-Whitney $U=11.0$, $P=0.031$). At mid and high elevation sites, ponds and edges had similar amounts of bat activity, but there was a significant difference at mid elevation sites during May, when ponds had greater activity (Mann-Whitney $U=15.5$, $P=0.024$).

Big bats

<u>Activity across elevations</u>

Presence and activity of big bats were strongly influenced by elevation. At ponds

and edges, big bats had greater occurrence and greater activity at low than at high

elevation sites (Figs. 8-10, Tables 9 and 10). Big bats were present at several mid

elevation ponds in 1997, and at many mid and several high elevation ponds in 1998.

There was a more consistent presence of big bats, but still low activity, at mid and high

elevation edges.

<u>Seasonal activity</u>

In 1997, use of mid elevation ponds (the upper limit of occurrence of big bats)

was restricted to July, August and September. In 1998, big bats were detected at high

ponds during June and July as well. Use of high elevation edges was longer, with big bats

detected from May to September.

<u>Comparison of activity at ponds and edges</u>

Unlike for *Myotis* bats, there was little difference in the activity of big bats at

ponds versus edges, at any elevation. The two statistically significant differences were:

greater activity at ponds than at edges at mid elevations in May (Mann-Whitney

U=17.50, P=0.040) and greater activity at edges instead of ponds at high elevations in

June (Mann-Whitney U=25.00, P=0.036). Presence of big bats was not statistically

different between pond and edge sites, when all sites were considered (CMH χ^2,

a) occurrence
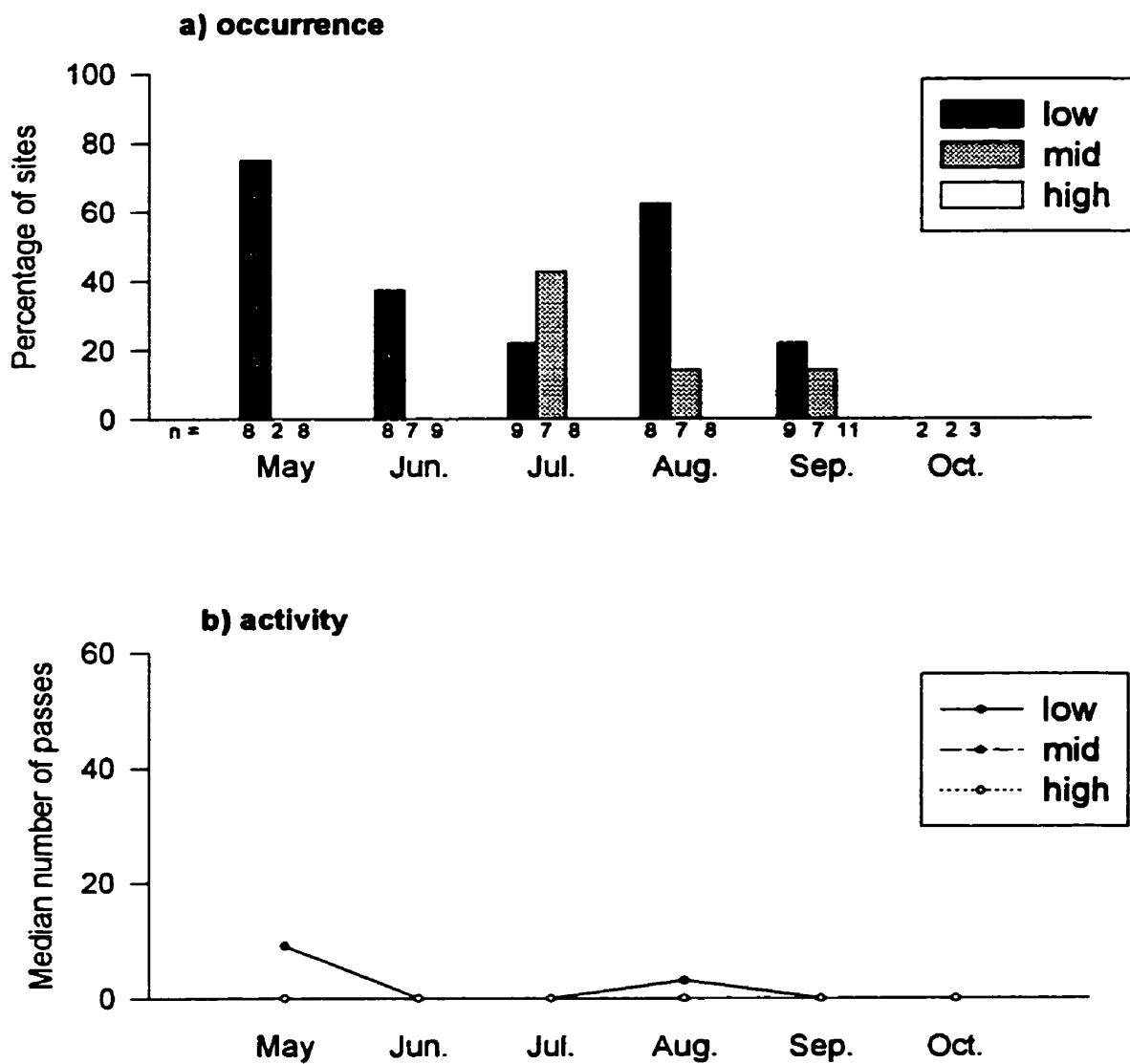
b) activity

Figure 8. Big bats at ponds, 1997. Percentage of sites sampled that had at least 1 detection of a big bat (a), and activity represented as median number of passes (b). 'n' is the number of sites sampled. When median number of passes is zero at 2 or more elevations, only the highest elevation symbol is shown but all elevation classes were sampled.

a) occurrence
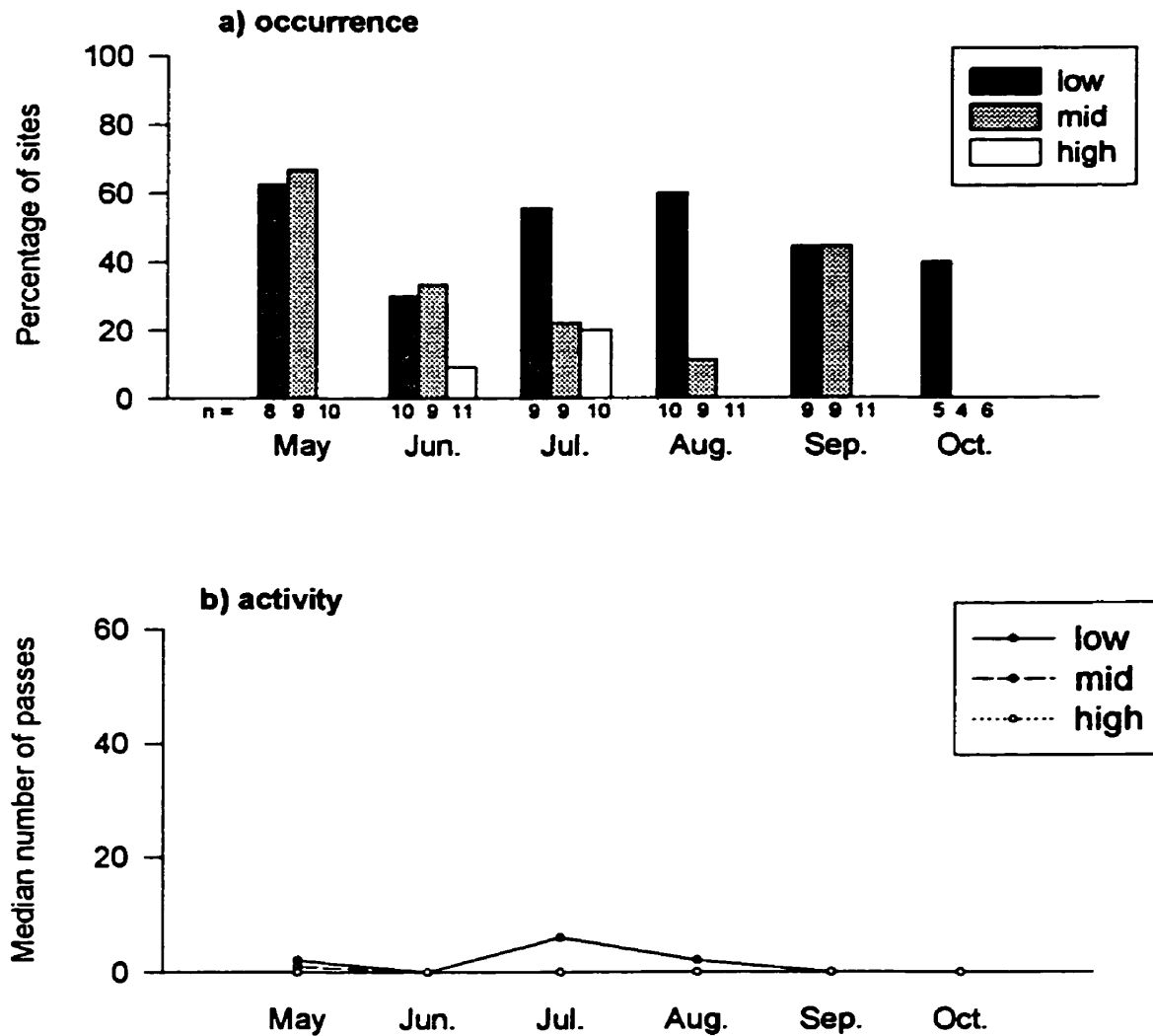
b) activity

Figure 9. Big bats at ponds, 1998. Percentage of sites sampled that had at least 1 detection of a big bat (a), and activity represented as median number of passes (b). 'n' is the number of sites sampled. When median number of passes is zero at 2 or more elevations, only the highest elevation symbol is shown but all elevation classes were sampled.

