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The summer ecology of *Myotis* species bats in the interior wet-belt of British Columbia

by

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ABSTRACT

Summers in the interior wet-belt of British Columbia have cool temperatures and high rainfall. This region is home to five species of insectivorous *Myotis* bats, including two gleaning species. I predicted that gleaners, given their ability to feed on non-flying insects, would have a diet unlike that of aerial hawkers, would emerge later after sunset, forage later and forage in different habitats than strict aerial hawkers. I further predicted that the foraging advantages of gleaning in cooler environments may allow more gleaning individuals to reproduce. I found there was no difference in diet and temporal foraging activity between foraging guilds, although there was evidence of spatial partitioning. Only 11% of captured *Myotis* females were obviously reproductive. Roost preferences of long-eared species were found to be similar to those of other forest-dwelling bats. However, *M. septentrionalis* may be more selective in the types of roosts it uses.

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CHAPTER ONE

General introduction

Over the past decade, the use of forested environments by temperate-zone bats has been closely examined (Barclay 1991, Crampton 1995, Law 1996, Lunney et al. 1988, Sasse and Pekins 1996, Thomas 1988, Vonhof 1995). As forests are an important natural resource, human use of forests has resulted in loss and fragmentation of older forest stands. In the interest of conserving forest-dwelling bat populations, the characteristics of forests selected by bats have been investigated (e.g. Crampton 1995, Lunney et al. 1988). Forest habitats vary across climatic and altitudinal gradients (Meidinger and Pojar 1991). Thus investigating the use of many distinct forest habitats will provide information on which characteristics may be relevant to bats in all forest types and what variation in habitat use exists among species and forest habitats.

The overall purpose of my study was to examine the summer ecology of a group of *Myotis* bats in the interior cedar-hemlock forests of British Columbia. I tested hypotheses regarding bat behaviour developed from studies on similar bat species in other forested habitats. A significant contributing factor to the selection of the study site was the presence of a rare (in British Columbia) species, *M. septentrionalis*. Thus, as I tested hypotheses related to the summer ecology of *Myotis* species, I focused on *M. septentrionalis* to try and elucidate why *M. septentrionalis* is consistently found in the interior wet-belt when it is relatively rare in other parts of British Columbia.

Through either hibernation or migration, temperate-zone bats are adapted to cope with long, cold winters with few foraging opportunities. Northern temperate bats that hibernate (i.e. all the *Myotis* species in this study) generally mate before entering hibernation, at the hibernaculum. In preparation, males undergo spermatogenesis during the summer. Females store sperm until the onset of spring. Gestation is short (but is influenced by temperature, heterothermy, and a female's foraging success) and a single offspring is born in June or early July. There is a brief lactation period (2-3 weeks) and then weaning occurs. During the remainder of the summer, juveniles and reproductive females must gain fat reserves to prepare for the next hibernation period (Racey 1982). The summer months are thus occupied with reproducing, weaning offspring and gaining fat reserves for the following winter. As temperate summers are short, any delay in the cycle (such as extensive use of torpor slowing fetal development) will have consequences on the probability of successful reproduction and juvenile survival.

Bats may minimize energetic expenditure through the use of torpor (reducing their body temperature to ambient, McNab 1982). However, the reproductive process is slowed in females that extensively use torpor over the summer (Audet and Fenton 1988, Racey 1982, Racey and Swift 1981). Thus reproductive female bats tend to avoid torpor. Instead, reproductive females will modify their roosting and foraging behaviour to minimize energetic expenditure without the use of torpor. Males and non-reproductive females do not experience the same constraints and generally use torpor in the summer more often than reproductive bats (Audet and Fenton 1988, Grinevitch et al. 1995, Hamilton and Barclay 1994).

Maximizing energetic gains and minimizing costs during the summer are reflected in the foraging and roosting ecology of temperate-zone bats and vary depending on reproductive status. Reproductive bats adjust the amount of time spent foraging depending on their current stage of reproduction (Barclay 1989, de Jong 1994, Rydell 1993) whereas non-reproductive bats do not show marked seasonal changes. Similarly, the roosting requirements of reproductive and non-reproductive bats differ, with non-reproductive males and females generally choosing cool, solitary roosts to facilitate the use of torpor (Hamilton and Barclay 1994). In many species, reproductive females form large maternity colonies and select warm roosts so as to maintain a high body temperature at minimal cost (Kurta 1986). The climatic conditions of the summer home-range will also affect bat behavioural decisions. In locations where night-time temperatures are low or rainfall is abundant, insect availability will be low (Williams 1961) and thus foraging opportunities are reduced. Cool environments will also facilitate the use of torpor but have increased costs for reproductive bats that avoid entering torpor (Barclay 1991, Thomas 1988). In these environments, males and non-reproductive females may outnumber reproductive females or reproductive females may migrate to warmer or drier areas.

Study Area

My study took place in the Columbia River valley in British Columbia. The study area included Glacier National Park and Mount Revelstoke National Park. Its southern limit was the Illecillewaet River valley, parallel to the Trans-Canada Highway, and the northern limit was the Goldstream River basin, 80 km northwest of the town of Revelstoke along Highway 23 (Fig. 1.1). The study area was bounded by the Columbia River valley to the west and the Beaver River valley in Glacier National Park to the east (between 51° 00' and 51° 41' N and between 117° 25' and 118° 35' W).

The study took place in the Interior Wet Belt (Achuff et al. 1984). It is a mountainous zone ranging from 550m (river valleys) to over 2000m. The mountains are steep and the valleys are narrow. Within the study area, the high altitude forests are dominated by subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*) (Achuff et al. 1984). However, all bat trapping and monitoring occurred around river valleys between 500-900m in elevation, as this is where bats were most active. This elevation is in the Interior Cedar - Hemlock (ICH) biogeoclimatic zone and the specific variants in the study area were ICHwk (wet cool ICH) and ICHvk (very wet cool ICH; Braumandl and Curran 1992). The mature climax forests are dominated by western red cedar (*Thuja plicata*) and western hemlock (*Tsuga heterophylla*). The forest consists of large, widely spaced trees which results in an irregular canopy. Climax understory in moist ICH forests is patchily distributed with well developed shrub layers, mostly in canopy gaps, and moderate to dense herb and moss cover under the canopy. The narrow valleys do not allow for the development of extensive wetlands but there are scattered riparian skunk cabbage (*Lysichiton americanum*) swamps and small bogs (Achuff et al. 1984, Braumandl and Curran 1992, Ketcheson et al. 1991).

Summers (May to August) at Revelstoke experience average daily highs of 19.2 (May) to 25.3°C (July) and corresponding overnight lows are 5.5 and 11.1°C

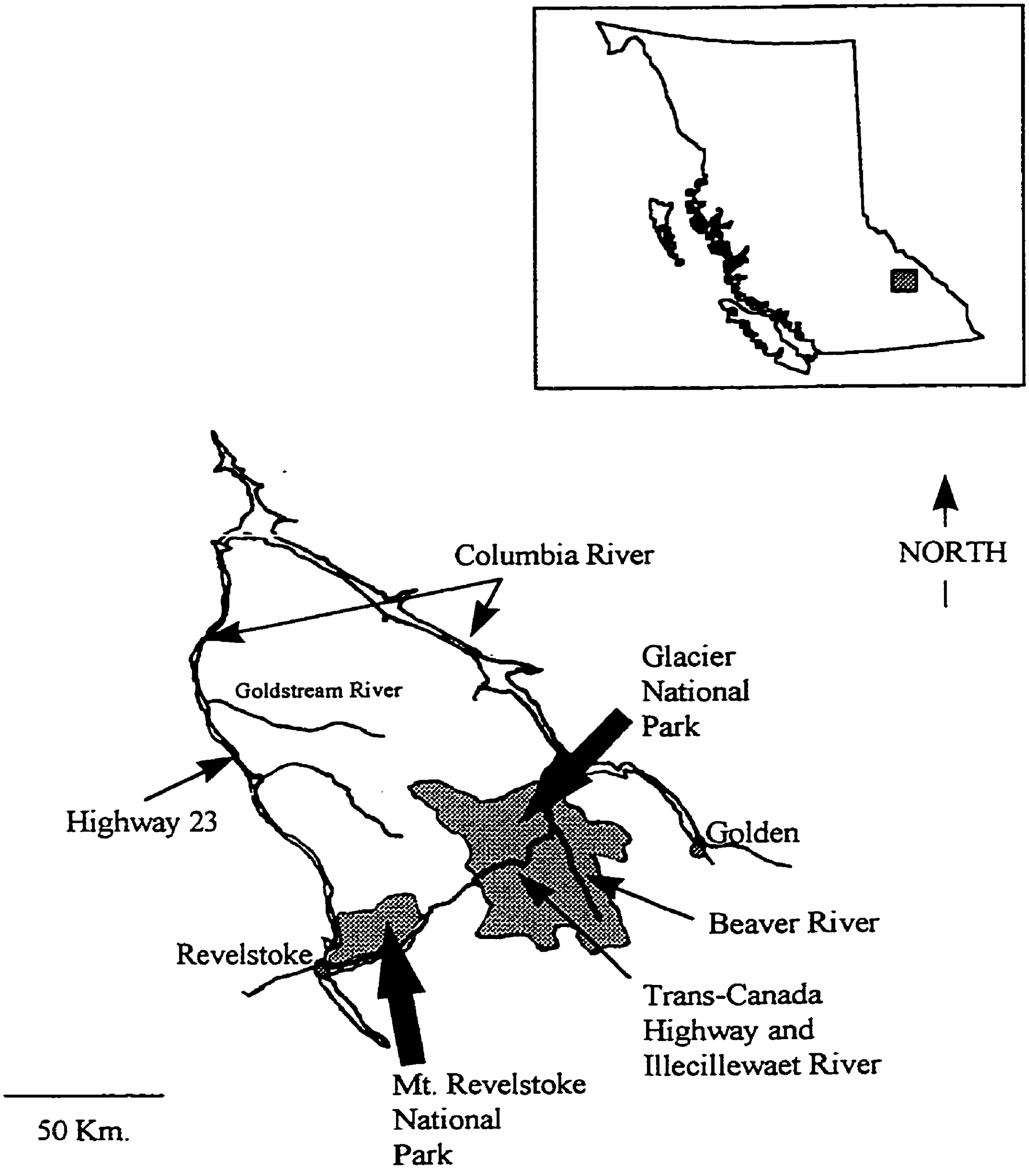


Figure 1.1. Schematic map of the study area including the national parks and some landmarks. Inset shows the location of the study area within British Columbia

(Environment Canada Climate Services, Pacific and Yukon Region). Revelstoke is located in a valley, at 450m in elevation. However, temperatures will decrease at higher elevations, which cover most of the study area. Normal total summer precipitation is 256mm and annual precipitation is 1000-1700mm (most of which falls as snow, Ketcheson et al. 1991).