a) occurrence
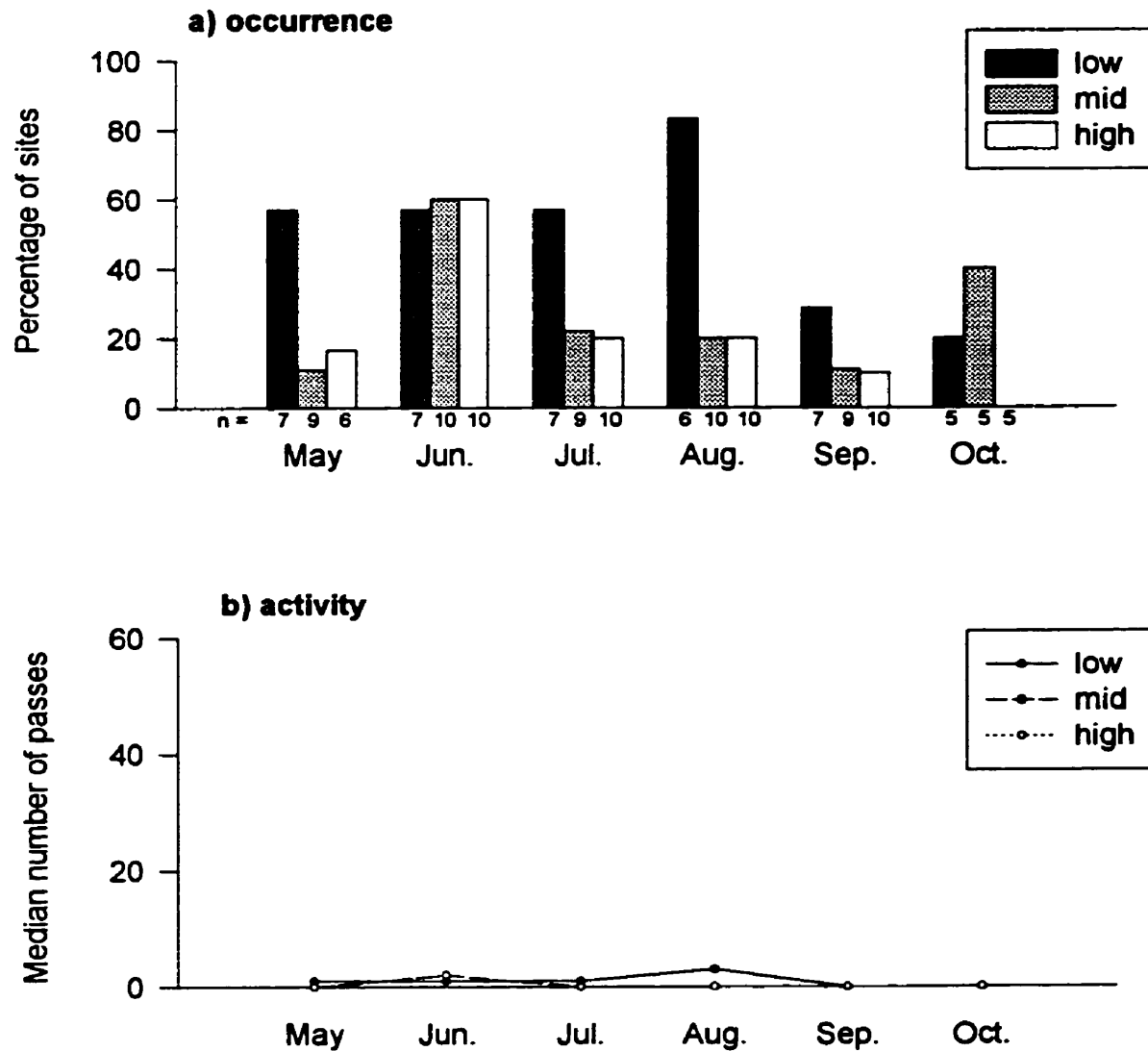
b) activity
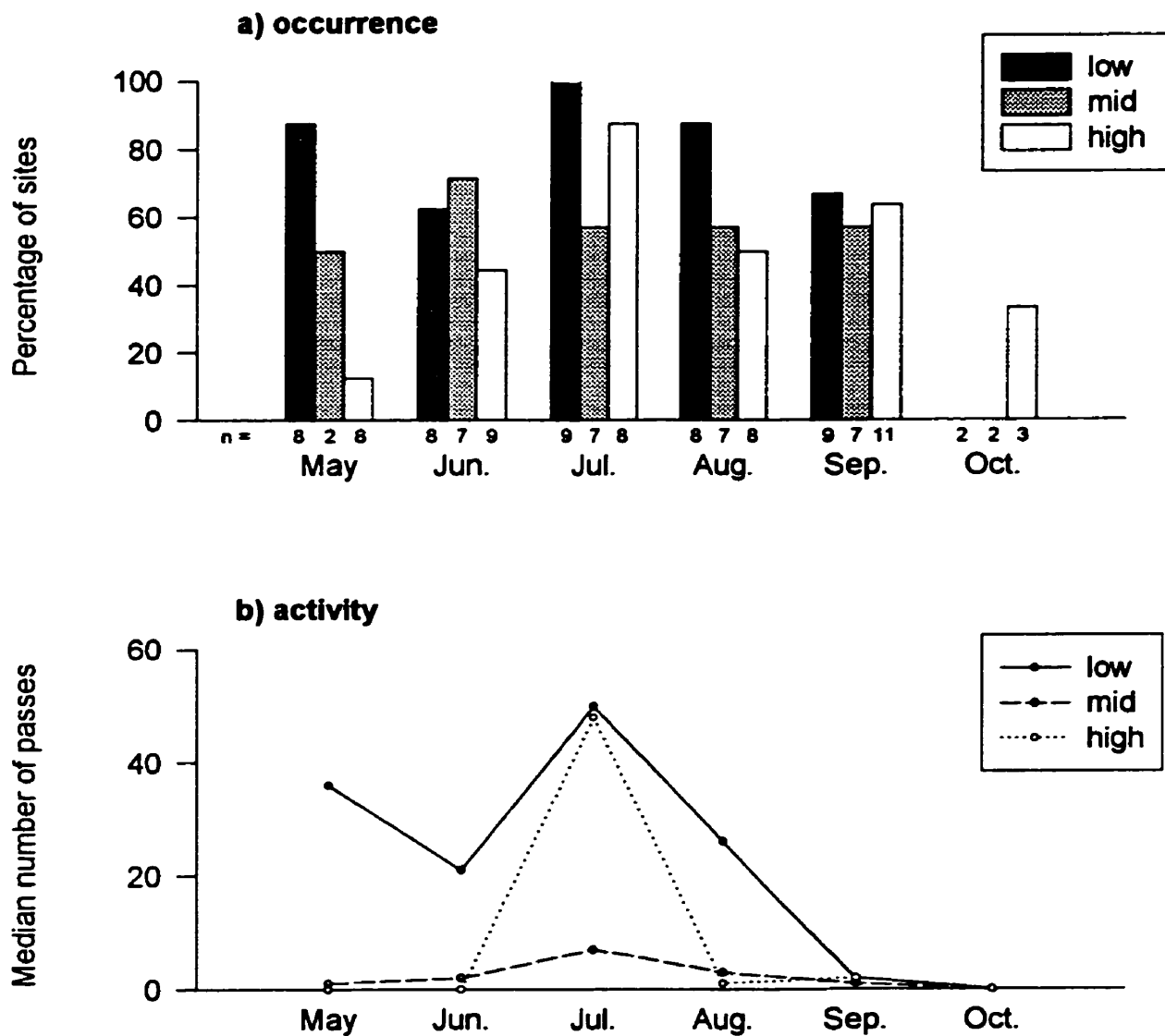

Figure 10. Big bats at edges, 1998. Percentage of sites sampled that had at least 1 detection of a big bat (a), and activity represented as medi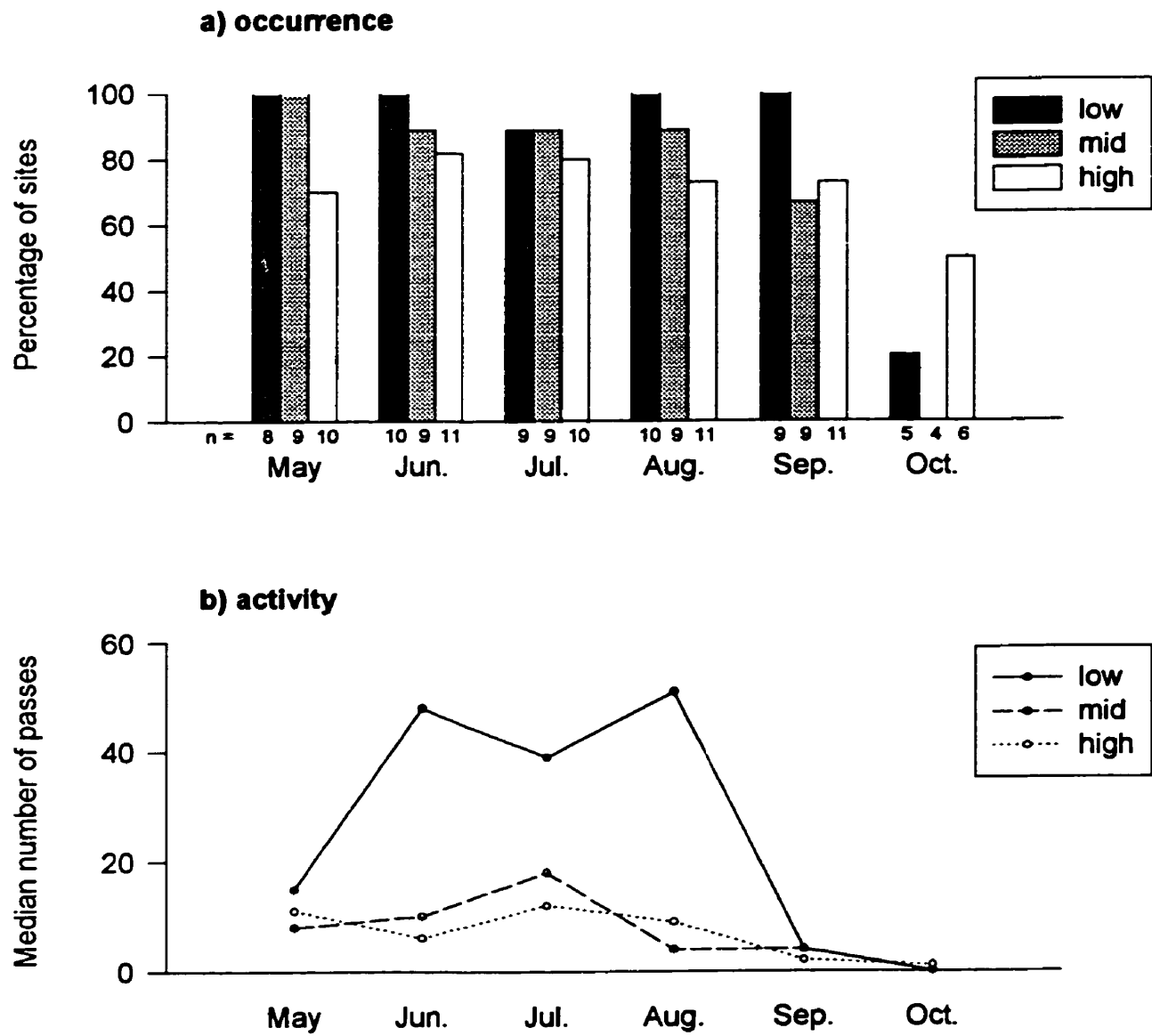an number of passes (b). 'n' is the number of sites sampled. When median number of passes is zero at 2 or more elevations, only the highest elevation symbol is shown but all elevation classes were sampled.

Table 9. Results of Cochran-Mantel-Haenszel chi-square tests for general association between elevation and the presence of big bats, blocked by month, and results of Fisher's exact tests for differences between the 3 elevations, within each month.

Habitat	Year	Month	CMH chi-square test (df=2)		Fisher's exact test
			χ^2	P	P
Ponds	1997		23.83	0.001 •	
		May			0.003 *
		Jun.			0.045 •
		Jul.			0.170
		Aug.			0.012 *
		Sep.			0.327
		Oct.			-
Ponds	1998		27.23	0.001 •	
		May			0.002 *
		Jun.			0.370
		Jul.			0.282
		Aug.			0.002 •
		Sep.			0.018 •
		Oct.			0.152
Edges	1998		10.24	0.006 •	
		May			0.159
		Jun.			1.000
		Jul.			0.275
		Aug.			0.024 •
		Sep.			0.642
		Oct.			0.725

Table 10. Results of one-way Kruskal-Wallis tests on the activity levels of big bats across elevations, by month. Elevations with different letters were significantly different (Dunn's Q, P<0.050).

Habitat	Year	Month	Kruskal-Wallis (df=2) χ^2	P	Elevation in order of mean rank		
Ponds	1997	May	10.10	0.006 *	Low (a)	Mid (a,b)	High (b)
		Jun.	6.537	0.038 *	Low (a)	Mid (a)	High (a)
		Jul.	3.932	0.140			
		Aug.	9.280	0.010 *	Low (a)	Mid (a, b)	High (b)
		Sep.	2.476	0.290			
		Oct.	0.000	1.000			
Ponds	1998	May	9.648	0.008 ●	Low (a)	Mid (a)	High (a)
		Jun.	2.305	0.316			
		Jul.	4.343	0.114			
		Aug.	11.69	0.003 ●	Low (a)	Mid (a)	High (a)
		Sep.	6.351	0.042 ●	Mid (a)	Low (a)	High (a)
		Oct.	4.308	0.116			
Edges	1998	May	3.763	0.152			
		Jun.	0.021	0.990			
		Jul.	1.967	0.374			
		Aug.	8.685	0.013 *	Low (a)	Mid (a)	High (a)
		Sep.	1.248	0.536			
		Oct.	2.299	0.317			

Q=1.262, P= 0.261). However, big bats were detected at high elevation edges from May to September more consistently than at high elevation ponds.

Insects

At ponds, there was a significant effect of elevation on insect abundance (Fig. 11a; 1997, F=20.996, P<0.001; Fig. 11b; 1998, F=9.582, P<0.001). Insect abundance decreased with increasing elevation in spring and early summer. Insect abundance peaked at low elevations in July, then declined. By August, numbers of insects at ponds were similar among all elevations. At edges, there was no significant overall effect of elevation (Fig. 11c; F=1.665, P=0.193), although number of insects peaked at low elevations in July, as it did at ponds.

When I examined the counts of Diptera alone, they exhibited the same pattern of abundance as all insects combined. This is not surprising because they comprised 50.4% of all insects caught. The number of Lepidoptera, however, showed no significant effect of elevation, at ponds nor edges.

Within each elevation class, there was no significant effect of habitat (ponds or edges) (blocked by month) (low, $F_{habitat} = 0.115$, P = 0.735; mid, $F_{habitat} = 2.460$, P = 0.121; high, $F_{habitat} = 1.345$, P = 0.249). Hence, although numbers of insects decreased with increasing elevation, numbers were the same between ponds and edges.

Foraging activity across elevations

I recorded a total of 1,104 buzzes and 10,892 passes for *Myotis* bats (foraging rate 9.2%), and 70 buzzes and 1,607 passes for big bats (foraging rate 4.2%). Foraging
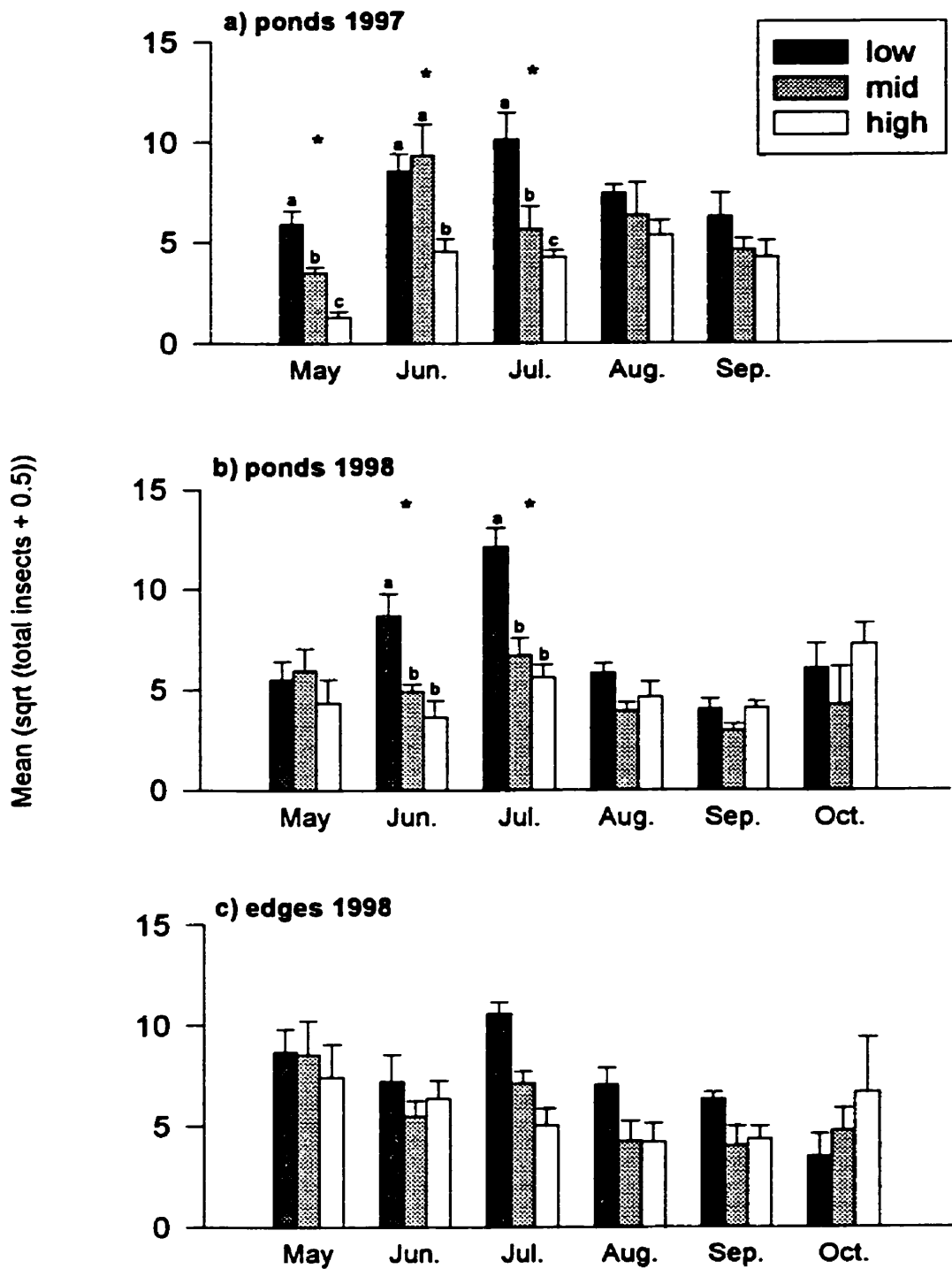
Figure 11. Insect abundance across elevations, by month, at ponds 1997 (a), ponds 1998 (b), and edges 1998 (c). Asterisks indicate months with significant differences in insect numbers. Within these months, bars with the same letter are not significantly different.

activity of *Myotis* bats occurred at all sites where I detected bats, with the exception of May 1997 (foraging was detected only at low elevation sites) and October of all years, when I did not record any foraging activity. The foraging rate was significantly greater at ponds (7.1 %, 406/5701) than at edges (2.7 %, 47/1739) in 1998 (χ^2=45.504, P<0.001).

Foraging buzzes of big bats were detected only from May to August, and 63 of the 70 buzzes were at low elevation ponds (foraging rate 6.4%, 63/977). Two were at mid elevation ponds (0.6%, 2/321), and the remaining 5 at high elevation edges (5.5%, 5/91).

Elevation and nocturnal activity patterns

The nocturnal activity of *Myotis* bats followed a similar pattern at all elevations (Fig. 12), with at least 50 % of all activity occurring in the first 3 hours after sunset. Nevertheless, the timing of activity was significantly different between elevations (Kolmogorov-Smirnov goodness of fit tests, P<0.001). The initial peak of activity was smaller at mid and high elevation ponds, where a greater proportion of calls were heard later in the night (Fig. 13a). At mid and high elevation edges, the initial activity period was extended even later. This distribution of activity is not apparent in the cumulative distribution for edges (Fig. 13b) due to the pre-dawn peak that occurred at low elevation edges. The low numbers of calls of big bats recorded at mid and high elevations prevented analysis by elevation. As seen for *Myotis*, big bats had an initial peak in activity at ponds and edges just after sunset (Fig. 14).
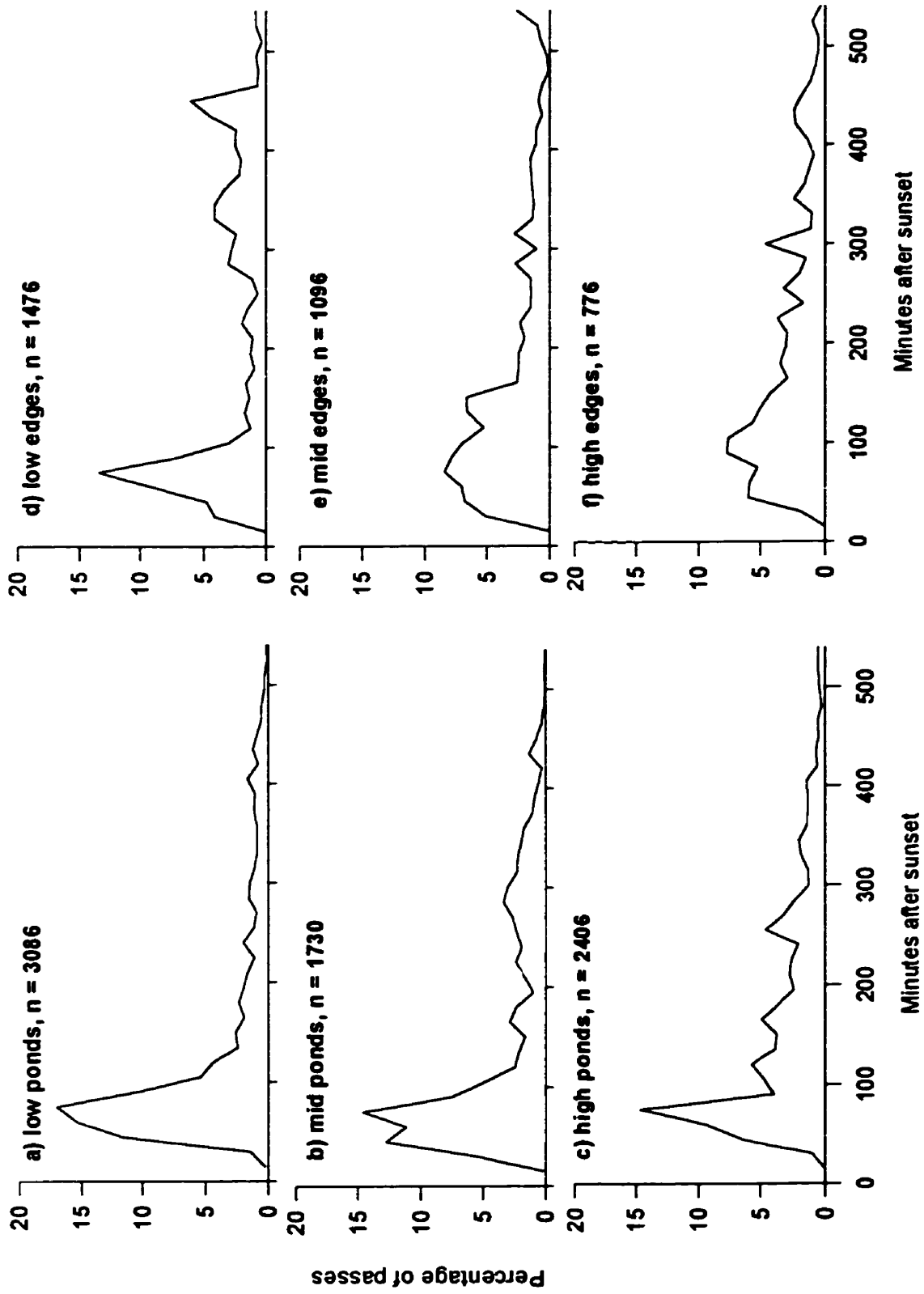
Figure 12. Nocturnal activity patterns of *Myotis* bats at ponds (a-c) and edges (d-f) at low, mid, and high elevations.

a) ponds 1997 and 1998

low   n=3086
mid   n=1730
high n=2406

Minutes after sunset

b) edges 1998

low   n=1476
mid   n=1096
high n=776

Minutes after sunset

Cumulative percentage of passes
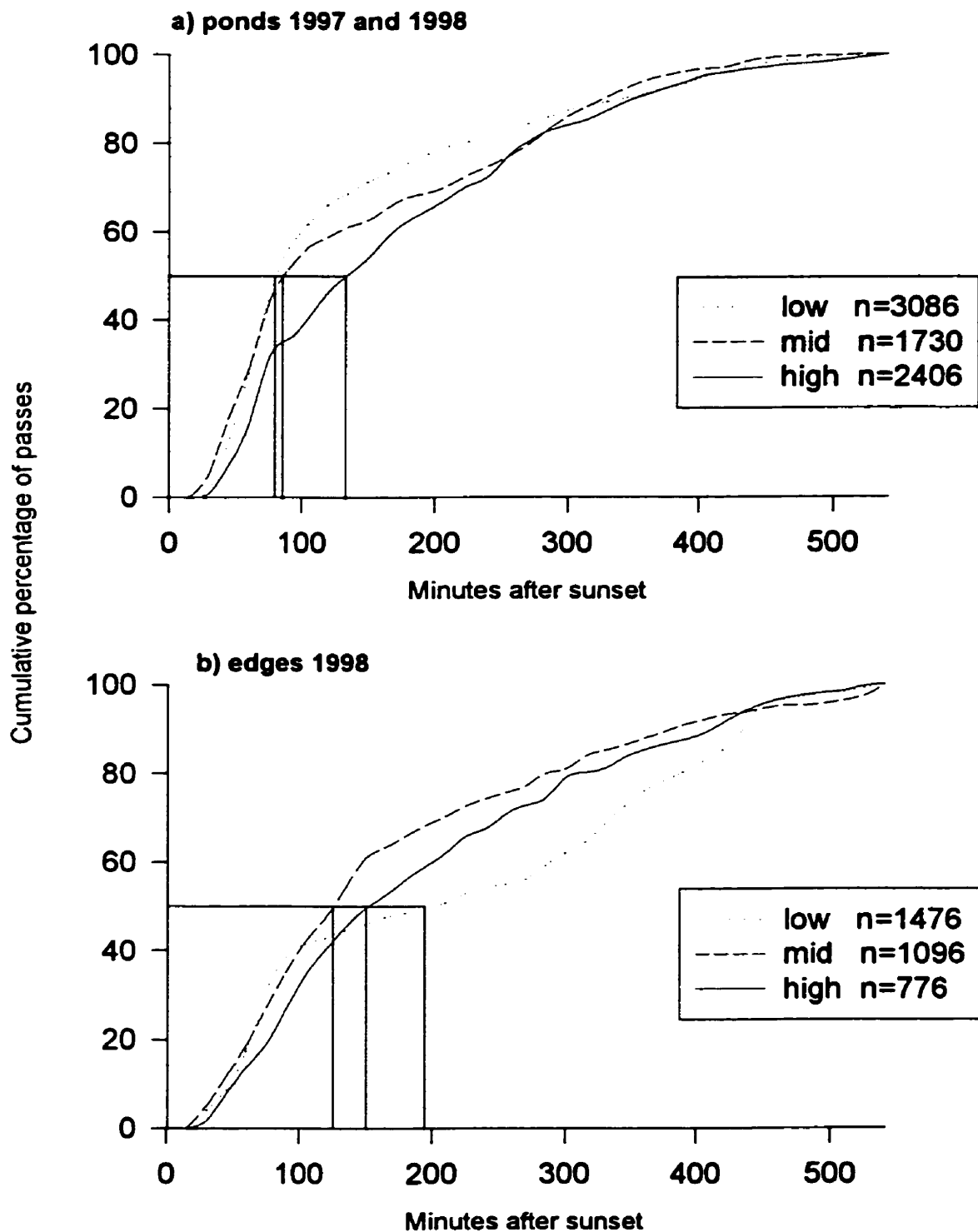
Figure 13. The cumulative distribution of activity of *Myotis* bats at a) ponds and b) edges, at low, mid, and high elevations. Straight lines indicate the time at which 50% of nightly calls had been detected, for each elevation.
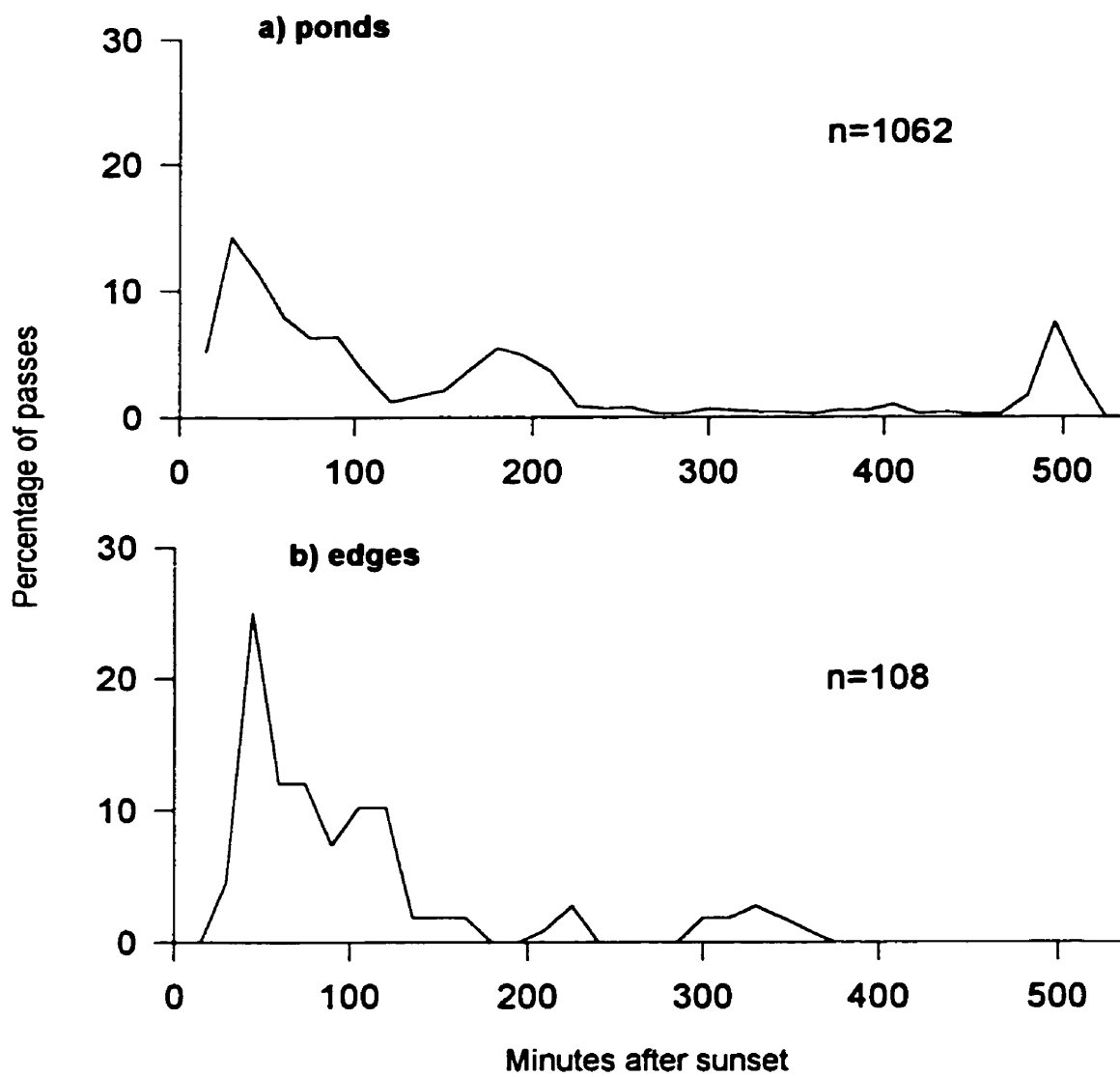
Figure 14. Nocturnal activity patterns of big bats at ponds (a) and edges (b).