Study Species

Eight species of insectivorous bats are found in the study area, including five species of *Myotis* (Nagorsen and Brigham 1993, van Zyll de Jong 1985). The non-*Myotis* species are *Lasiurus cinereus* (the Hoary Bat), *Lasionycteris noctivagans* (the Silver-haired Bat), and *Eptesicus fuscus* (the Big Brown Bat). These are the largest species of bats in the area and are each quite distinct, both from each other and from *Myotis* bats. *Myotis* is divided into three subgenera, each of which have representatives in the study area. The species and subgenus of *Myotis* in the study area are *M. evotis* and *M. septentrionalis* (subgenus *Myotis*), *M. lucifugus* and *M. volans* (subgenus *Leuconoe*), and *M. californicus* (subgenus *Selysius*). The bats range in mass from 5g (*M. californicus*) to 8g (*M. lucifugus*; van Zyll de Jong 1985). Three of these species (*M. evotis*, *M. lucifugus*, and *M. californicus*) are fairly common in other regions of British Columbia (Nagorsen and Brigham 1993). *M. septentrionalis* (the Northern Long-eared Bat) is red-listed in British Columbia (Stevens 1995). This means that it is considered a rare and possibly endangered species. However, previous surveys have consistently found it in Mt. Revelstoke National Park, within the study area (Fenton et al. 1983, Holroyd 1993, Rasheed and Holroyd 1995, van Zyll de Jong et al. 1980).

Species Identification

I based my identification of species on species accounts in van Zyll de Jong (1985) and Nagorsen and Brigham (1993). There was the potential to confuse the Northern Long-eared Bat (*M. septentrionalis*) with the Western Long-eared Bat (*M. evotis*) or the Little Brown Bat (*M. lucifugus*) as these three are superficially similar in size and appearance. In my study area, the average forearm lengths of *M. septentrionalis*, *M. evotis* and *M. lucifugus* were 36.6, 36.8, and 36.7mm, respectively. I distinguished *M. septentrionalis* from *M. evotis* by fur and membrane colour and ear length. *M. septentrionalis* is a more uniform brown in both pelage and membranes. *M. evotis* had distinct black membranes contrasting with a brown pelage, and very long black ears (Manning and Knox Jones 1989). *M. evotis* within the study area was darker than individuals caught in the dry interior of British Columbia (Nagorsen and Brigham 1993). *M. evotis* is reported to be larger physically and cranially than *M. septentrionalis*, but this characteristic was not evident externally and I did not use it for diagnosis.

Distinguishing *M. septentrionalis* and *M. lucifugus* was not as straightforward. I distinguished the species by a combination of features. I used the slightly longer ears, longer tail, and lack of hairs on the toes to identify *M. septentrionalis*. Both bat species tended to have dark brown fur and brown membranes. *M. lucifugus* varied in membrane colour within the study area. *M. lucifugus* individuals captured north of Revelstoke, along the Columbia River basin, had dark membranes, a characteristic of *M. l. alascensis* (subspecies of the study area; Fenton and Barclay 1980, van Zyll de Jong 1985). Individuals caught in and around the National Parks were more variable in colour, with some individuals having lighter brown membranes. Note that colour of bats is a highly variable trait (Nagorsen and Brigham 1993, van Zyll de Jong 1985) and the diagnosis I used may not be the same for individuals in other geographic regions.

My assistants and I independently identified each individual to species. All long-eared species were marked with yellow (1996) or red (1997) plastic split-ring arm bands. I performed a discriminant functions analysis using the measurable characteristics (ear length, tragus length, tail length, and forearm length) of all *M. evotis*, *M. lucifugus* and *M. septentrionalis* caught in 1996 and 1997. I measured ear length, tragus length, and tail length to the nearest millimeter with a metric ruler. I measured forearm length with vernier calipers, measuring to the nearest 0.05 mm. Species were significantly discriminated (Wilks' lambda =0.104, $F_{8,106}$ =27.84, $p<0.0001$, Fig. 1.2). Forearm length, ear length, tragus length and tail length accounted for 47% of the variation between species (Table 1.1). The individuals were classified into three distinct groups with only one misclassification (Fig 1.2) and the overall error rate was 2%.

As the study area has high summer rainfall and low overnight temperatures, I expect low insect (prey) abundance (Williams 1961), poor foraging opportunities and high thermoregulatory costs for bats. However, despite being climatically marginal, there is a relatively diverse bat fauna. Therefore, I examined the summer ecology of the

Myotis bats with special attention to the red-listed species, *Myotis septentrionalis*. I hypothesized that foraging, roosting and reproduction would be greatly influenced by the climatic conditions of the study area.

Table 1.1. Summary of discriminant functions analysis on morphological characteristics of *M. evotis*, *M. septentrionalis* and *M. lucifugus*.

Variable	$F_{2,53}$	P	Partial R^2	Standardized Coefficients	
				Root 1	Root 2
Forearm	3.55	0.036	0.156	0.374	-0.324
Ear length	27.5	<0.0001	0.047	-0.772	-0.278
Tragus length	8.71	0.0005	0.129	-0.569	-0.025
Tail length	11.74	<0.0001	0.141	-0.487	0.951

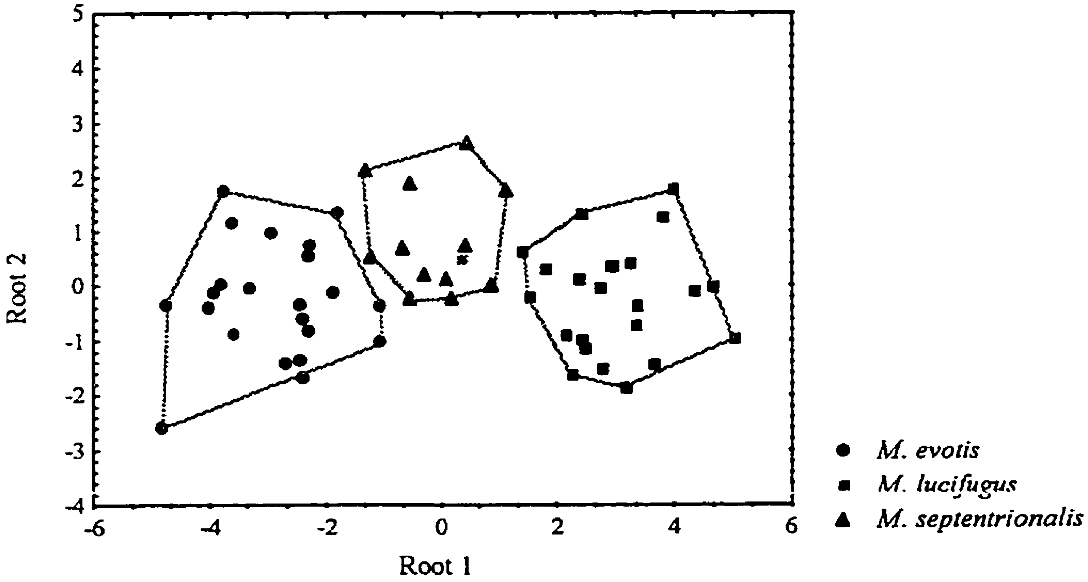


Figure 1.2. Canonical coefficients for *M. evotis, M. septentrionalis* and *M. lucifugus*. Outer boundaries of each group are shown. Note the presence of one *M. lucifugus* in the *M. septentrionalis* group. Ear length weighs highly negatively on root 1. Tragus and tail length weigh negatively on root 1 and forearm length weighs positively.

CHAPTER TWO

Population structure, foraging activity and diet of two foraging guilds of *Myotis* in the interior wet-belt, B.C.

INTRODUCTION

Of major importance to temperate-zone bats (especially reproductive females) is the amount of energy and nutrients they can garner in the short summer season (Barclay 1991, Grindal et al. 1992, Lewis 1993, Racey 1982). The behavioural decisions as to where and when to forage are critical to this goal. The challenge faced by bats in the interior wet-belt is to successfully reproduce and achieve fat reserves for hibernation in a climatically marginal habitat. My predictions for this investigation stem from the question: how does a diverse community of morphologically similar species of *Myotis* use the resources available given climatic constraints?

The species of *Myotis* I studied fall into two distinct foraging guilds. While all the bats can use echolocation to aerial hawk for insects, the long-eared species (*M. evotis* and *M. septentrionalis*) are also gleaners (Faure and Barclay 1992, Faure et al. 1993). Gleaning is the capture of prey items from a surface, such as the ground or foliage. Gleaners (specifically *M. evotis* and *M. septentrionalis*) can use passive listening to detect the sounds of insects moving on a surface (Entwistle et al. 1996, Faure and Barclay 1994, Faure et al. 1993). Species that use gleaning are less dependent on the presence of flying insects for foraging (Audet 1990, Barclay 1991, Entwistle et al. 1996). Gleaners may also be able to effectively capture auditive insects

(Faure et al. 1993). These insects can hear echolocation calls and may avoid being captured by hawking bats. Many species of moth (Lepidoptera) as well as some lacewings (Neuroptera) have ears designed for detecting bat echolocation (Fenton and Fullard 1979, Miller 1975). If a gleaning bat does not use echolocation, or uses low intensity calls (Faure and Barclay 1994) to detect an auditive insect, the insect has less warning of the approaching predator.

The existence of two foraging guilds may result in niche separation between species. Nocturnal insects have peaks of flying activity shortly after sunset and shortly before sunrise (Jones and Rydell 1994, Lewis and Taylor 1965, Racey and Swift 1985, Swift 1980, Taylor and Carter 1961). These peaks are important for aerial hawkers and hawking bat activity peaks generally correspond to peaks in insect activity (Erkert 1982, Racey and Swift 1985, Swift 1980, Taylor and O'Neill 1988). Gleaning bats, however, are not dependent on flying insect activity and can be more flexible in the time of night they forage. They may forage throughout the night despite cooler mid-night temperatures because insects, incapable of flying, may still be active on foliage (Barclay 1991, Entwistle et al. 1996). Gleaners emerge from roosts and begin foraging later than strict aerial hawkers (Barbour and Davis 1969, Entwistle et al. 1996, Jones and Rydell 1994, Rydell et al. 1996). As the interior wet-belt experiences cold overnight temperatures, gleaning may be a significant foraging advantage. I predicted that gleaning bats would emerge from their roost and forage later than non-gleaning bats.

Augmenting foraging opportunities may be particularly important to reproductive females who need resources not only for hibernation fat reserves, but also to produce and wean offspring. Barclay (1991) found gleaning Western Long-eared bats (*M. evotis*) were reproducing in the Kananaskis valley of Alberta whereas the non-gleaning sympatric species, *M. lucifugus*, the Little Brown Bat, was not. He supposed the advantages of gleaning in cooler conditions were enough to allow female gleaning bats to be able to reproduce in the area. Similarly, I predicted that the cold overnight environment of the interior wet-belt would result in proportionally more female gleaners (*M. evotis* and *M. septentrionalis*) than non-gleaners being reproductive.