Discussion

Amount of activity

Bats were detected at all elevations, from low elevation (300 m a.s.l.) to montane

parkland forests (1200 m a.s.l.). However, presence and activity of bats decreased with

increasing elevation. Big bats were influenced more by elevation than were the *Myotis*

group. I expect that differentiating between *Myotis* species would reveal other species-

specific responses. Barclay (1991) proposed that bats with more flexible foraging

strategies, such as the ability to glean prey, should be able to exploit harsher

environments. Foraging strategy of bats is influenced by body shape and characteristics

of echolocation calls (Fenton 1990). Perhaps big bats, which fly faster than *Myotis*

species and have a constant frequency component to their call, rather than a frequency

modulated call, forage less effectively in montane environments than in lower elevation

forests. This could occur, for example, because of differences in species, size, or spatial

distribution of insects between elevations. The larger size and corresponding greater

energy requirements of big bats may also constrain their use of high elevations.

The spatial distribution of *Myotis* activity is different between low and higher

elevations. Low elevation sites showed a more 'typical' distribution of activity between

ponds and edges. Activity tended to be greater at ponds than at forest edges, similar to

that found by Grindal (1998). This may reflect greater numbers of bats at ponds, or a

difference in flight patterns used at ponds and edges. *M. lucifugus* foraging at ponds use

circling flight (Fenton and Bell 1979), and many passes can be recorded per bat. Edges

are used as foraging habitat by some species (e. g., *M. evotis* Barclay 1991, *M. volans*

Saunders and Barclay 1992), but are also used extensively as commuting routes (Limpens

and Kapteyn 1991). Even when foraging, bats probably use predominantly linear flight at edges, resulting in 1 pass detected per bat.

At mid and high elevation sites, median activity of *Myotis* bats recorded at edges was similar to that at ponds. This could be evidence of a different community of bats at mid and high elevations, with fewer pond-foraging species. However, this is unlikely, because I caught many *M. lucifugus* at high elevation sites, and they forage primarily near water. Instead, I propose that bats are exhibiting different foraging behaviour because, unlike at lower sites, it is less profitable at high elevations to forage intensely at 1 pond than to travel between and forage at many ponds. This could occur because of reduced insect numbers, or the different spatial arrangement of water on mountains compared to valley bottoms. In montane forests, water is widely distributed and generally in numerous small ponds. Perhaps this spatial configuration allows bats to move quickly between many nearby ponds. Foraging rates were up to 4 times greater at ponds than at edges, hence most foraging occurred at ponds. However, there is a potential for bias in under-estimating the importance of edges for foraging, because bats do not make foraging buzzes when gleaning (Fenton and Bell 1979).

Seasonal changes in activity

The timing of the appearance of bats in montane forests during spring was correlated with environmental conditions, but once the snow had begun to melt, *Myotis* bats were detected at most high elevation sites throughout the summer. Big bats exhibited a more temporally constrained period of use of montane forests.

By September, the elevational gradient in activity had disappeared. Median activity of *Myotis* was similar at low, mid, and high elevation ponds. Activity at low sites had declined from amounts in August, while activity remained the same at mid and high sites. This may reflect bats' responding to similar insect abundance at different elevations, but bats are also beginning to migrate and hibernate at this time. Birds are thought to use mountain tops and montane forests as stop-overs during migration, to avoid losing elevation or following valley routes (Kathy Martin, pers. comm., University of B.C.). Although I do not know where bats from the study area hibernate, *Myotis* elsewhere travel 40 to 200 km to hibernacula, and *Lasionycteris noctivagans* may migrate south to the United States (Nagorsen and Brigham 1993). Bats may also be swarming and gathering before hibernating nearby. Although no hibernacula are known around Mt. Cain, high elevation (900 m) karst cave systems are used as hibernacula on the west coast of northern Vancouver Island (Davis et al. 1998). There is no karst at Mt. Cain, but there are steep cliffs with many deep cracks and crevices, which may be deep enough to provide suitable conditions for hibernating bats.

Correlation with prey abundance

Some differences in bat activity between elevations are correlated with insect abundance. In particular, insect numbers decreased sharply with increasing elevation in May 1997, when a heavy snowpack was still present at high elevation sites. Presence and activity of bats also decreased sharply with increasing elevation. Although prey abundance is not correlated with bat activity on a smaller scale (i. e., at forest interior,

edges and clearcuts, Grindal 1996), on the larger scale of watersheds and on a time scale of months, bat distribution is correlated with prey abundance.

The numbers of insects, as I measured them, do not explain all the variation in bat activity. Presence and activity of big bats did not coincide with patterns of total insect number, or number of Diptera, one of their primary prey. Furthermore, in August of both years, activity and presence of all bats remained much greater at low elevations, in spite of the insect counts being similar at all elevations. Other factors besides insect numbers must determine the distribution of bats and maintain a gradient of bat activity. One possibility is that cool temperatures keep bat activity reduced at higher sites. Another factor may be insect biomass. I counted insects but did not measure biomass. Insect biomass could have differed among elevations.

Montane forests as extreme environments

The annual variation of bat activity suggests that montane forests are on the upper limit of use for some bat species. *Myotis* bats showed significantly different timing in their use of higher forests, and big bats had very different vertical distributions between 1997 and 1998. Both of these changes corresponded to the different weather between years. These changes in activity could be a consequence of daily or nightly temperatures, the length of the short summer season, or the effect of climatic factors on insects, although I did not detect changes in insect numbers.

Nocturnal activity patterns

Nocturnal activity patterns have been used to make inferences about behaviour of bats. For example, activity limited to early evening has been assumed to reflect bats leaving roosts and commuting to foraging areas (Thomas 1988). I found no such restriction on the timing of activity of big or *Myotis* bats, at ponds or at edges. Activity patterns were similar to those described for foraging bats in other areas, with an initial peak of activity immediately after dusk. The length of the initial peak, of over 2 hours, is similar to that at riparian areas in the western Washington Cascades (Erikson and West 1996) and southeastern Alaska (Parker et al. 1996). A second, predawn, activity peak was found for *Myotis* bats at low elevation edges and for big bats at ponds. Predawn peaks at other sites may have been obscured by seasonal variation in night length.

When I compared low and high elevations, nocturnal activity patterns were opposite to what I had predicted. If, at high elevations, nights were cooler and temperatures dropped more quickly after sunset, I predicted that most activity would occur earlier in the evening, closer to sunset. Instead, activity at high elevation was more spread out during the night at ponds, and even more so at edges, with a reduced initial peak. One possible explanation is that foraging at high elevations was less profitable at dusk relative to at low elevations, perhaps because of fewer insects, and this forced bats to extend their foraging period. This hypothesis is supported by the similar amount of activity at ponds and edges, suggesting continual movement and insufficient foraging returns at a single pond. Another possibility is that the different timing across elevations

reflects a different species composition of bats, because species potentially emerge and forage at different times (Nagorsen and Brigham 1993).

Limitations of my study

Unfortunately, given the differences in activity that I observed among elevations, I probably excluded a greater proportion of the nightly activity at high sites than at lower sites by limiting sampling to the first 2 hours of the night. Another problem with my sampling design was the low power of the statistical tests. My target sample size of 10 sites of each type was too low, given the huge variability in my data. Large ranges in amounts and patterns of activity have been described for 2 sites in Oregon (Hayes 1997). It appears that large sample sizes are required even when the sites to be compared are paired. I did not calculate the power of the tests that I used because there are no straightforward methods to calculate power for non-parametric statistics (Murphy and Myors 1998).

Estimates of insect numbers can only be used as a rough index of insect densities. I sampled only at ground level, which is the height where some bats forage (e. g., *M. lucifugus*), but other bats forage high along edges or at canopy height (e. g., *M. volans, L. noctivagans*) (Fenton and Bell 1979, Saunders and Barclay 1992, Nagorsen and Brigham 1993). The traps that I used sampled only flying insects, and not potential prey of gleaning bats. Finally, there is the unavoidable problem that my estimates of insect abundance were not equivalent to the number of insects actually available to foraging bats, and this suite of available insects varies with species of bat.

Data on the nightly timing of activity are pooled data from nights of varying

length, from 7.5 hours between sunset and sunrise in June to 15 hours in early October.

This undoubtedly obscures morning activity peaks, because sunrise occurs at a different

time each day. However, these peaks, if present, represent only a small proportion of

activity, as shown by the cumulative distribution of calls.

Chapter 3. Use and selection of roosts by bats

Introduction

Roost selection has immediate consequences for bats. Roosts can influence the energy balance of roosting bats by providing favourable microclimates and shelter from the elements. Use of a particular roost also influences the energetic costs of foraging, because of the location of the roost relative to foraging areas. During the day, roosts must provide bats with protection from semi-arboreal predators such as marten (*Martes americana*). As bats emerge in the evening, they risk predation by northern goshawks (*Accipiter gentilis*) and other raptors, hence the ease and speed of exiting a roost may be important in avoiding capture.

Roost selection depends also on the availability of structures in a landscape - roosts must be present and accessible to a flying bat (Kunz 1982b). From a management perspective, we need to describe roosts and express roost selection using identifiable and measurable attributes, such as tree species, size, and decay class, and density of surrounding vegetation. The number of roosts and the areas required by bats also need to be determined for effective habitat retention.

Numerous studies have shown that particular roost and site characteristics are important to tree-roosting bats. Several species of bats (e. g., *Eptesicus fuscus* and *Lasionycteris noctivagans*, Betts 1996, Vonhof 1996; *Myotis californicus*, Brigham et al. 1997; *Myotis volans*, Ormsbee and McComb 1998) generally select large trees, in moderate stages of decay, which are located in relatively open patches of forest. On the other hand, *Myotis evotis* has been found roosting in accessible stumps in clearcuts

(Vonhof and Barclay 1997). Preference for tree species has been identified in some habitats, such as for Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) in the Oregon Cascades (Ormsbee and McComb 1998) and western white pine (*Pinus monticola*) in south-eastern British Columbia (Vonhof and Barclay 1996). Bats select cavities (Kalcounis and Brigham 1998), bark (Vonhof and Barclay 1997), or a combination of structures (Vonhof and Barclay 1996, Crampton and Barclay 1998) depending on the study area and habitat type. Complementary studies in other habitats are the only practical way to determine if these requirements are species- or habitat-specific (Brigham et al. 1997).

Roost selection in coastal temperate rainforests has been investigated by Ormsbee and McComb (1998) in the western Cascades, Washington. In coastal British Columbia, 2 low elevation studies have documented the use of trees and rock crevices (Grindal 1998, van den Driessche et al. 1999). Other research in coastal B.C. focuses on use of caves (Davis et al. 1998) and unique hotspring environments (Burles 1999).

Coastal forests are home to a diverse fauna of forest-dwelling bats, but are also subject to logging. On Vancouver Island, few old growth stands remain in low elevation forests, and logging is extending into high elevation forests as the wood supply diminishes at low elevations. To provide guidelines for the retention and provision of roosts and roosting habitat for bats, my study focused on:

a) the characteristics of roosts used by bats in high elevation coastal forests; and

b) roosting ecology – the number of roosts per bat, the frequency of roost switching, and the location of roosts relative to each other.

Methods

I mistnetted bats over ponds or along forest edges and radio-tagged 15 bats, each weighing at least 6.0 grams (LB2 transmitters, 0.45 g, Holohil Systems, Ltd., Woodlawn, Ontario). All tagged bats were captured at sites 650 m or more above sea level. Four species were tagged: *Lasionycteris noctivagans* (3 males), *Myotis volans* (2 males, 2 females), *M. lucifugus* (5 males), and *M. evotis/keenii* (2 males, 1 female). I located the tagged bats daily, to identify a suspected roost (usually a tree) for each bat. Suspected roosts were watched at dusk to confirm that a bat left the roost and that the bat still carried a radio-tag, and to identify the specific roost structure used. Roosts were classified as 'visually confirmed' if I saw a bat exit from the roost, or 'suspected' if I was unable to watch the roost or could not positively identify where a bat emerged from.

Roosts were assessed according to British Columbia Resource Inventory Committee Standards for bats (Garcia and Barclay 1997) and Ministry of Forests' Coastal Montane Biodiversity Project protocol for wildlife tree and vegetation surveys (Scott McNay, pers. comm., B.C. Ministry of Forests). For each roost, I described or measured type of structure, aspect of entrance, height above ground, and relative height (roost versus tree height and roost versus canopy height).

I described the roost site by establishing a 10 m by 10 m square plot centered on the roost, and recording the elevation, slope, aspect, percent cover by species of trees (>10 m), tall shrubs (2-10 m), low shrubs (<2 m), and herbs. For all trees (with a diameter at breast height (dbh) >7.5 cm) within this plot, including the roost tree, I identified tree species, assigned a decay and bark class of 1-7 (BC Wildlife Tree classes, Tables 11 and 12), measured diameter at breast height (dbh), and measured tree height using a

Table 11. Decay classes used in roost classification.

Decay class	Description
1	Live, healthy
2	Live, unhealthy and dying
3	Dead - needles or twigs may be present
4	Dead - no needles/ twigs; 50% of branches lost; loose bark; top usually broken
5	Dead - most branches and bark absent; some decay
6	Dead - no branches or bark; advanced decay
7	Dead - extensive decay

After: B.C. Wildlife Tree classification, B.C. Ministry of Environment

Table 12. Bark classes used in roost classification.

Bark class	Description
1	All bark present
2	Bark lost on damaged areas only (<5% lost)
3	Most bark present, bare patches, some may be loose (5-25% lost)
4	Bare sections, firm and loose bark remains (26-50% lost)
5	Most bark gone, firm and loose bark remains (51-75% lost)
6	Trace of bark remains (76-99% lost)
7	No bark (100% lost)

After: B.C. Wildlife Tree classification, B.C. Ministry of Environment

clinometer and meter tape. For roost trees, I measured distance to the nearest tree with dbh >7.5 cm, distance to the nearest tree as tall or taller than the roost tree, and distance to the nearest snag >2 m high.

Each roost plot was paired with a random plot situated in the same forest stand. I walked 100 m in a random direction from each roost tree, and designated the nearest tree with dbh >7.5 cm as the 'random' tree. Random trees and 10 m by 10 m plots around them were described as for roost plots. I plotted capture sites, roosts, and random sites on 1:20,000 maps provided by Canadian Forest Products Ltd.

Results

Confirmed and suspected roosts

Of the 47 roosts located in trees, 32 were visually confirmed by watching each tree at dusk to determine if and where a bat exited from the tree. I compared confirmed roost trees and suspected roost trees to determine if the 2 groups could be pooled (Table 13). Confirmed roost trees were significantly smaller in dbh than suspected roost trees. This may be as a result of practicing 'triage' for roost watching – I occasionally had to choose one of several roost sites to watch, and generally chose to watch the roost tree for which I was least confident in the identification of the tree, based on telemetry data. Visually confirmed and suspected trees did not differ in species of tree, decay class, height, or bark class, and so I pooled them for further analyses.

Table 13. Comparison of 32 roost trees that were visually confirmed and 15 suspected roost trees that were identified solely by telemetry.

Variable	Visually confirmed trees	Suspected trees	P	Test
	(mean ± SE)			
Decay class	-	-	0.178	Fisher's exact
% bark remaining	62.2 ± 5.5	55.7 ± 7.5	0.482	t-test
Species of tree	-	-	0.090	Fisher's exact
Dbh (cm)	64.2 ± 3.7	75.5 ± 4.3	0.041 *	t-test[1]
Height (m)	27.5 ± 2.5	33.9 ± 3.3	0.078	t-test[1]

[1]Data were transformed using natural logarithms to normalize distributions before analysis.

Roost characteristics

Forty-seven of 50 roosts were in trees, primarily under loose tree bark but also in cracks in the tree bole. The remaining 3 roosts were in rocks; 1 in a crevice in a cliff (used by a male *Myotis lucifugus*), and 2 in crevices in a granite quarry (used by a male *Myotis evotis/keenii*) (Table 14).

Known roost entrances (n = 21) were all south-facing (mean 171°, range 134 – 267 °, P < 0.001, Rayleigh's test for random distribution) (Zar 1999, p. 618). Among 26 visually confirmed tree roosts, 21 (81 %) were located in the top third of the tree, 4 (15 %) in the middle third, and 1 (4 %) in the lower third. The heights of 24 of the visually confirmed tree roosts ranged from 3.2 - 34.4 m above the forest floor. When expressed as a percentage of roost tree height, roosts were located from 16 to 95 % of the tree height, with a mean of 68 %. The lowest roosts belonged to 2 male *M. evotis/keenii*; 1 used a tree roost situated well below canopy height (3.2 m, 16 % of tree height), and the other used 2 roosts in a granite quarry. Of the latter, 1 roost was 5 m and the other, 1 m, above the base of the quarry.

Roosts were located primarily in or above the main canopy. Thirteen of 31 roosts (42 %) were 'above' the main canopy, 15 (48 %) 'in', and 3 (10 %) 'below'. Access by bats to roosts in or below the main canopy level was not constrained because the roosts were always located beside natural gaps. All bats roosted alone, except for one lactating female who used a bark roost on a western white pine along with 18 other bats.

Table 14. Structures used as day roosts.

Roost structure	Number	Percent
Tree bark	35	70
Tree crack	7	14
Tree unknown	5	10
Rock crevice	3	6
Total	50	100

Characteristics of roost trees

I compared 47 roost trees to other trees in the roost plot, and to trees in the paired random plot. As well, I compared roost plots (including and excluding the roost tree) to random plots. I examined differences in decay class, bark class, tree species, dbh, and height. Roost trees were also compared to random trees for distance to the nearest tree (dbh >7.5 cm), distance to the nearest tall tree (as tall or taller than the roost tree), and distance to the nearest snag (height >2 m) (Table 15).

Although roosts were located in trees exhibiting decay classes 2 to 5, bats selected decay class 4 and avoided decay class 2 (Fig. 15). Other decay classes were used in proportion to availability. Bark class is one of the considerations when assigning a decay class to wildlife trees. However, because many roosts were located under bark, bark class may be more relevant than the general decay class when examining roost selection. Bats used bark classes 2 through 7 (Fig. 16). Bark class 2 was used less than available, while all other classes were used in proportion to availability.

All tree roosts were in western or mountain hemlock (*Tsuga heterophylla or T. mertensiana*), yellow-cedar (*Chamaecyparis nootkatensis*), western white pine (*Pinus monticola*), amabilis fir (*Abies amabilis*), or western redcedar (*Thuja plicata*) (Fig. 17). Within roost plots, bats preferred hemlock and avoided amabilis fir and trees of other than the 5 main species (i. e., avoided red alder (*Alnus rubra* Bong.), western yew (*Taxus brevifolia* Nutt.), and Douglas-fir (*Pseudotsuga menziesii*)). When roost trees were compared to trees in random plots, amabilis fir was avoided, and hemlock and all other species were used as available. The apparent selection for hemlock as a roost tree species compared to other trees in roost plots is likely a consequence of small plot size, because

Table 15. Results for comparisons of roost tree, roost plot, and random tree or random plot characteristics.

Variable	Roost trees	Roost plot	Random tree or plot	P values for Mann-Whitney U or Pearson χ^2 tests		
				Roost tree - roost plot	Roost tree - random plot	Roost plot - random plot
	(n or mean ± SE)					
Decay class						
2-5	47	109 [1]	105	0.001 *	0.001 *	0.770 [2]
2	10	58	62	< 0.001 *	< 0.001 *	
3	4	13	6	0.530	0.520	
4	20	13	12	< 0.001 *	< 0.001 *	
5	13	25	25	0.528	0.612	
Bark class						
2-7 in decay classes 2-5	47	87 [1]	68	< 0.001 *	< 0.001 *	0.302 [2]
2	7	35	31	0.003 *	0.001 *	
3	14	20	10	0.388	0.050	
4	11	12	9	0.159	0.157	
5	6	7	7	0.378	0.681	
6	6	12	5	0.868	0.332	
7	3	1	6	0.089	0.632	
Tree species						
All trees in decay classes 2-5	47	109 [1]	105	0.002 *	0.082	0.805 [2]
Hemlock (*Tsuga* spp.)	25	28	42	0.002 *	0.203	
Yellow-cedar	9	33	27	0.248	0.556	
Western white pine	8	8	8	0.067	0.081	
Amabilis fir	3	24	20	0.018 *	0.044 *	
Western redcedar	2	6	3	0.746	0.655	
Other	0	10	5	0.032 *	0.128	

Table 15. continued.

Variable		Roost trees	Roost plot	Random tree or plot	P values for Mann-Whitney U or Pearson χ^2 tests		
					Roost tree - roost plot	Roost tree – random plot	Roost plot - random plot
		(n or mean ± SE)					
Dbh (cm)	Trees >30 cm dbh, decay class 2-5	68.5 ± 2.9	53.4 ± 2.9 [1]	52.9 ± 2.5	< 0.001 *	< 0.001 *	0.984 [1]
			61.0 ± 2.2 [2]				0.022 * [2]
Height (m)	Trees > 5 m, decay class 2-5	29.9 ± 2.0	16.7 ± 0.8 [1]	17.0 ± 0.9	< 0.001 *	< 0.001 *	0.895 [1]
			20.9 ± 1.0 [2]				0.017 * [2]
Distance to nearest tree (m)		2.4 ± 0.2		2.4 ± 0.2		0.538	
Distance to nearest tall tree (m)		7.1 ± 0.9		3.6 ± 0.3		0.001 *	
Distance to nearest snag (m)		6.6 ± 0.7		5.7 ± 0.7		0.405	