Gleaners and non-gleaners may have preferences in the type of habitat they forage in (Fenton 1990). Studies of sympatric species have found gleaners tend to be associated with habitats that have more environmental clutter (i.e. presence of foliage) whereas strict aerial hawkers rely on more open habitats (Barclay 1991, Fenton 1990). Gleaning species have lower wing loading (mass/wing area) which presumably make them more adept at maneuvering through cluttered environments than non-gleaners (Barclay 1991, Norberg and Rayner 1987). Studies of gleaners and non-gleaners in forest environments have found that gleaners are associated with forest edges or under the canopy whereas non-gleaners are above the canopy or over open water bodies (Audet 1990, Barclay 1991, Crampton 1995, Krull et al. 1991). I predicted that this pattern of spatial separation would also occur in the interior wet-belt.

I examined the diet and activity pattern of the two foraging guilds in the interior wet-belt to assess how *Myotis* species are using available resources. I expected spatial (habitat) and temporal separation between the two foraging guilds. Different habitats and different periods of night vary in the numbers and proportions of insect orders present (deJong 1994, Ekman and deJong 1996, Lewis and Taylor 1965, Taylor and Carter 1961). Thus the separation of foraging guilds is reflected in differences in their diet. I predicted that diet composition would differ between the two gleaning long-eared species (*M. septentrionalis* and *M. evotis*) and the strict aerial hawkers (*M. lucifugus*, *M. californicus* and *M. volans*), with the strict aerial hawkers (particularly *M. lucifugus*) expected to have significantly higher proportions of dipterans (Anthony and Kunz 1977, Barclay 1991, Fenton and Bell 1979, Jones and Rydell 1994) and gleaners having higher proportions of lepidopterans (Barclay 1991, Fenton and Bell 1979) in their diets.

METHODS

Study Sites

The study took place from mid-May until the end of August 1996 and 1997. I conducted field work on all possible evenings when weather conditions permitted. I was unable to work on evenings with heavy rain, electrical and thunder storms or strong winds. In the field, I monitored for bat echolocation activity with Petersson ultrasonic detectors (D100) and I captured bats to assess the bat population structure and amount of nocturnal activity occurring in the Interior Cedar-Hemlock biogeoclimatic zone.

I chose trapping sites based on success in previous surveys (Fenton et al. 1983, Holroyd 1993, Rasheed and Holroyd 1995), accessibility, and habitat features believed to be attractive to bat activity, such as the presence of water or open flyways (e.g. along a trail, Barclay 1991, Racey and Swift 1985, Thomas 1988)

Each night, I measured ambient temperature at sunset, one hour after sunset and two hours after sunset. I noted the conditions at the start of the evening as either clear, cloudy (between 10% and 75% cloud cover, visually estimated) or overcast (>75% cloud cover) and as either dry, damp (rain had occurred within 24h) or drizzle (a light rain was occurring). The total rainfall and average monthly overnight temperatures for the Revelstoke airport were obtained from Environment Canada, Climate Services, Pacific and Yukon Region.

Captures and Echolocation Monitoring

I captured bats in mist nets or harp traps (Tuttle 1974). On arrival at a site, prior to sunset, I set up three or four mist nets and one or two traps depending on availability of appropriate spaces. I opened mist nets at sunset, or shortly after, in order to avoid the majority of bird activity. I trapped for a minimum of 2.5 hours after sunset and continued beyond the minimum if weather conditions, ambient temperature and bat activity merited it. As various numbers of capture devices were used each night, I measured effort as "net-nights". One net-night is the use of one trapping device (mist net or harp trap) for one night (2.5 hour trapping session).

I monitored bat echolocation activity using a Pettersson ultrasound detector (D100). I divided each evening into four half-hour time blocks beginning at one half-hour after sunset. During each half-hour block, I monitored the site with the bat detector for a minimum of 10 minutes (or as long as possible given circumstances). I monitored only for the presence of *Myotis* bats (ultrasound detector set at 40kHz, Kunz and Brock 1975). The similarity between calls makes it impossible to accurately determine the species of a *Myotis* bat producing a call, although it is possible to separate *Myotis* calls from those of the other genera of bats present (Kunz and Brock 1975, Thomas et al. 1987). An audible clicking sound indicated the presence of a bat. As the bat approached the vicinity of the detector, the clicking sounded louder. Thus I considered a bat "pass" to end when the audible clicks became faint. I also noted when the first *Myotis* was heard each evening.

I measured activity in three habitats: "canopy" included any area which occurred under a tree canopy; "water" included areas over an open (no canopy) body of water; and "edge" was activity which occurred at the boundary of a forest and open habitat such as a road, clear-cut or field. I did not monitor edges between water and forest.

Activity data were not uniformly collected from different sites or habitat types. As some trapping sites were more successful for bat captures, these were visited more frequently and thus were monitored for bat activity more often. Furthermore, only a few sites had more than one habitat category present. Consequently, my analysis of bat activity attempted to incorporate the variation due to different monitoring nights, sites, and habitats by examining components of the complete activity data set. In the analysis, I compared the number of bat passes occurring in the first monitoring hour (by pooling the first two monitoring half-hour sessions) to the second. My analysis involved multiple-factor analysis of covariance (ANCOVA) on subsets of the complete data set.

Activity had usually diminished by the end of the two-hour sampling period. In 1997, I monitored on some nights until dawn either with an Anabat II remote bat detector and delay switch (Titley Electronics Ltd., Ballina, New South Wales, Australia) connected to a sound activated cassette recorder, or with a hand held ultrasonic detector. This was to confirm the marked drop in bat activity that occurred shortly after sunset, as noted in 1996.

Bat Processing Protocol

Once captured, a bat was removed from the net or trap and placed in a cloth holding bag. I held the bat for a minimum of one hour after its capture to collect a fecal sample. At the end of the trapping session, all bats were identified to species, sexed, and aged (based on ossification of the epiphyseal cartilages of the fourth metacarpal-phalangeal joint, Kunz and Anthony 1982, Racey 1974). Females were assessed for reproductive condition. I detected pregnancy by noticeable abdominal swelling or by gently palpating the abdomen. Lactation was detected by expression of milk or bare patches and swelling around the nipples and post-lactation was indicated by hair starting to re-grow around the nipples (Hamilton 1996, Racey 1982). Hair re-growth is slow and would not be complete by the end of the summer trapping season, thus allowing late summer females to be classified as either non-reproductive or post-lactating. I weighed each individual in the cloth bag on an electronic balance (PT 600 Sartorius portable) to the nearest 0.1 grams. I measured ear length, tragus length, tail length, and forearm length (see Species Identification, Chapter 1). If the bat was a long-eared species, I assessed it for radio-tagging (see Chapter 3).

Diet Analysis

A fecal sample is the total amount of feces collected from one captured individual. Each sample consisted of one to many fecal pellets. I air dried the entire sample and then weighed it, and divided it into pellets of approximately equal size. I analyzed each sample one pellet at a time. All individual samples were coded such that I did not know the species the sample came from until I had analyzed all samples. In 1996, I randomly chose five individuals' samples from each of three species (*M. evotis*, *M. lucifugus* and *M. californicus*) and four individuals samples from *M. septentrionalis* for a total of 19 samples. I divided each individual's sample in half and analyzed one half immediately. The other half was stored. Once I finished analyzing fecal samples collected in the 1997 field season, I analyzed the stored half of the 19 samples from 1996. I compared the diet composition of the samples with paired t-tests to gauge the amount of change in my identification due to experience.

I loosened each fecal pellet in 50% ethanol to separate the insect remains. Under a dissecting microscope, I isolated and identified insect remains to Order. For each pellet, I visually estimated the percent volume composition of all insect Orders. Wing remains were the most diagnostic characteristic distinguishing between Orders. Lepidopterans were identified primarily by the presence of wing scales and secondarily by wing remains. Coleopterans were identified by the presence of hard orange cuticle remains as well as wing remains (M^{c}Aney et al. 1991, Whitaker 1989). I also estimated the proportion of "unknown" in each pellet based on the amount of insect remains which may have been diagnostic (small wing pieces for example) but were not conclusively identifiable. Once the entire fecal sample was examined, I pooled results of all pellets in the sample to calculate the diet composition for each individual bat. Data were arc sine square-root transformed (Zar 1984). I used multivariate analysis of variance (MANOVA) to compare diet composition between species.

I also calculated diet diversity of individuals using Levins' standardized niche-breadth index, B_A (Hamilton 1996, Hurlbert 1978, Levins 1968).

(Equation 2.1)

$$B = \frac{1}{\Sigma P_j^2}$$

where B = Levins' measure of niche-breadth

P_j = proportion of the diet that is of food type j.

(Equation 2.2)

$$B_A = \frac{B - 1}{n - 1}$$

where B_A = the standardized niche-breadth index

n = the number of possible resource states (the number of insect orders in the diet of all bats).

This method assigned each individual a niche-breadth index value between 0.0 and 1.0, where 1.0 refers to a diet which evenly incorporates all food types. I used ANOVA to compare dietary niche-breadth of species.

To assess prey availability, I initially collected insect samples using 37.5cm long sections of 10.5cm diameter PVC pipe coated with Tanglefoot ® insect adhesive (sticky traps). I chose sticky traps over light traps to obtain an unbiased sample of the flying insect fauna. Light traps sample primarily phototactic insects such as moths. Traps were set in one of the three previously mentioned habitat categories (water, canopy or edge) at approximately the same height as the mist nets. Traps were removed and insects counted after the two hour trapping session had ended. I also checked (visually) the insect traps after one hour and noted the number and order of insects caught at that point.

I also examined fecal samples collected in 1997 from 29 individual *Myotis* bats by A. Yu and S. McNalley in the Fort Nelson (B.C.) region (59° 00' N, 122° 50' W). This sample was treated in the same manner as the interior wet-belt samples I collected. A. Yu had analyzed the diets of *Myotis* bats caught in 1996 in Fort Nelson and found significant differences between the diets of gleaning and non-gleaning species (A. Yu pers. comm.). I analyzed samples collected from individuals of the Fort Nelson region to determine if my methodology could detect diet differences similar to those detected by A. Yu. Fecal analysis is an effective non-destructive method of estimating diet composition (Kunz and Whitaker 1983). However, visual estimation of diet composition is subjective, making it difficult to compare between observers. Thus, by analyzing samples collected from the same species in two distinct geographic locations, I could be confident that differences in diet composition I might find are not due to biases from interpretation of someone else's analysis. I used the same statistical tests for analysis of the Fort Nelson samples as I did for the interior wet-belt samples. I also compared niche-breadth and diet composition between species caught at the two geographic locations.