[1] Roost plot without the roost tree included.
[2] Roost plot with the roost tree included.
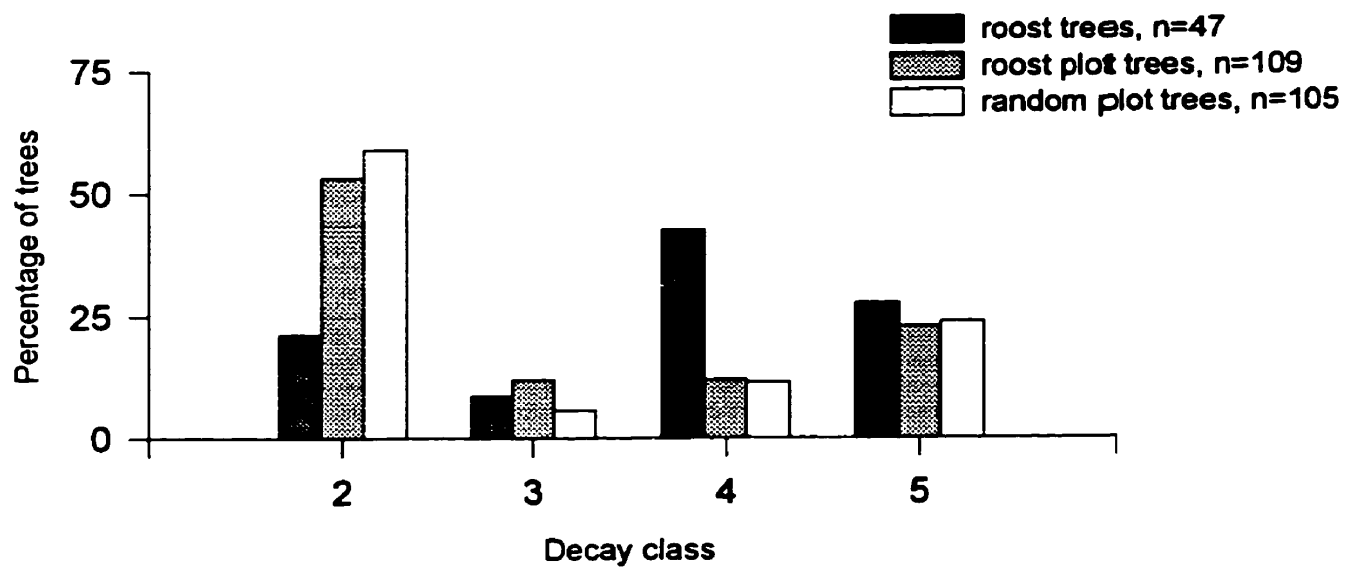
Figure 15. Decay classes of roost, roost plot, and random plot trees. Only trees in decay classes used for roosting (classes 2-5) are included.
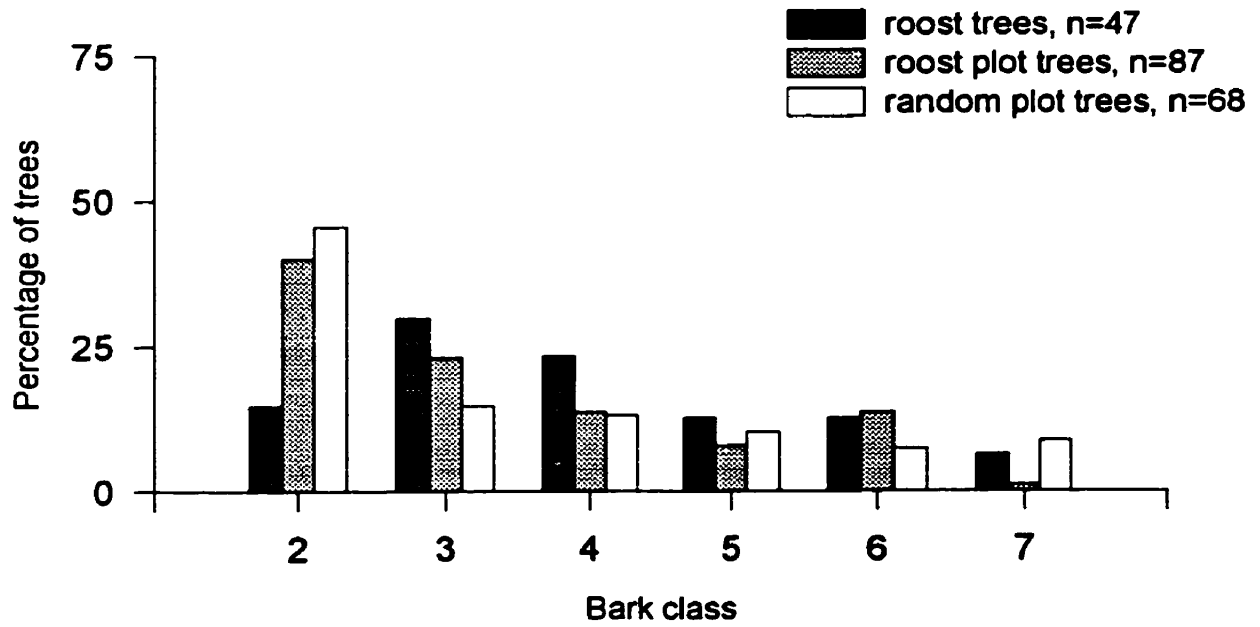
Figure 16. Bark classes of roost, roost plot, and random plot trees. Only trees in decay and bark classes used for roosting are included (decay classes 2-5, bark classes 2-7).
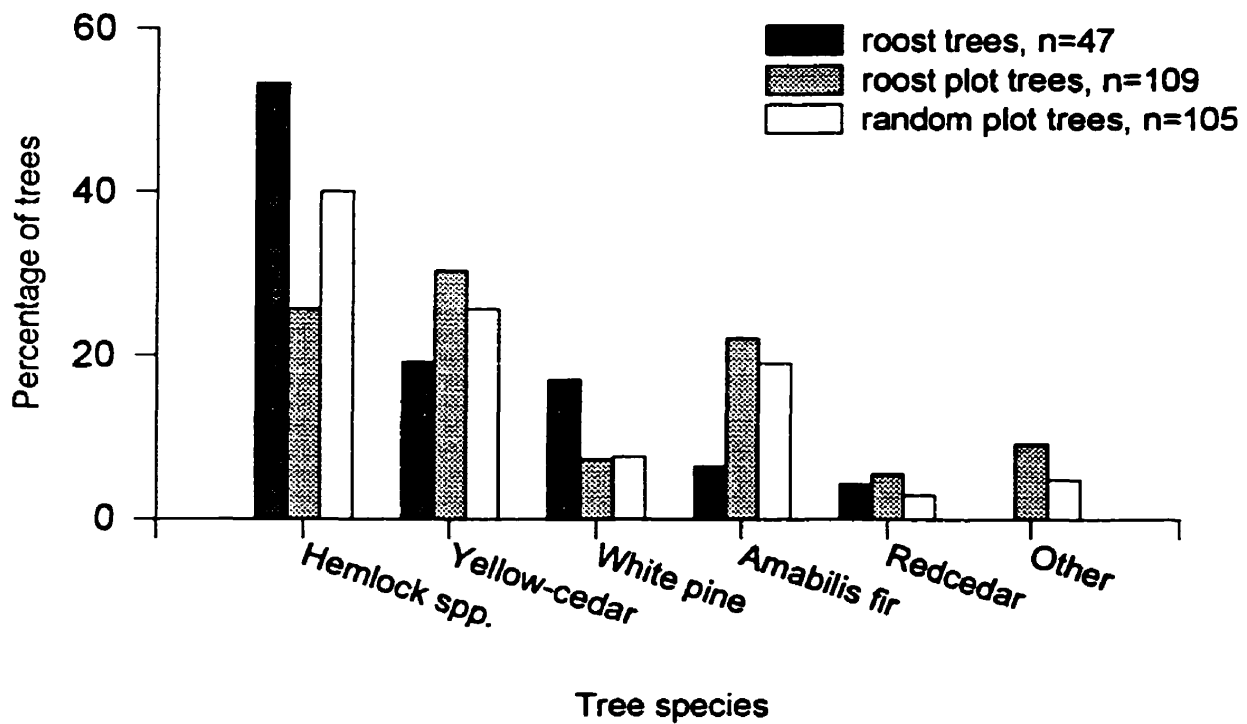
Figure 17. Tree species of roost, roost plot, and random plot trees. Only trees in decay classes 2-5 are included. Species are presented in order of decreasing occurrence as roost tree species.

roost and random plots did not differ in species composition (see site characteristics, Table 15).

Bats selected large trees for roosting. Roost trees were larger in diameter (Fig. 18) and taller (Fig. 19) than trees in both roost and random plots. Dbh and height were strongly positively correlated for roost trees (Spearman's rho=0.52, P<0.001) and all roost and random plot trees (rho=0.78, P<0.001).

The only significant measurement on the distance of the roost to the nearest tree, snag, or tall tree was the distance to the nearest tall tree. Roost trees were farther than random trees from other tall trees. This agrees with the result that roost trees were themselves tall trees, and were often the tallest trees around.

Year-of-death for snags

I cored 18 roost trees with an increment borer, and determined the year-of-death for the samples at the University of Victoria Tree Ring Lab (Table 16). Details of the methdology are dscribed by Laroque and Kellner (1999). Cores from western white pine were crossdated using the hemlock chronology. Year-of-death was variable within each tree because trees died slowly, not all at once. The 3 species sampled (yellow-cedar, hemlock, and western white pine) decayed at different rates, and within a species, the time since death for each decay class ranged widely (Fig. 20). In spite of variability, the data indicate that snags, and particularly yellow-cedar snags, are potentially very long-standing structures in montane forests. As well, some of these snags retain their bark for long periods.
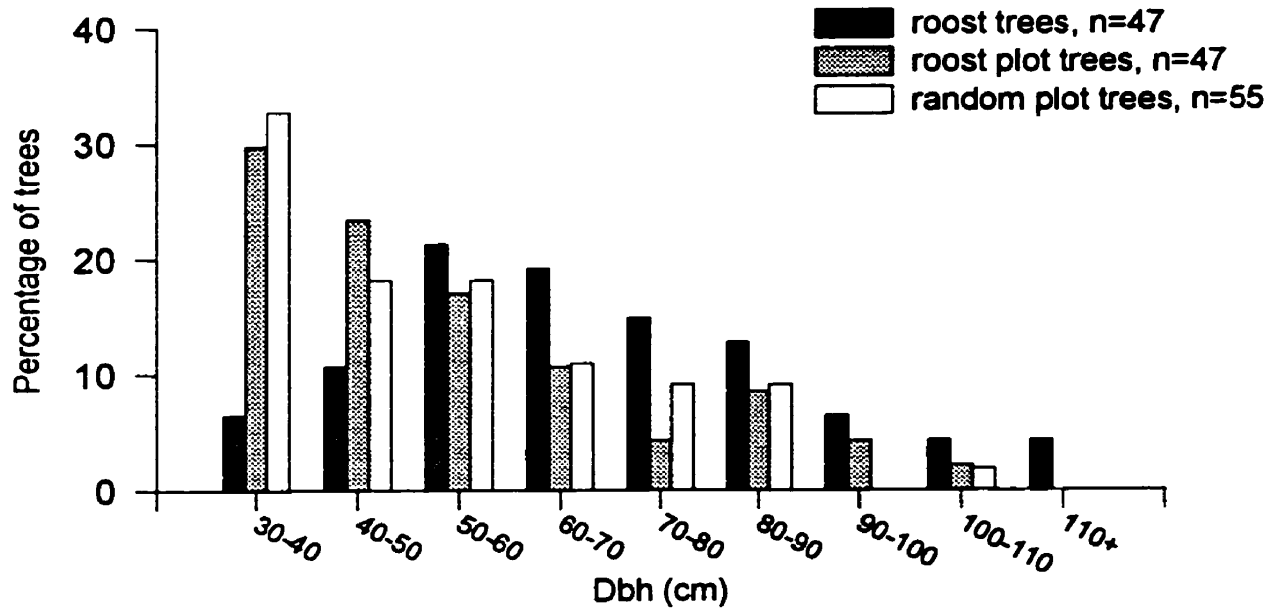
Figure 18. Diameter at breast height (cm) of roost, roost plot, and random plot trees. Only trees as large as roost trees (>30 cm dbh) and in decay classes used as roost trees (2-5) are included.
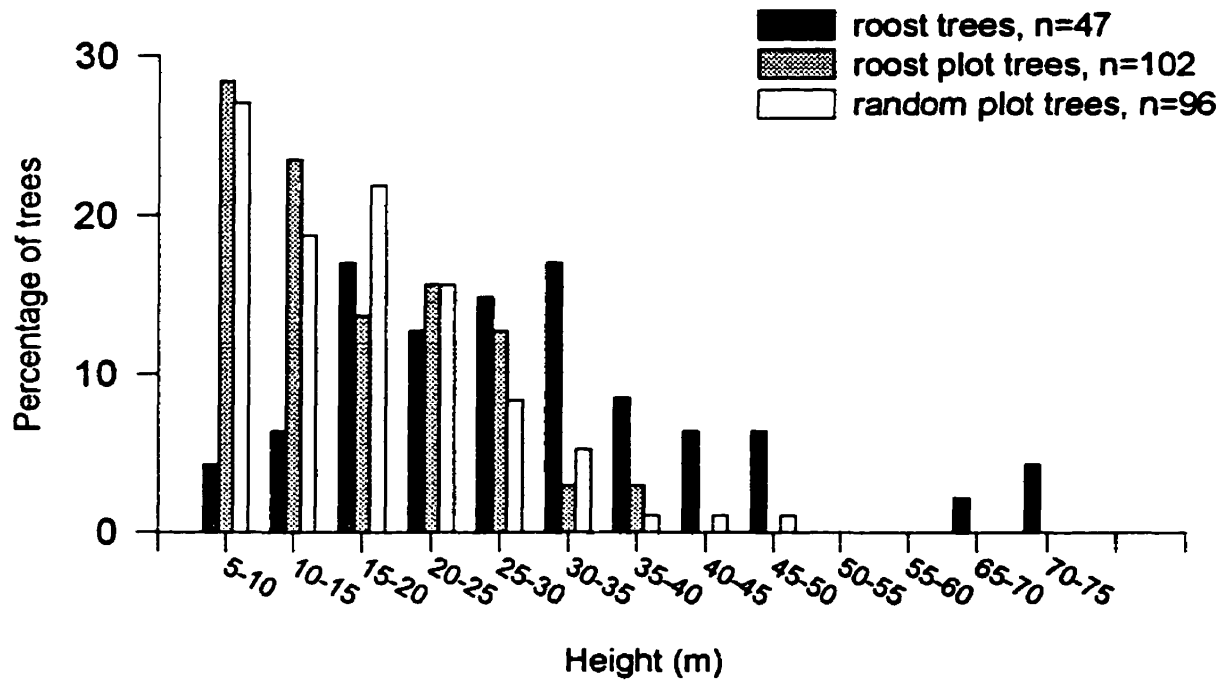
Figure 19. Height of roost, roost plot, and random plot trees. Only trees as tall as roost trees (>5 m) and in decay classes used as roost trees (2-5) are included.