RESULTS

Netting effort and Bat Captures

I spent a total of 99 nights trapping (48 in 1996 and 51 in 1997). On 25 nights I was unable to trap due to heavy rain (10 in 1996 and 15 in 1997). In two years, I sampled for a total of 332 net-nights (166 in 1996, 166 in 1997). Trapping primarily occurred at the lower elevations along the Beaver River valley (in Glacier National Park), along the Illecillewaet River valley (which included Glacier and Mt. Revelstoke National Park), and in logged areas north of Revelstoke, including the Downie River valley and the Goldstream River valley. The most successful and most repeatedly sampled sites were in the Beaver valley at the Copperstein trail head (Glacier National Park), the Giant Cedars Boardwalk and the Skunk Cabbage Boardwalk (Mt. Revelstoke National Park) and along the French Creek road at small ponds between km 6 and km 7 (Goldstream River valley). A total of 58% of trapping time and 84% of all bat captures (n = 98) occurred in these locations (Fig. 2.1).

In 1996, I caught 64 bats on 25 nights while, in 1997, I caught 34 bats on 18 nights. On average 0.40 captures per net-night (1996) and 0.20 captures per net-night (1997) occurred. The majority of nights, and the majority of bats caught, were in the southern regions in and around Glacier and Mt. Revelstoke National Parks (Table 2.1). Of the eight species expected to be present, I caught six. Most commonly caught was the Little Brown Bat (*M. lucifugus*), followed (in order) by the Western Long-eared Bat

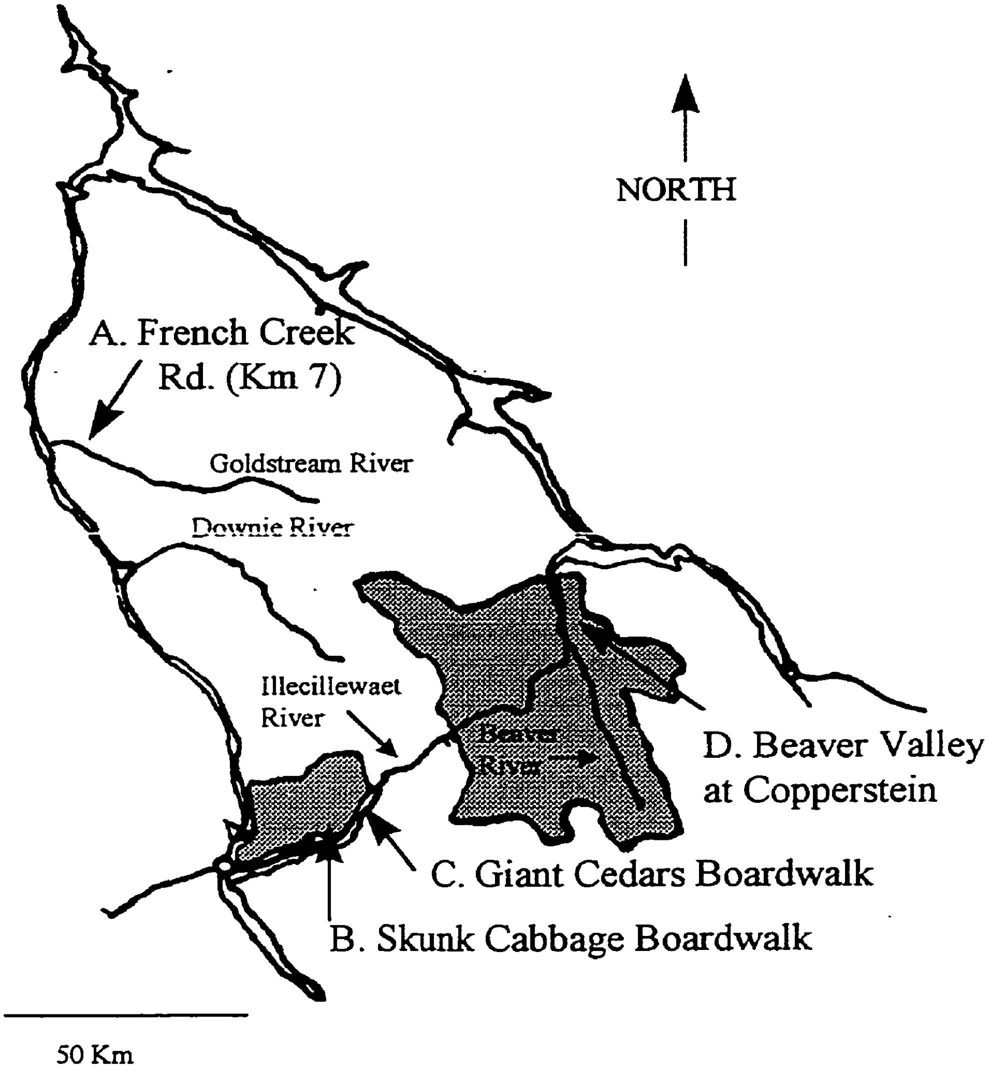


Figure 2.1. The four (A, B, C, and D) most successful trapping sites within the study area.

Table 2.1. The number and general geographic distribution of adult bats captured in the Columbia Basin area in 1996 and 1997. Parks refers to captures which occurred at sites within Glacier National Park or Mount Revelstoke National Park, Highway refers to captures which occurred at sites around the trans-Canada highway but not directly in the national parks and North refers to captures which occurred at sites in the logging regions north of the town of Revelstoke. n= the number of nights spent trapping in each of the three geographic areas. Individual trapping sites are given in Appendix 1.

Species	1996			1997			
	Parks n=30	Highway n=4	North n=14	Parks n=32	Highway n=8	North n=11	TOTAL
Myotis septentrionalis	11	1		3			**15**
M. evotis	10		6	3		8	**27**
M. lucifugus	6		10	8	4	2	**30**
M. californicus	15	1	1	2			**19**
M. volans	1			2		2	**5**
Lasionycteris noctivagans	2						**2**
TOTAL	**45**	**2**	**17**	**18**	**4**	**12**	**98**

(*M. evotis*), the California Bat (*M. californicus*), Northern Long-eared Bat (*M. septentrionalis*), the Long-Legged Bat (*M. volans*) and the Silver-haired Bat (*Lasionycteris noctivagans*, Table 2.2). The species not caught were the Hoary Bat (*Lasiurus cinereus*) and the Big Brown Bat (*Eptesicus fuscus*). This is not unexpected as these bats tend to forage high above the canopy (van Zyll de Jong 1985) and most of my trapping occurred at lower heights (a maximum of 5m off the ground). This may also partially explain the low capture incidence of *M. volans*, the Long-legged Bat, as it also tends to forage above the forest canopy (Saunders and Barclay 1992, van Zyll de Jong 1985).

Of all bat captures, 54 (55%) were females and only six (11%) of these were determined to be reproductive (Table 2.3). I first observed pregnancy on June 1 (1996) and July 22 (1997). Of the 54 females I captured, 22 were caught after June 1 (1996) and 13 after mid-June (1997), when I would expect pregnancy to be apparent (Barclay 1991, Racey 1982). Thus 17% of females caught when reproductive condition should have been visibly assessable, were reproductive. I did not catch any juveniles.

In 1996, captures of the sexes were not evenly distributed in time; more female bats were caught in the first two months of the summer and more males in the second two months ($\chi^2 = 7.82$, df=1, $p<0.02$). This skew did not occur in 1997; each sex was approximately equally represented in bat captures in both halves of the season ($\chi^2 = 1.84$, df=1, $p>0.05$).

I caught the *M. septentrionalis* (the Northern Long-eared Bat) at five sites in 1996 and two in 1997. In 1996, the sites were the Beaver River valley at the

Table 2.2. The number of adult male and female bats caught in the Columbia basin area in 1996 and 1997.

Species	1996		1997		**TOTAL**
	Male	Female	Male	Female	
M. septentrionalis	9	3	1*	2	**15**
M. evotis	7	9	6	5	**27**
M. lucifugus	9	7	2	12	**30**
M. californicus	6	11	2		**19**
M. volans	1			4	**5**
L. noctivagans	1	1			**2**

* The male *Myotis septentrionalis* caught in 1997 was a re-capture from 1996. Thus although 15 bats were caught in 1996 and 1997, only 14 different individual *M. septentrionalis* were caught.

Table 2.3. The total number of females caught in the Columbia Basin including the date, location, and condition of reproductive females caught.

Species	Total Females	Female (June+)[A]	No. Repro[B]	Condition[C]	Date	Location[D]
M. septentrionalis	5	5	1	P. Lact.	Aug 21, 97	R. Park
M. evotis	14	11	2	Preg. Preg.	Jun 1, 96 July 22, 96	R. Park R. Park
M. lucifugus	19	8	1	Preg.	July 22, 97	G. Park
M. californicus	11	7	1	Preg.	July 28, 96	G. Park
M. volans	4	4	1	Lact.	Jun 28, 97	North
L. noctivagans	1	0	0			
TOTAL	**54**	**35**	**6**			

[A] Females caught after detection of the first pregnant female (June 1, 1996) or after mid-June (1997), when pregnancy should be apparent (see results)

[B] Number of reproductive females

[C] Condition refers to reproductive condition where Preg. is pregnant, Lact. is lactating and P. Lact. is post-lactating

[D] Location refers to the general area where the female was caught. R. Park refers to captures in Mount Revelstoke National Park, G. Park is Glacier National Park and North is north of Revelstoke.

Copperstein trail head (Glacier National Park), Skunk Cabbage Boardwalk, Giant Cedars Boardwalk (both in Mt. Revelstoke National Park), a forest stand 300m east of the Giant Cedars Boardwalk, and a forest patch just west of the Jumping Creek Forest Service Road. In 1997, *M. septentrionalis* was found only in Mt. Revelstoke National Park at the two boardwalk trails (Fig. 2.2). In both 1996 and 1997, the same male *M. septentrionalis*, as identified by an arm band, was captured at the Skunk Cabbage boardwalk. This was the only recapture within or between years.

Myotis bats were captured in all habitat categories. Of the four commonly caught *Myotis* species, the majority (93%) of *M. lucifugus*, both in and out of the parks region, were caught over water (Table 2.4). *M. septentrionalis* was caught only in or near the parks and was generally (73%) caught under a tree canopy. In the parks, *M. evotis* was only caught under a canopy (100%). However, the majority (86%) of *M. evotis* captures outside the park occurred at a small (diameter <10m) pond along French Creek road. This pond was bordered on three sides by forest remnants and was separated from more continuous forest on the fourth side by a logging road. Finally, *M. californicus* was caught mostly along trails under a canopy (89%), especially at the Skunk Cabbage boardwalk.