Table 16. Tree species, age range of tree cores, minimum time since death, and decay class for 18 roost trees.

Tree species and sample #	Core	Time span of core (AD)	Time since death (years)	Decay class	Roost structure
Yellow-cedar 1	A	1671 –1962	36	2	bark
	B	1667 –1987	11		
Yellow-cedar 2	A	1426 –1950	48	4	bark
Yellow-cedar 3	A	1744 –1996	2	2	crack
Yellow-cedar 4	A	1164 –1609	389	5	bark
	B	1429 –1689	309		
	C	1222 –1784	214		
	D	1376 –1789	209		
Hemlock 1	A	1678 – 1998	0	2	bark
Hemlock 2	A	1779 – 1998	0	2	unknown
	B	1728 – 1905	93		
	C	1708 – 1988	10		
Hemlock 3	A	1816 – 1986	12	4	bark
	B	1702 – 1810	188		
Hemlock 4	A	1767 – 1985	13	4	unknown
Hemlock 5	A	1823 – 1969	29	4	bark
	B	1811 – 1989	9		
Hemlock 6	A	1691 – 1905	93	4	bark
Hemlock 7	A	1611 – 1991	7	5	bark
	B	1617 – 1948	50		
Hemlock 8	A	1703 – 1897	101	5	bark
White pine 1	A	1802 – 1979	19	4	unknown
White pine 2	A	1849 – 1971	27	4	bark
White pine 3	A	1729 – 1964	34	4	bark
White pine 4	A	1814 – 1920	78	4	bark
	B	1800 – 1934	64		
	C	1827 – 1939	59		
White pine 5	A	1742 – 1985	13	5	unknown
White pine 6	A	1760 - 1983	15	5	bark

From: Laroque and Kellner 1999.
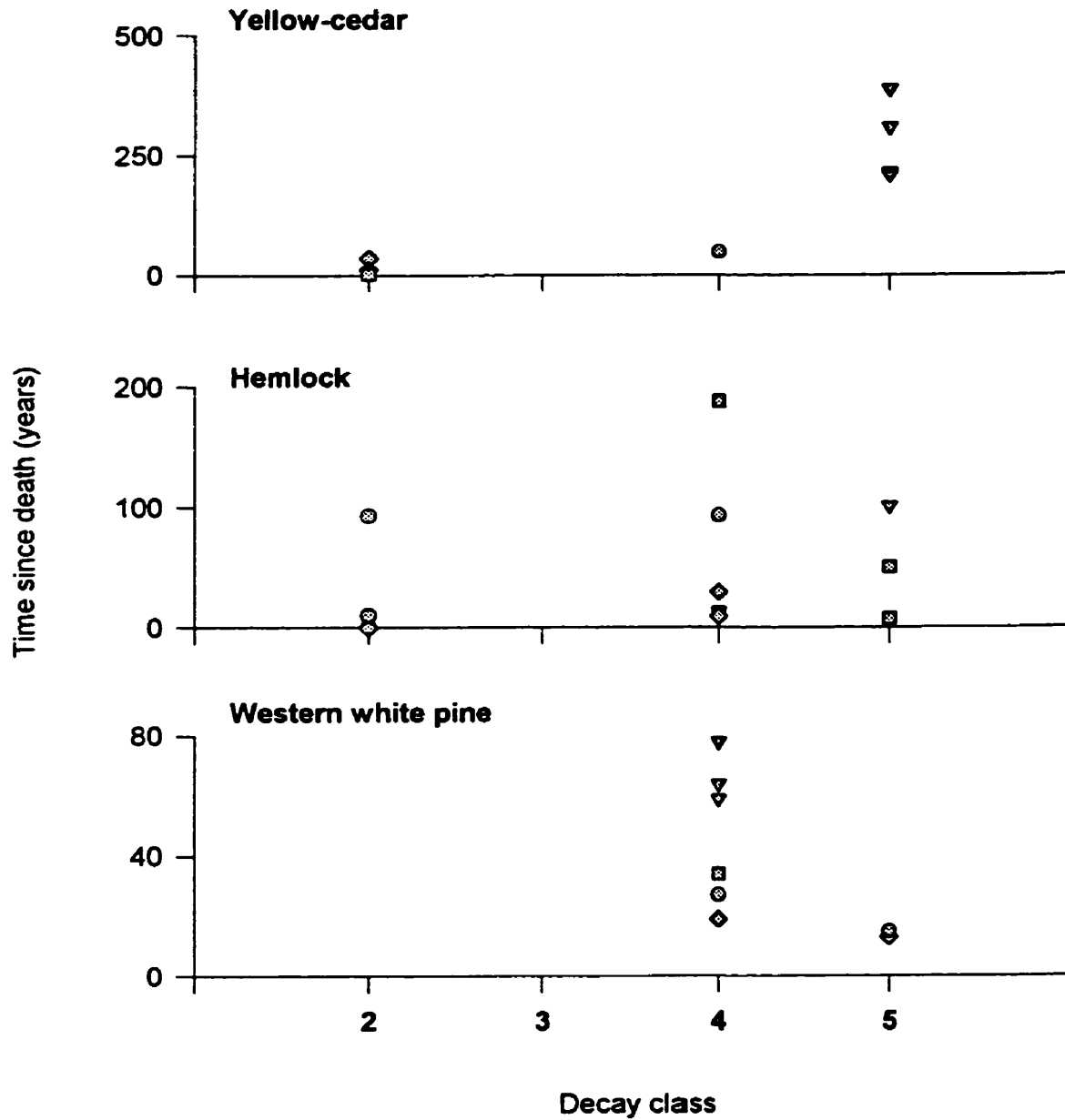
Figure 20. Time since death versus decay class, for yellow-cedar, hemlock, and western white pine trees. Data are from 29 cores from 18 roost trees. Within each decay class, different symbols represent different trees. Note different time axes for each species.

Site characteristics

Roost plots did not differ from random plots in decay class or bark class

distribution, or in species composition (Table 15). Roost plots contained significantly

larger trees, based on dbh and height. However, this difference was driven by the large

size of roost trees. The exclusion of roost trees from roost plots resulted in no significant

differences in dbh (P = 0.984) or height (P = 0.895).

Although bats were captured solely at montane sites (>600 m elevation), they

roosted at all elevations (Table 17). Mean aspect of roost sites (221°) was significantly

different from the mean aspect of random sites (246°), in spite of constraints on random

plot location due to the paired sampling design. Roost sites were on a wide range of

slopes, and were not significantly different from slopes at random sites. Of the vegetation

variables measured, only percent canopy cover of trees (>10 m tall) showed significant

differences. Roost sites had less canopy cover than did random sites. This agrees with the

observation that roost sites almost always incorporated a natural gap.

Movements between capture and roost sites and between roosts

Bats travelled variable horizontal and vertical distances from their capture site to

their initial roost site (Table 18, capture-roost1 distances; Fig. 21). Thirteen of 15 initial

roosts were below the elevation of the capture site. Subsequent roosts were closer

together, with less change in elevation (Table 18, roost-roost distances). Bats for which I

located multiple roosts showed fidelity to a roost area, although they moved between sites

Table 17. Results for comparison of roost and random site characteristics.

Variable	Roost plots	Random plots	P	Test
	(value or mean ± SE)			
Elevation (m)	836 (range 280 - 1275)			
Aspect (°)	221	246	0.040 *	Watson-Williams
Slope (%)	25.2 ± 3.5	22.0 ± 3.3	0.656	Mann- Whitney U
Tree cover (%)	19.5 ± 2.0	28.1 ± 2.3	0.002 *	Paired t-test
Tall shrub cover (%)	19.5 ± 2.5	17.8 ± 1.8	0.538	"
Short shrub cover (%)	37.2 ± 3.0	40.9 ± 2.7	0.300	"
Herb cover (%)	22.5 ± 2.9	23.0 ± 3.1	0.911	"
Stem density (# stems/plot)	9.7 ± 0.7	9.5 ± 0.7	0.743	"

Table 18. Horizontal and vertical distances between capture and initial roost sites (roost1) and between subsequent roost sites. Data from 'Fluffy1' are excluded.

Measurement	n	Horizontal distances (m)			Vertical distances (m)[1]		
		Mean ± SE	Min.	Max.	Mean ± SE	Min.	Max.
Capture - roost1	14	1827 ± 451	78	6384	237 ± 61	20	830
Roost – roost	34	395 ± 65	5	1640	52 ± 15	0	380

[1] Absolute value of change in elevation.
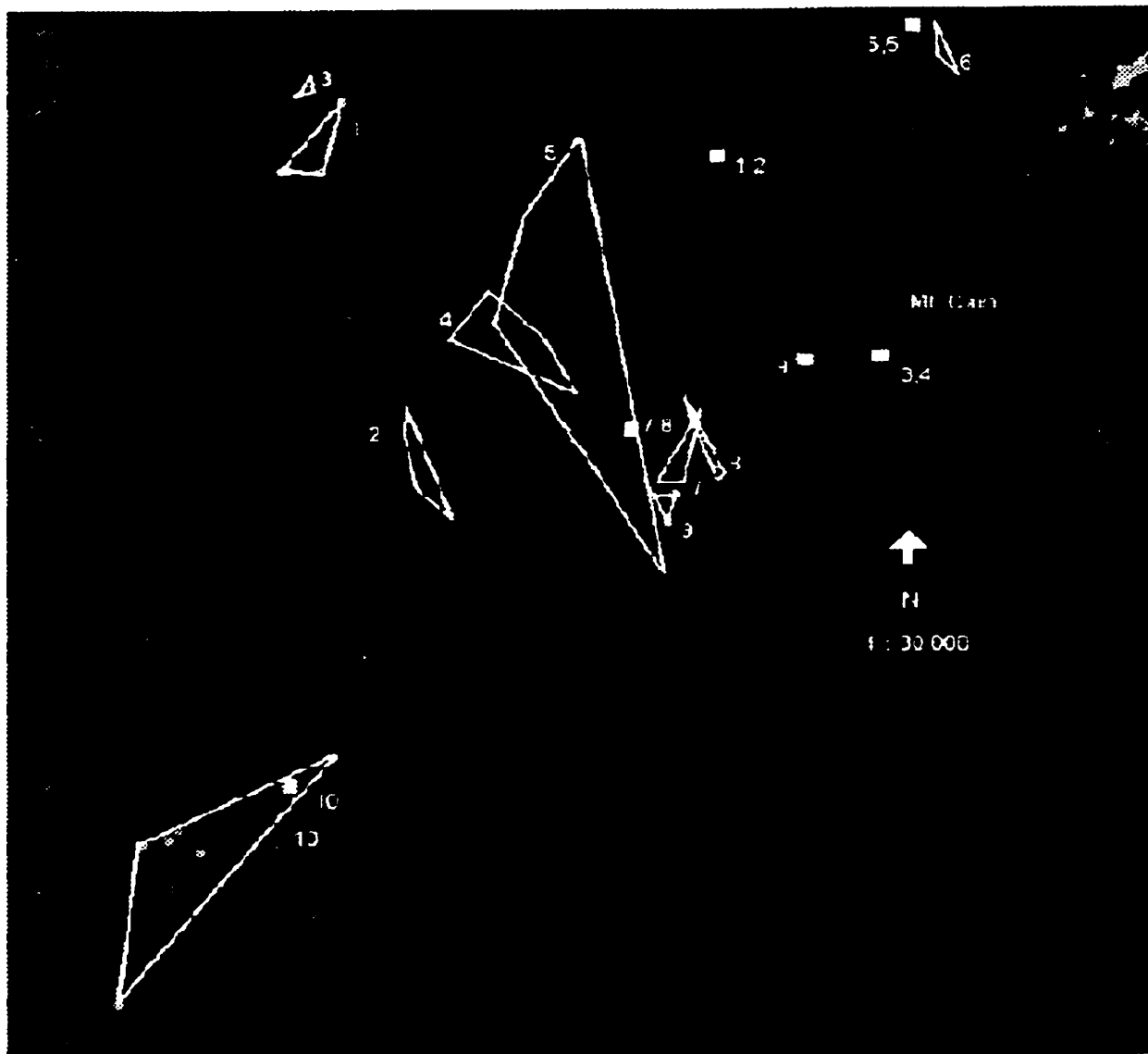
Figure 21. Capture sites (squares) and roost areas (polygons) for 10 radio-tagged bats. Numbers represent different individuals.

and roosts within the area. In spite of the stresses of capture, the first roost after capture was in the roost area, with the exception of 1 male *M. lucifugus* ('Fluffy1') who initially roosted far from his capture site and subsequent roost area.