Bat Activity

I examined bat activity in relation to temporal changes and habitat features. Habitat categories are "water", "canopy" and "edge" as defined earlier. All analysis of bat activity was performed with analysis of covariance (ANCOVA) using length of time

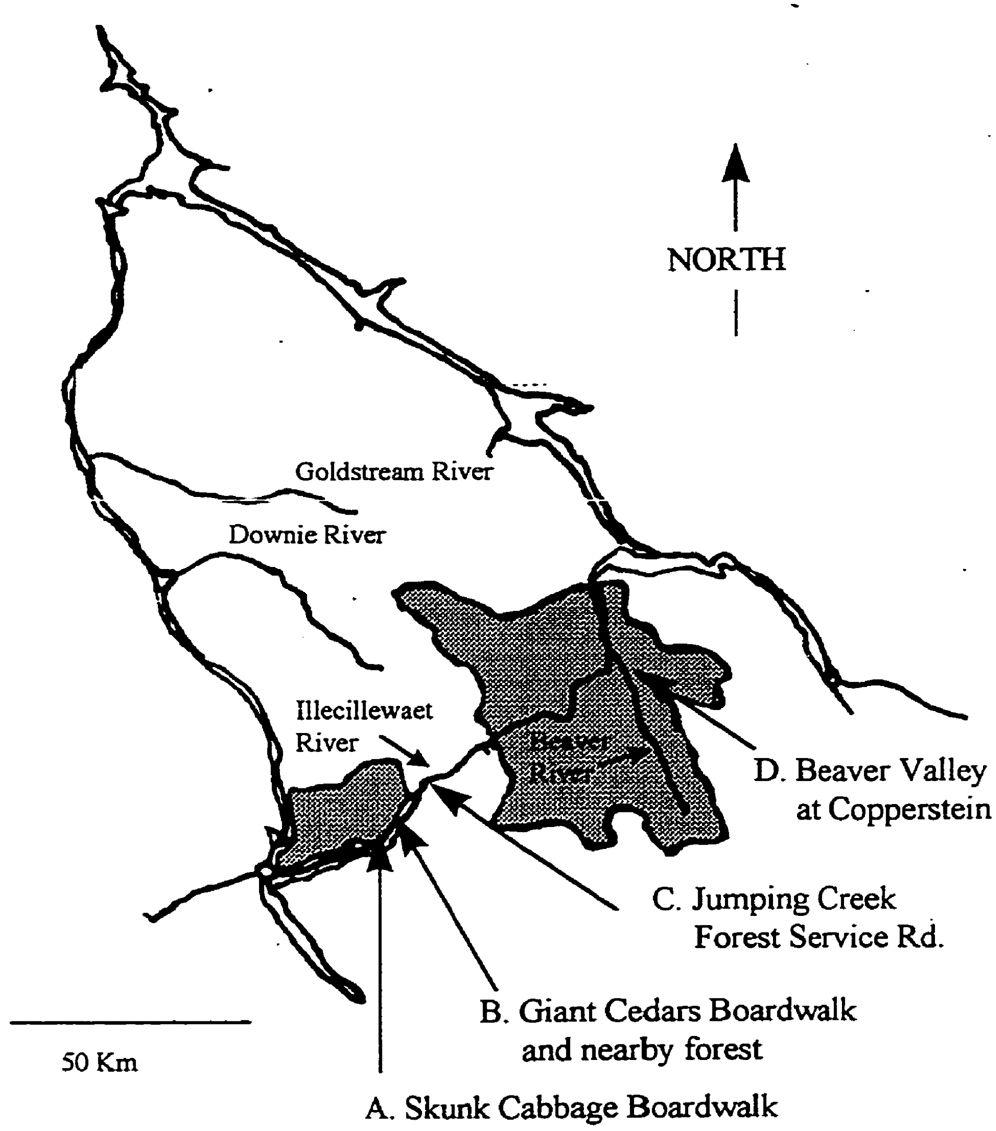


Figure 2.2. Sites (A, B, C, and D) where *M. septentrionalis* was caught in 1996 and 1997.

Table 2.4. Distribution of bat captures by habitat category for the four most commonly captured *Myotis* species. Parks, Highway and North include those sites listed in Appendix 1. Canopy captures are those which occurred under or at the edge of a forest canopy. Water captures occurred directly over open bodies of water.

Species	Parks and Highway		North	
	Canopy	Water	Canopy	Water
M. septentrionalis	11	4	0	0
M. evotis	13	0	2	12[B]
M. lucifugus	2	15	0	13
M. californicus	17[A]	1	0	1

[A] 10 *M. californicus* were captured at Skunk Cabbage Boardwalk on a trail through riparian willow scrub.

[B] These 12 *M. evotis* were all captured over a small pond at French Creek road.

monitoring as a covariate. Ambient temperature is often found to affect bat activity (Anthony et al. 1981, Vaughan et al.1997) and is generally used as a covariate. However, my preliminary analysis indicated that ambient temperature did not have significant effects on the amount of bat activity heard. In the wet-belt, temperature did not vary greatly over the night and the night-time low temperature was usually reached shortly after sunset (Table 2.5).

I sampled activity for two-hours on 133 separate occasions (two habitat categories sampled on the same night are considered separate occasions in this case) over 95 nights. In total, I heard 5173 bat passes over two seasons (3528 passes in 1996, 1645 in 1997). The maximum number of passes heard during a two-hour monitoring session was 317, the minimum was zero. Data were skewed as on 54 nights, or 102 monitoring sessions, less than 50 bat passes were heard over the entire monitoring period. Thus, prior to analysis, all activity data were log (x+1) transformed and tested for a normal distribution. The raw activity data is available with R. Barclay, University of Calgary, Department of Biological Sciences.

I examined the activity patterns of *Myotis* at three frequently sampled sites. These sites (Giant Cedars Boardwalk, Skunk Cabbage Boardwalk, Beaver valley at Copperstein) each had more than one habitat category monitored in one night. These sites were monitored on 41 nights, on 20 of which at least one bat was caught and at all sites there were at least three trapping nights when no bats were caught. Of all *Myotis* bat captures, 47% (45 of 96 captures) occurred at these sites. Most (37) of the captures

Table 2.5. Mean ambient temperature (°C) at sunset, one hour after sunset (at the middle of the first monitoring hour) and two hours after sunset (at the middle of the second monitoring hour) for all monitoring nights (n=95). Minimum and maximum recorded temperature is also shown.

Time of night	Mean temp. (°C) ± S.D.	Min. temp. (°C)	Max. temp. (°C)
Sunset	13.0 ± 2.8	7	20
1 hour post-sunset	11.8 ± 3.0	6	20
2 hours post-sunset	10.6 ± 2.9	4	18

occurred at Giant Cedars or Skunk Cabbage Boardwalk, under a canopy. Individuals of the four main *Myotis* species in the study area were caught at all these sites with the exception of *M. evotis* which was not caught at the Beaver valley site. I caught 14 *M. septentrionalis*, 11 *M. evotis*, 6 *M. lucifugus*, 13 *M. californicus* and 1 *M. volans* at these sites.

I performed a four-factor ANCOVA with site, habitat category, time of night (first hour, second hour) and day (nested within site as a random effect) as main effects. The use of day (as a way of controlling for seasonal and day-to-day variation) required a large number of degrees of freedom and thus, year and temperature could not be incorporated into the model. Similarly, all possible interactions could not be tested and I did not include higher order interactions. Lower order interactions (two-way) were sequentially removed from the model if not significant. The habitat categories at each site were edge and canopy at Giant Cedars, canopy and water at Skunk Cabbage, and edge and water at Beaver valley at Copperstein. The model explained a significant part of the variation in the number of passes heard ($F_{61,43}=3.35$, $r^2=0.83$, $p=0.0001$). There was no effect of habitat category or time of night on the amount of activity heard (Table 2.6). However, a drop in activity from first to second hour in "water" and "canopy" habitats occurred and an increase in activity in the "edge" habitat. There was a significant time of night by habitat category interaction (Table 2.6, Fig. 2.3). The "edge" analysis included data collected on only six nights. A day(nested in site) by habitat category interaction occurred suggesting that daily variation influences *Myotis* activity. This variation could be attributed to daily environmental (climatic) fluctuations, for

Table 2.6. Final ANCOVA model for the effects of habitat category and time of night on *Myotis* passes (log +1 transformed) heard at three sites (Skunk Cabbage, Giant Cedars and Beaver valley). Random effects were day(nested in site) and day(nested in site)*habitat category.

Source of variation	df	df (error)	F	P
Habitat category	2	21.95	0.86	NS
Time of night	1	43	2.48	NS
Site	2	50.11	0.40	NS
Day (nested in site)	34	19.23	1.24	NS
Day (nested in site)*habitat category	19	43	2.41	0.009
Time of night*habitat category	2	43	4.56	0.02
Duration of time spent monitoring (covariate)	1	43	0.14	NS

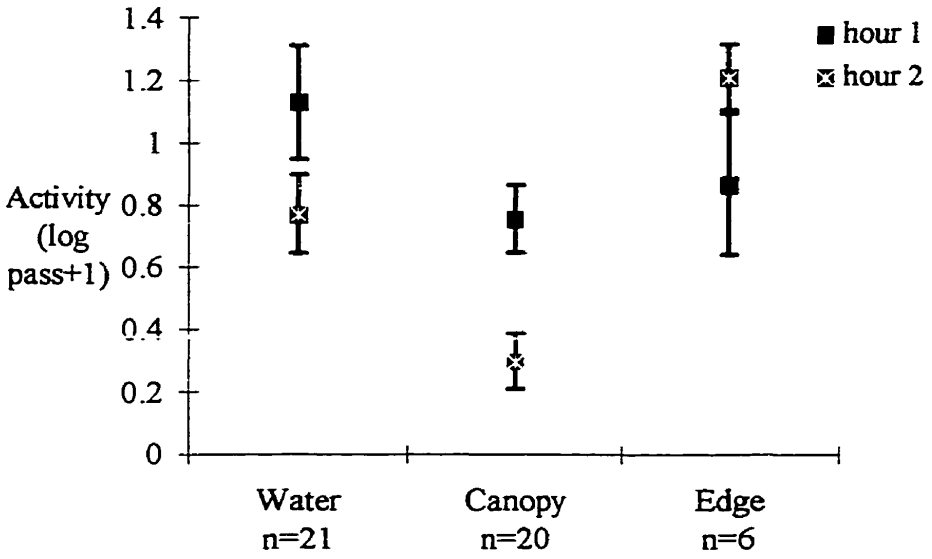


Figure 2.3. *Myotis* activity in three habitat categories for three selected locations. Beaver valley (water and edge habitat), Skunk Cabbage Boardwalk (water and canopy habitat) and Giant Cedars Boardwalk (canopy and edge habitat). Activity was measured in log (bat passes heard +1) ± S.E. Hour 1 and hour 2 refer to the first and second hour of monitoring starting one half hour after sunset. n refers to the number of sampling nights in each habitat category.

example.

I examined activity (passes) in other less frequently sampled sites, each of which contained only one habitat category and which was sampled on at least two separate nights. These sites (n = 14) tended to be less successful in terms of bat captures, particularly of long-eared species. A total of 20 bats, one of which was a long-eared species, *M. septentrionalis*, were caught at these sites (13 *M. lucifugus*, 5 *M. californicus* and 1 *M. volans*). I used a four-factor ANCOVA with habitat category, site (nested within habitat category as a random effect), date (nested within habitat category and site) and time of night, as the main effects. Interactions were tested and sequentially removed if not significant, starting with higher order interactions. Year was not included as all sites were not monitored in both years. The model explained a significant part of the variation in the number of passes heard ($F_{34,27} = 7.34$, $r^2 = 0.90$, $p = 0.0001$). This was attributable to a significant effect of habitat category (Table 2.7, Fig. 2.4), with the highest activity occurring over water and the lowest under canopy, and to time of night (Table 2.7, Fig. 2.4) with a drop in activity between the first and second hour in all habitat categories. Activity also differs among sites and among days (Table 2.7).