Roost areas

For bats with more than 2 roosts, I calculated the size of the roost area, based on the minimum convex polygon outlined by their first 3 roosts, first 4 roosts, etc. (Table 19, Fig. 21). Data from 'Fluffy1' were not included. This provided an estimate of a minimum roost area used by each bat. Although sample size was small, females appeared to use larger roost areas than males. Roost area may vary among species of bat, with *M. volans* using larger areas than the other species monitored.

Roost switching and site fidelity

Bats showed fidelity to a roost area, but switched roosts frequently. Within a roost area, bats used 1 to 6 sites (a particular tree or rock) and 3 to 8 roosts (a particular crack, crevice, or bark flake), using 1 to 5 roosts at each site (Table 20). Bats returned to previously used sites, but often used a different roost at that site. Continuous residence time at any particular roost was from 1 to 11 days, with a mean stay of 1.7 days per roost and 1.8 days per site. There were no trends between species or sex and residence time.

Table 19. Roost areas (ha) for bats with >2 roosts.

# of roosts	Roost area (ha, 100% minimum convex polygon)										
	Myotis lucifugus				Myotis evotis		Myotis volans			Lasionycteris noctivagans	Mean ± SE
	Male1	Male2	Male3	Male4	Male1	Female1	Male1	Male2	Female1	Male1	
3	0.1	0.1	0.1	0.42	0.4	2.7	1.8	4.3	13.5	0.9	2.4 ± 1.3
4	0.2	3.7	2.7	5.9			3.9	78.4	15.0		16.0 ± 11.0
5		3.9	4.5				13.8	78.4	15.0		23.0 ± 14.0
6									40.1		40.1

Table 20. Number of roosts and roost sites, residence time, and site re-use for 15 radio-tagged bats.

Species	Sex	# days monitored	Total # sites	Total # roosts	# days/ site	# days/ roost	# returns to a site	# days used on return
M. lucifugus	Male	2	1	1	2	2		
	Male	15	5	5	1	1	0	
	Male	12	4	4	1- 5	1- 5	0	
	Male	13	5	8	1- 4	1- 2	1 to site 1	2
							1 to site 5	2
	Male	5	5	5	1	1	0	
M. evotis	Male	8	3	4	1-2	1	1 to site 1	1
	Female	4	3	3	1	1	1 to site 1	1
	Male	7	1	2	7	2- 5		
M. volans	Male	6	5	5	1	1	1 to site 1	1
	Male	11	5	5	1- 5	1- 5	0	
	Female	18	6	6	1- 2	1- 2	2 to site 2	1,1
							3 to site 3	1, 2, 1
	Female	1	1	1	1	1		
Lasionycteris noctivagans	Male	1	1	1	1	1		
	Male	18	3	3	1-11	1- 11	1 to site 1	2
	Male	6	2	2	1- 5	1- 5	0	

Discussion

Roost selection

The roost structures and sites chosen by bats at Mt. Cain may be explained in terms of solar heating and ease of access. Cool temperatures at Mt. Cain may play a strong role in roost selection. Although male and non-reproductive female bats frequently use deep torpor, and select cool roosts to facilitate this behaviour (Hamilton and Barclay 1994), rewarming can be a major energetic cost (Hamilton and Barclay 1994). Bats in the cool Mt. Cain environment selected south facing roosts and roost sites, perhaps to take advantage of solar radiation. Solar-heated roosts may limit the drop in body temperature and reduce costs of re-warming.

Roost selection at Mt. Cain may also reflect the need for accessibility. Bats are agile flyers, and most of the species present at Mt. Cain have been described as "clutter-tolerant" (Bradshaw 1996). Nevertheless, bats forage in the more open areas of the forest (Bradshaw 1996), and presumably navigation through the canopy presents some difficulties, to varying degrees for different species. An open area around a roost allows for ease of landing, and a quick exit to avoid predators.

Bats at Mt. Cain roosted in the upper portions of large trees, above or at canopy height. There was low canopy cover at roosts. All rock roosts (3 of the 50 roosts) were in completely unobstructed rock faces. These characteristics would contribute to easy location and access by bats as well as to solar heating of the roosts. Solar heating may also be enhanced in dark-coloured bark roosts on hemlock and pine trees (30 of the 50 roosts), and by roost aspect, as mentioned above.

Bats used roost trees in intermediate stages of decay, and selected trees in decay

class 4. Presumably these snags are used because they provide the preferred roost

structures in the form of loose bark flakes or cracks in the boles, and easy access because

they had few branches. The trend to avoid use of *Abies amabilis* as a roost tree species

may reflect the decay pattern of this species and a lack of the preferred structural

characteristics usually associated with intermediate decay classes. Roost selection by bats

at Mt. Cain has many factors consistent with other studies, where bats selected large trees

in moderate stages of decay, in open areas (e. g., Betts 1996, Vonhof and Barclay 1996,

Brigham et al. 1997, Ormsbee and McComb 1998).

Roost fidelity

Bats at Mt. Cain switched roosts and roost sites frequently. This behaviour has

been reported for other tree-dwelling bats (Betts 1996, Kurta et al. 1996, Ormsbee 1996,

Vonhof and Barclay 1996, Brigham et al. 1997). Fidelity is related to the permanence of

roosts and inversely related to the availability of roosts (Lewis 1995). At Mt. Cain, there

currently appears to be high roost availability, and most roosts are under tree bark, which

are generally regarded as non-permanent roosts. However, results from the analyses on

age-since-death suggest that bark and tree crack roosts in montane ecosystems may be

very stable with respect to the lifespan of a bat, due to the slow decay rates of standing

snags (Laroque and Kellner 1999).

Number of trees and size of roost areas

The number of trees used by individual bats is unknown due to the limitations of

current technology of radio-telemetry. A longer observation period led to the discovery of more roosts for bats at Mt. Cain and in other studies (Kurta et al. 1996, Ormsbee 1996). Therefore, numbers of roosts that I report are likely extreme underestimates of the numbers actually used by bats. Longer monitoring of bats at Mt. Cain led to an increase in the roost area used by bats, contrary to the findings of Ormsbee (1996).

Multiple day roosts in single areas have been described for various species of bats (e. g., Kunz 1982b, Taylor and Savva 1988, Lewis 1995, Betts 1996, Kalcounis and Hecker 1996, Vonhof 1996, Vonhof and Barclay 1996) including *M. volans* in the Oregon Cascades (Ormsbee 1996). Area fidelity could be due to favourable structures having a clumped distribution, but at Mt. Cain, potential roosts appear to be distributed throughout the landscape. Indeed, forests in the Mountain Hemlock Biogeoclimatic zone have been noted for the large number of standing dead trees and the high proportion of canopy gaps (Lertzman and Krebs 1991), characteristics which provide roosting habitat for bats. It is more likely that bats remain in one area because of the benefits of home range familiarity.

Size of roost area may vary with species and sex of bat. Male *Myotis evotis* and *M. lucifugus* have been described as philopatric and nomadic, respectively (Barclay 1991). I found that both these species tended to use smaller roost areas than did *M. volans*. In southeastern B.C., however, there was greater inter-individual than inter-specific variation in roost area for *M. evotis*, *M. volans*, and *Lasionycteris noctivagans* (Vonhof and Barclay 1996). Although my sample size is small, *M. evotis* and *M. volans* females at Mt. Cain tended to use larger areas than did most males.

Roost areas at Mt. Cain (13.8 - 78.4 ha) were larger than those reported for *M. volans* in Oregon (11.4 ha, Ormsbee 1996). Horizontal and vertical distances between capture and initial roost sites and between subsequent roost sites were also larger at Mt. Cain than in southeastern B.C. (Vonhof and Barclay 1996). However, area based data must be interpreted within the context of the landscape. Most roosts at Mt. Cain were in contiguous old growth forest. The only exceptions were a low elevation tree roost in a riparian leave strip, and 2 rock roosts in a quarry within a clearcut. Presumably, in a more fragmented landscape, the size of remaining forest patches could influence the size of roost areas.

Chapter 4. Summary and implications for habitat management

I found a diverse community of bats in montane forests. Bats were possibly at lower density in montane forests relative to low elevation forests, based on lower capture rates and reduced relative activity. Nevertheless, there was evidence of reproductively active populations of *Myotis lucifugus*, *M. volans*, and *M. evotis/keenii*. The diets of bats at Mt. Cain were similar to those reported for bats in other areas, with perhaps an increased reliance on dipterans.

Increasing elevation resulted in decreasing occurrence and abundance of bats, and of big bats in particular. It is probable that there are differences in response to elevation between *Myotis* species as well, given the variety in diet found here and in other studies, and the range of foraging strategies and habitats used by the various species. Increasing elevation also led to an extended nocturnal activity period, suggesting different foraging patterns between elevations. In spite of decreased activity at higher elevations, bats were present in montane forests from May to October. Evidence from telemetry and bat detectors indicated that bats use montane habitats for foraging and roosting. Movement patterns from several radio-tagged bats showed that some bats may commute regularly to and from lower elevations, while others spend extended periods in montane forests.

Management of montane forests for bats must therefore provide for both foraging and roosting habitat at high elevations. Although I did not attempt to identify prime foraging habitat, I found foraging activity at ponds and along human-generated old growth edges. Other studies report limited foraging activity within old growth stands

(Thomas 1988, Grindal 1996, Parker et al. 1996), although old growth is used extensively for roosting (this study, Crampton and Barclay 1998, Grindal 1998).

In my study, bats roosted primarily beneath loose bark or in cracks in large dead or dying trees. Roost trees were in open patches within old growth forest. I think that exposure to sun is a critical factor in roost selection at Mt. Cain, although factors generating exposure to sun probably also result in ease of roost location and ease of access. Regardless of the underlying cause for roost tree and patch selection, the ability to identify roost trees on the basis of physical tree and site characteristics suggests that it may be possible to retain or provide appropriate roosts in managed forests.

Because of the selection of large trees for roosts, dominant or co-dominant snags and live trees should be provided as potential roosts. The slow decay rate of roost trees at Mt. Cain means that these trees may provide viable roosts for a long time, as shown by the dating of one yellow-cedar snag at 209 to 389 years since death. However, the rate of decay varied greatly among and within tree species. Within a species, the lack of a strong correlation between decay class and time since death of a snag (this study, Daniels et al. 1997) means that predicting the future decay class distribution of snags is difficult. Recruitment of dominant trees into the snag population is also very slow (Edmonds et al. 1993). Therefore, to provide roosting habitat over time, there must be an emphasis on retaining large trees and snags in a variety of decay classes. Some of these trees should be healthy trees, which will eventually be recruited as wildlife trees in future stands.

The provision of suitable roosting habitat must take into account not only the roost characteristics selected by bats but also the need for multiple roosts in one area. Bats switched roosts frequently but were faithful to roost areas up to at least 78 ha in size.

Therefore, single wildlife tree or small patch retention may not adequately address habitat requirements of bats. Instead, the retention of patches or stands of forest containing many potential roosts should be favoured, and may also aid in maintaining the microclimate of roosts, as suggested by Ormsbee (1996).

The location of old growth patches should be considered in relation to potential foraging and drinking sites such as ponds and wetlands. The average distance between capture site and initial roosting area was 1.8 km in my study, with a maximum of 6.4 km. In the Oregon Cascades, bats commuted an average 2.5 km between roost and foraging areas (Ormsbee 1996). These distances provide considerable flexibility to managers attempting to locate forest patches 'near' foraging areas. Nevertheless, the relatively inhospitable nature of recent clearcuts and regenerating forest (Lunde and Harestad 1986, Thomas 1988, Parker et al. 1996, Crampton and Barclay 1998, Humes et al. 1999) may affect commuting distances because bats follow forest edges instead of crossing open spaces (Limpens and Kapteyn 1991).

Protection and provision of habitat for forest-dwelling bats is not explicitly considered under forest management guidelines. The exception to this is the protection of hibernacula of the red-listed *Myotis keenii* (B.C. Ministry of Forests and B.C. Ministry of Environment, Lands and Parks 1999). Instead, the recommendations of the Forest Practices Code Biodiversity and Riparian Management Area Guidebooks (B.C. Ministry of Forests and B.C. Ministry of Environment, Lands and Parks 1995a, 1995b) are expected to protect habitat for bats. Because the trees used by roosting bats in my study are typical Wildlife Trees, and as such are recognised as important to many species, these trees are likely to be considered for protection and inclusion in Wildlife Tree patches.

Furthermore, given the high number of snags and openings in montane forests (personal

observation, Lertzman and Krebs 1991) and the wide distribution of water, measures for

the protection and spatial location of old growth forest for other species, such as marbled

murrelets (*Brachyramphus marmoratus*), mule deer, and black bear (*Ursus americanus*),

are likely to provide suitable roosting and foraging habitat for bats.

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