All species were not caught equally at all trapping sites. *M. lucifugus* was caught at the greatest number of different trapping sites and the long-eared species were found at the least number of different trapping sites (Table 2.8). At one trapping site, the Giant Cedars Boardwalk, 10 out of 15 *Myotis* bat captures were long-eared species. All bat captures occurred under the canopy. I performed a three-factor ANCOVA on

Table 2.7. Final ANCOVA model for the effects of habitat category and time of night on *Myotis* passes heard at many sites (n=14), each containing one habitat category. Site (nested in habitat category) was a random effect.

Source of variation	df	df (error)	MS	F	P
Habitat category	2	11.4	37.88	15.51	0.0006
Time of night	1	27	2.42	4.48	0.04
Site (nested in habitat category)	12	27	2.24	4.16	0.001
Day (nested in site and habitat category)	18	27	1.30	2.40	0.02
Duration of time spent monitoring (covariate)	1	27	4.58	8.49	0.007

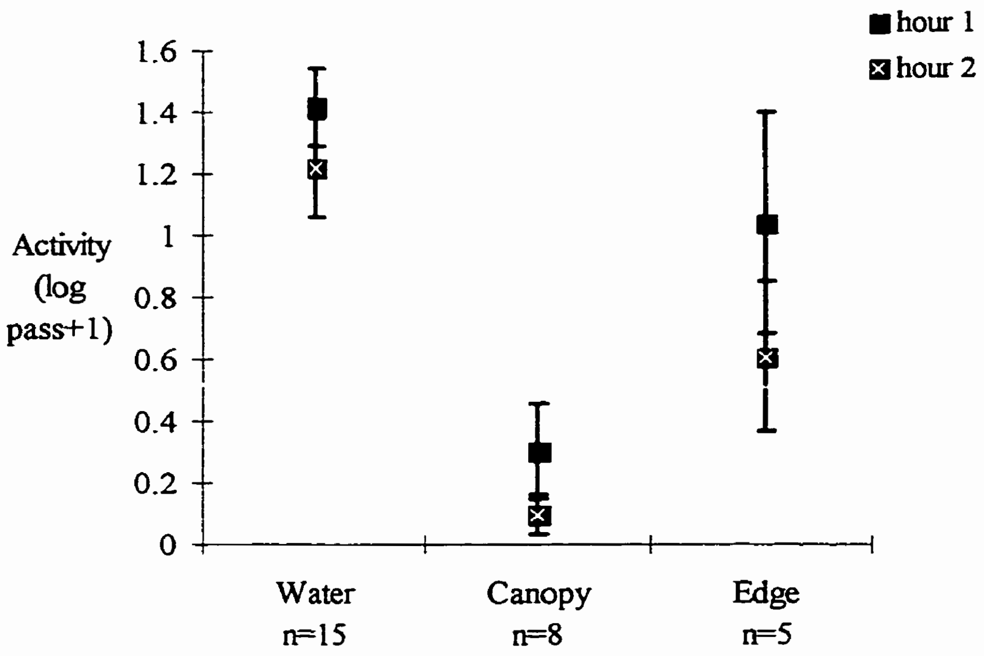


Figure 2.4. *Myotis* activity measured at many trapping sites each consisting of one habitat category. n refers to the number of nights spent sampling in each of the habitat categories. In total, 6 water sites, 5 canopy sites and 3 edge sites were used. Activity is measured in log (bat passes+1) ± S.E . Hour 1 and hour 2 refer to two consecutive hour-long monitoring periods starting at one half hour after sunset.

Table 2.8. The number of sites which contributed to captures of each of the *Myotis* species.

Species	No. sites	No. captured
M. septentrionalis	5	15
M. evotis	5	27
M. lucifugus	11	30
M. californicus	7	19
M. volans	5	5

the amount of activity I heard under the canopy. Time of night, season (early or late) and year were main effects. Non-significant interactions were removed sequentially beginning with the highest order interactions. Early season refers to activity heard in May and June, and late season is activity heard in July and August. Ambient temperature was used as a covariate as there were sufficient degrees of freedom. At this site (Giant Cedars Boardwalk), the model explained a significant part of the variation in the number of passes heard ($F_{5,17}$ =6.29, r^2 =0.65 p =0.001). There was a significant time of night effect on activity ($F_{1,17}$=14.18, p =0.002, Fig. 2.5) and a significant season effect ($F_{1,17}$=7.98, p =0.01). Activity in this location was almost zero in May and June but increased in July and August (Fig. 2.5). There was no effect of year ($F_{1,17}$= 2.11, p =0.17), ambient temperature ($F_{1,17}$ =1.00, p =0.33) or duration of time spent monitoring ($F_{1,17}$ =3.03, p =0.10). There were no significant interactions. This was the only site where I observed a seasonal effect on the amount of activity heard.

On average, the first *Myotis* bat was heard (by ultrasonic detector) 30 min (± 15min S.D., n = 95) after sunset (i.e. during twilight conditions). Radio-tagged *M. evotis* and *M. septentrionalis* (n = 10; see Chapter 3) left their roost from 60 min before sunset to 60 min after sunset ($\bar{x}$ = 15 minutes after sunset for n = 18 nights, or $\bar{x}$ = 28 minutes after sunset using average individual emergence times to calculate an overall average, n = 10 bats). Thus, although the first *Myotis* bat heard could not be identified to species, long-eared species are likely among those *Myotis* bats foraging as early as 30 minutes after sunset. There was no bat activity heard during the pre-dawn periods monitored by Anabat or hand held detector (n = 4).

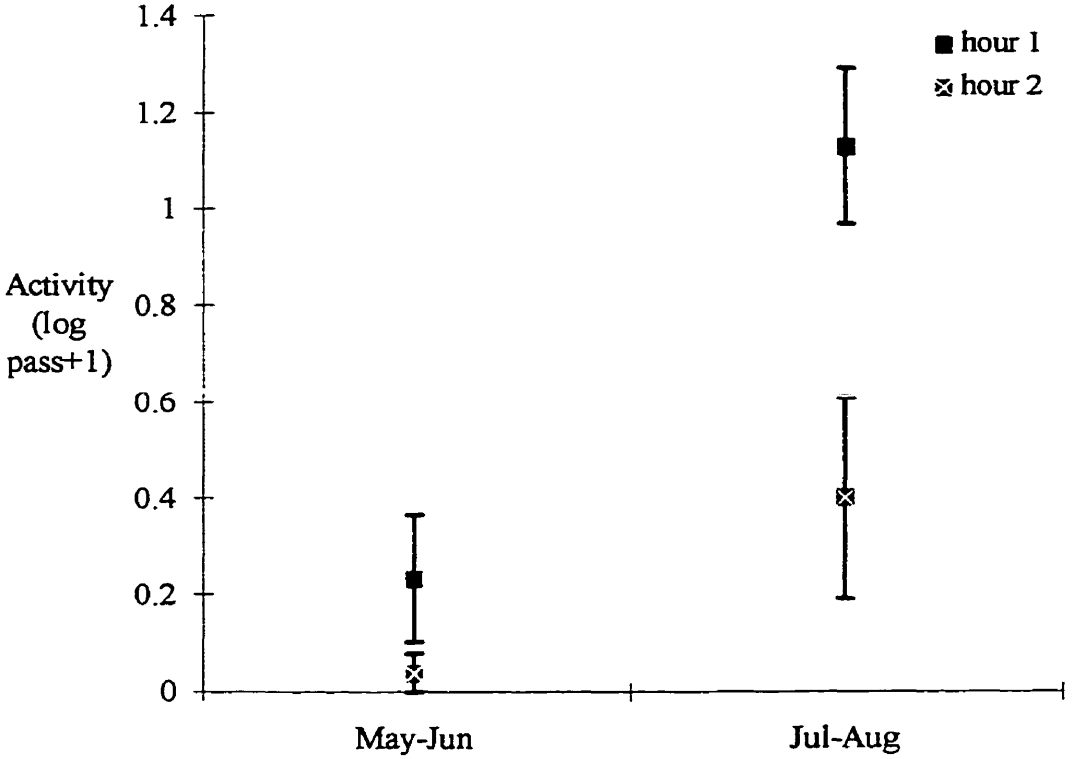


Figure 2.5. The numbers of passes heard under the canopy at Giant Cedars Boardwalk in 1996 and 1997. Passes are log+1 transformed and shown for both the first and second monitoring hour early in the season and late in the season. There is a significant increase of activity in July and August.

Diet

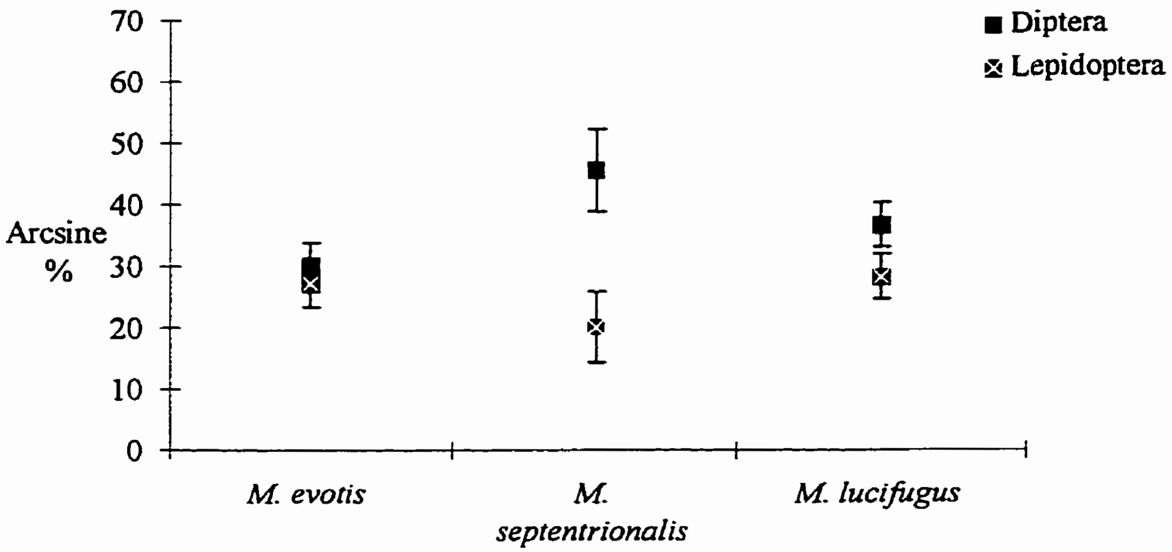
Insect trapping was relatively unsuccessful and an inefficient use of time. I set out 21 sticky traps (4 in edge habitat, 10 under a canopy and 7 over water) on 12 nights between 21 May and 15 July, 1997. A total of 19 insects were caught on six nights (9 traps). The other six nights yielded no insects. The majority of insect trapping time yielded no insects (12 out of 21 traps). By order, 15 Diptera (flies, primarily mosquitoes (Culicidae) and other unidentified insects with body lengths <3mm), 3 Lepidoptera (moths) and 1 Coleoptera (beetle) were caught. As a consequence of the low capture success, I did not continue insect trapping and can not compare insect abundance among habitats.

Analysis of a total of 82 fecal samples from four *Myotis* species (*M. septentrionalis, M. evotis, M. lucifugus,* and *M. californicus*) indicated that there were four major orders of insects that the bats of the wet-belt relied on: Lepidoptera (moths), Diptera (flies), Neuroptera (lace wings) and Coleoptera (beetles). Other orders of insect were rarely represented and only in samples from a few individuals. Of the four major orders, Lepidoptera and Diptera were proportionally the most commonly consumed. I performed a paired t-test on the proportion (arc sine square-root transformed) of Lepidoptera and the amount of Diptera found in 19 samples I had set aside for self-testing. The amount of Lepidoptera and Diptera found in an individual's fecal sample did not vary significantly between pellets I analyzed in 1996 and those analyzed in 1997 (Lepidoptera: $t = 0.95$, $df = 18$, $p = 0.36$; Diptera: $t = 0.55$, $df = 18$, $p = 0.59$).

I used a multivariate analysis of covariance (MANCOVA) to examine differences in arc sine square-root transformed proportion diet composition. The main effects used in the model were species, sex and year, as well as all interactions between effects. In this and all subsequent analyses, non-significant interactions were removed sequentially beginning with highest order interactions. Sample mass was used as a covariate in this and subsequent diet composition analyses. There were no significant differences in the diets of the four species (Wilks' lambda =0.818, $F_{12,190.8}=1.26$, p =0.25, n =82). There was no effect of sex, year or sample weight on diet and no interactive effects. I also repeated the analysis removing *M. californicus* as it is a smaller bat with a smaller jaw, potentially influencing diet simply due to morphology. Among the three similarly sized *Myotis* species, there was no difference in diet (Wilks' lambda =0.878, $F_{8,110}=0.92$, p =0.50, n =64). Again there were no sex, year, sample weight or interactive effects. Bats relied heavily on Lepidoptera and Diptera (over 55% of the fecal sample for all species). Thus, I examined species differences (excluding *M. californicus*) in the amount of Lepidoptera and Diptera consumed in two separate three-factor ANCOVA's with species, sex and year as main effects. The models were not significant (Lepidoptera: $F_{5,58}=0.83$, $r^2=0.07$, p =0.53, n =64; Diptera: $F_{5,58}=0.63$, $r^2=0.05$, p =0.68, n =64, Fig. 2.6a).

I analyzed fecal samples collected in the vicinity of Fort Nelson, British Columbia from three bat species, *M. lucifugus*, *M. evotis* and *M. septentrionalis*. I used species and sex as main effects in a MANCOVA. The small sample (n = 29) did not show significant variation in the amount of Lepidoptera, Diptera, Neuroptera and

2.6a. Interior wet-belt.



2.6b. Fort Nelson

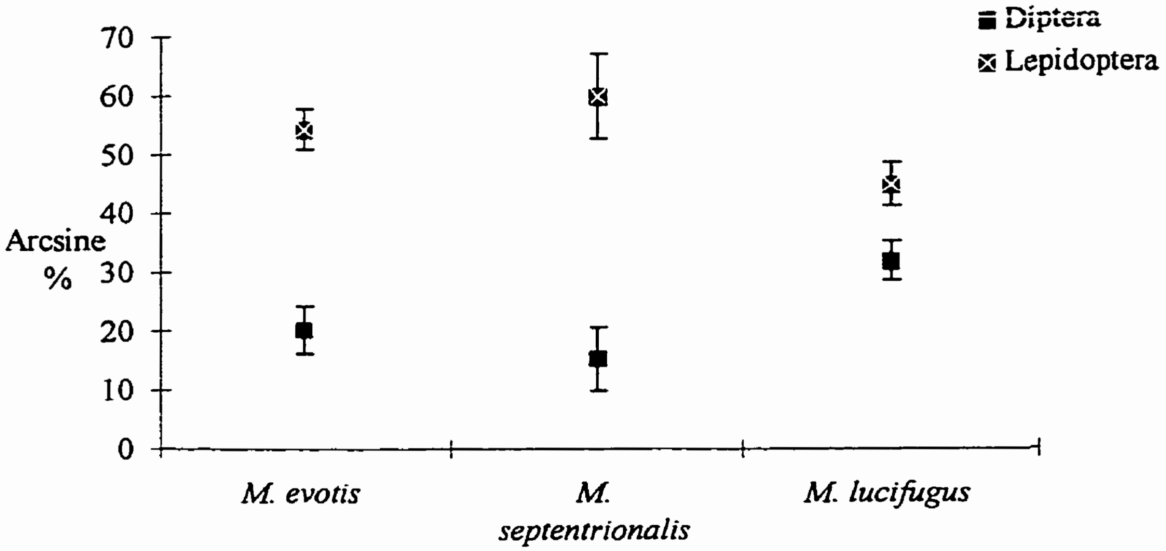


Figure 2.6. The proportion (arcsine square-root transformed % ± S.E.) of flies (Diptera) and moths (Lepidoptera) found in the diet of three species of *Myotis* (*M. evotis*, *M. septentrionalis* and *M. lucifugus*) in both the interior wet-belt study area (a) and in the Fort Nelson region (b). 23 *M. evotis*, 12 *M. septentrionalis* and 28 *M. lucifugus* samples were analyzed from the interior wet-belt and 9 *M. evotis*, 9 *M. septentrionalis* and 11 *M. lucifugus* samples from Fort Nelson.

Coleoptera ingested in one foraging session between the three species (Wilks' lambda =0.557, $F_{8,42}$=1.78, p =0.108). There were no sex or sample weight effects and no significant interactions. As in the interior wet-belt, the diet of all individuals was primarily composed of Lepidoptera and Diptera (over 75%) with other orders contributing relatively little. However, unlike the wet-belt, there was significant variation in the amount of Lepidoptera and Diptera consumed (Lepidoptera: $F_{4,24}$ =3.02, r^2 =0.33, p =0.04; Diptera: $F_{4,24}$=3.18, r^2 =0.35, p =0.03, Fig. 2.6b). These differences were attributable to species differences (Lepidoptera: $F_{2,24}$ =4.97, p =0.02; Diptera: $F_{2,24}$ =5.58, p =0.01, Fig. 2.6b). There was no effect of sex or sample weight and no significant interactions.

I compared the amount of Lepidoptera and Diptera consumed by individuals caught in the vicinity of Fort Nelson to those caught in the interior wet-belt. I performed two three-factor ANCOVA's with location of capture (Fort Nelson or interior wet-belt), species and sex as main effects to examine these differences. There were significant differences in the amount of Lepidoptera and Diptera consumed (Lepidoptera: $F_{5,87}$=9.61, r^2 =0.36, p =0.0001; Diptera: $F_{5,87}$=2.81, r^2 =0.14, p =0.021) which were attributed to differences between individuals caught at Fort Nelson versus those caught in the interior wet-belt (Lepidoptera: $F_{1,87}$=35.37, p =0.0001; Diptera $F_{1,87}$ =10.19, p =0.002). The long-eared species at Fort Nelson ate more Lepidoptera and fewer Diptera than the long-eared species in the interior wet-belt. There were no species, sex, sample weight or interactive effects.

I compared dietary niche-breadth using a two-factor ANOVA with species and sex as main effects. The dietary niche-breadth index did not vary significantly in the interior wet-belt ($F_{3,61}$ =0.12, r^2 =0.01, p =0.95) but did differ in Fort Nelson ($F_{3,25}$ =4.16, r^2 =0.33, p =0.016). The variation at Fort Nelson was due to differences between species ($F_{2,25}$ =5.58, p =0.01, Fig. 2.7) and there was no sex effect. Individual long-eared bats (at Fort Nelson) consumed mostly moth whereas *M. lucifugus* individuals consumed a greater variety of insect orders during a foraging session. Overall there was no difference in the diversity of the diet between bats of the same species found in the interior wet-belt as compared to those in the Fort Nelson region ($F_{3,90}$ =1.65, r^2 =0.05, p =0 18, two-factor ANOVA with location and species as main effects) although gleaning bats (*M. evotis* and *M. septentrionalis*) from the wet-belt tended to have more diverse diets than those of the same species caught at Fort Nelson (Fig. 2.7).

DISCUSSION

Capture Success

The bat population in the wet-belt appears to be small when compared to those found during surveys conducted in other habitats and biogeoclimatic zones of British Columbia and Alberta. In the Pend d'Oreille valley, near Nelson, B.C., 1.9 bats per net-night and 1.8 bats per net-night were caught in 1995 and 1996 respectively (for a total of 326 bats in two seasons, Vonhof 1997). In the dry interior of B.C. (Holroyd et al. 1994), capture success was 2 bats per net-night (484 bats in 76 trapping nights) and, in

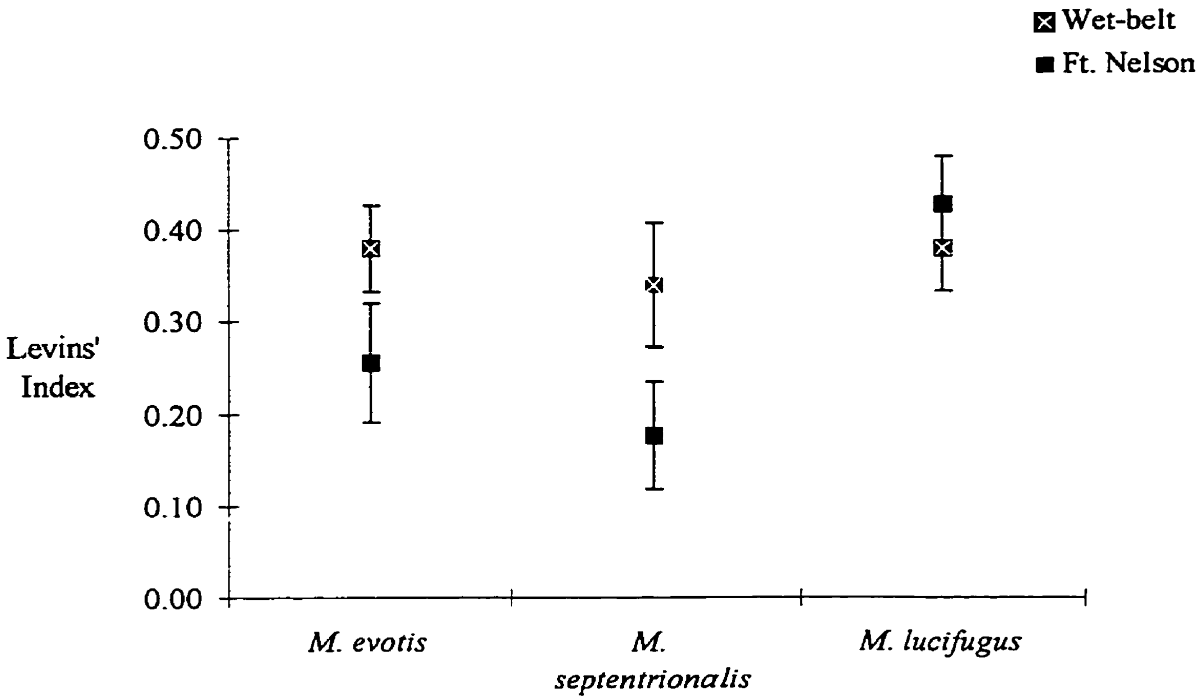


Figure 2.7. The diversity of diet of *Myotis* bats (± S.E.) as measured using Levins' standardized dietary niche-breadth index.

the Liard river region of Northern B.C. (Wilkinson et al. 1995), 80 bats were caught in 45 trapping nights (net-nights not given). Finally, in the Kananaskis valley of Alberta, 417 *M. evotis* and *M. lucifugus* were caught over the summers of 1985-1988 (Barclay 1991).

The Columbia basin, including the region where my study was based, was surveyed in 1993 (Holroyd 1993). The capture success reported was 0.38 bats per net-night, similar to my success in 1996, and higher than my success in 1997. That same year, the Columbia valley south of Golden was surveyed and had a success of 0.65 bats per net-night.

It is evident that the study area within the interior wet-belt has a relatively low capture rate, which suggests a small summer bat population when compared to other western Canadian habitats and biogeoclimatic zones. The interior wet-belt is distinct from other surveyed regions in that it experiences both cold over-night temperatures, similar to most mountainous zones (Barclay 1991), and high summer rainfall. The low numbers of insects I caught suggests that nocturnal, flying insects are not abundant in the wet-belt. The abundance of flying insects is greatly reduced by cold and rain (Williams 1961). This in turn contributes to fewer foraging opportunities for bats (Barclay 1991, Kunz 1973, Rydell 1992). The combination of these factors likely contributes to the comparatively small bat population in the study area, as has been suggested for the Cascade mountains (Thomas 1988).

Reproduction

I examined the population structure of the interior wet-belt *Myotis* to address my hypothesis of proportionally more long-eared bats being reproductive. The proportion of reproductive females I found was lower than that reported for other habitats and biogeoclimatic zones. In the dry interior, approximately 50% of all females were known to be reproductive (Holroyd et al. 1994). In the Liard river area, 63% (33 out of 52) of females were reproductive (Wilkinson et al. 1995), while in the Kananaskis valley, 30.5% of *M. evotis* females were reproductive (Barclay 1991). However, combining 1996 and 1997 data, I found only 11% of captured adult females were reproductive. Unlike the results in Kananaskis and contrary to my predictions, I found no difference between gleaners and non-gleaners in the proportion of reproductive females.

Cold and wet climatic conditions diminish the abundance of flying insects (Williams 1961) and increase the cost of maintaining a constant body temperature (Kurta 1986). These conditions make torpor more energetically favourable, at the cost to reproductive females of slowing fetal development and decreasing milk production (Audet and Fenton 1988, Racey 1982, Racey and Swift 1981). Lower temperatures or high rainfall have been correlated with delayed parturition and a lower proportion of reproductive females (Grindal et al. 1992, Lewis 1993). I suggest that the cold and rainy conditions of the interior wet-belt reduce foraging opportunities such that neither gleaning nor non-gleaning females can meet the high energetic requirements of reproduction.

An alternative explanation for the low reproductive rate of bats in my study area could be that the conditions of the previous season may affect a female's ability to reproduce in the current season. If males experienced poor summer conditions, they may not have been able to undergo spermatogenesis. However, a minimum of one healthy male is required to fertilize many females. At the hibernacula, individuals from many summer ranges gather (Barbour and Davis 1969), and it seems unlikely that all the males swarming at one hibernaculum experience poor summer conditions. The over-winter cost of storing sperm for a female is low, and the major costs of reproduction occur during late pregnancy and lactation. Thus it is likely, as has been suggested by Grindal et al. (1992) and Lewis (1993), that the female's decision whether or not to reproduce is based upon the current season's climatic conditions and occurs during pregnancy.

Habitat use

I predicted spatial and temporal partitioning of foraging habitat between the two foraging guilds. In the study area, four sites (Skunk Cabbage boardwalk, Giant Cedars boardwalk, Beaver valley at Copperstein trail and French Creek road) harboured most of the bat activity in the study area and were the most successful sites in terms of bat captures. Other sites that I monitored had low detection rates and either no bat captures or captures of primarily *M. lucifugus*. Although *M. lucifugus* and *M. evotis* were captured most often in both years, *M. lucifugus* was caught at many sites whereas *M. evotis* was caught at few sites and appears to be more patchily distributed within the study area. Localized distribution also appears to be the case for *M. septentrionalis*, although it was less common than *M. lucifugus* and *M. evotis*.

At three of the most successful capture sites with more than one habitat category (water, canopy or edge), activity among habitat categories did not differ significantly. Unlike in previous studies (Barclay 1991, Crampton 1995, Ekman and deJong 1996, Thomas 1988), "canopy" had comparable activity to water and edge habitat. There was a decrease in activity over the first two hours after sunset at these three locations (for activity measured over water or under a canopy), suggesting that *Myotis* bats using these sites forage only for a short time. All *Myotis* species were caught at these sites: *M. lucifugus* primarily over water and the long-eared species under a canopy. Thus, while echolocation monitoring could not reveal spatial partitioning among the species, the capture data suggest that there is spatial partitioning within a small (<200m between habitat types) area.

At the less frequently sampled locations, I did not capture any bats or the bats captured were not a long-eared species (with one exception). *M. lucifugus* was captured over water at these sites as in other studies (Barclay 1991, Fenton and Bell 1979, Saunders and Barclay 1992). My analysis of these sites showed significantly greater bat activity over water than under a canopy or at an edge. It appears that bodies of water attract more bat activity (Barclay 1991, Vaughan et al. 1997) and this is likely due primarily to activity of *M. lucifugus*. There was little activity under the canopy and intermediate activity at forest edges. This pattern is similar to the findings of other studies investigating forest bat activity (Barclay 1991, Crampton 1995, Ekman and deJong 1996) and mirrors the distribution of insect abundance in a forest (Barclay 1991, Ekman and deJong 1996, Racey and Swift 1985). There was a significant time of night effect at these sites with activity decreasing between the two one-hour sampling periods.

Captures suggest that long-eared bat species are found more often under a canopy. However, not all forest sites were equally active and only a few forest sites harbored *Myotis* bat activity. Bodies of water throughout the study area, however, appeared to consistently attract *Myotis* bats. Captures suggest specifically that *Myotis lucifugus* was active around open bodies of water. Thus the lack of an effect of habitat category on *Myotis* activity in the most active sites could be attributed to many *Myotis* species being present, but partitioned into the various habitats. In the sites I sampled less frequently few bats were present, except for *Myotis lucifugus*, and I suggest that the differences in activity between habitats could have been due to *M. lucifugus* foraging over water and the lack of gleaners under the canopy.

A striking aspect of the data is the high activity seen under the canopy at two sites (Giant Cedars Boardwalk and Skunk Cabbage Boardwalk) and little canopy activity at other sites. At the two active sites, I measured activity along wide (1 - 2m) boardwalks, which were not present in other canopy sites. At Skunk Cabbage, the development of these boardwalks involved the removal of dense willow bush and the creation of a clear flyway. It could be that the bats use the trail to travel along and thus there is an apparent increase in activity (see also Barclay 1991). At Giant Cedars the trees in the mature cedar-hemlock forest are widely spaced with little understory clutter for a bat to maneuver through and thus the boardwalks do not create an obvious flyway.

This forest patch appeared structurally similar to other canopy sites investigated (except for the presence of the boardwalk). It is possible Giant Cedars contained suitable roosting sites which attracted bats. However, no roosts near the boardwalk were found (Chapter 3). Cedar-hemlock forest 500-700m away from the boardwalk was used for roosting by a *M. septentrionalis* female (see Chapter 3), but activity levels in that forest were low (mostly zero). Giant Cedars also contains small streams and still pools of water which appear to attract long-eared bats (Fenton et al. 1983, van Zyll de Jong et al. 1980). However, at least one other canopy site monitored also had small still pools of water and only one bat pass was heard. The majority of bats captured at Giant Cedars were long-eared and their presence is well documented (Fenton et al. 1983, Holroyd 1993, Rasheed and Holroyd 1995, van Zyll de Jong et al. 1980, M. Vonhof pers. comm.). However, what makes Giant Cedars boardwalk attractive to long-eared bats is not clear.

In my study, *Myotis* bats of both foraging guilds emerged early and foraged for a short period early in the night. This is the typical pattern of activity expected for strict aerial hawking species (Rydell et al. 1996, Swift 1980, Taylor and O'Neill 1988). This pattern was also apparent at Giant Cedars, a site primarily used by long-eared species, contrary to my prediction of temporal partitioning. Long-eared *Myotis* may be roosting at Giant Cedars and the early bat activity may be linked to roost emergence. However, roost emergence occurred early (within 28 min after sunset, see Chapter 3), unlike previous studies of gleaning bats (Entwistle et al. 1996, Jones and Rydell 1994, Rydell et al. 1996). Overnight monitoring in very active sites, where all *Myotis* species were caught (French Creek road and Skunk Cabbage boardwalk), indicated that activity does diminish shortly after sunset and does not reoccur before sunrise. Thus, it appears long-eared bats emerge early and forage for a brief post-sunset period, as occurs for aerial hawking *Myotis* bats. As the majority of the population is non-reproductive, it is possible that short foraging periods, coupled with torpor, is enough to meet both gleaning and non-gleaning bats' energetic requirements.

Diet

The diet of the *Myotis* bats of the interior wet-belt did not vary significantly among species. This is contrary to my prediction that, between morphologically similar species, gleaning species will tend to have a distinct diet from non-gleaning species (Barclay 1991). When I analyzed fecal samples from bats in the Fort Nelson region, I found gleaning species ate more Lepidoptera (moths) and less Diptera (flies) than non-gleaning species. In 1996, A. Yu analyzed the diets of 18 individuals also from Fort Nelson. She found a significant difference in the diets of the gleaners (*M. evotis* and *M. septentrionalis*) and non-gleaners (*M. lucifugus*), again with gleaning bats eating more lepidopterans and fewer dipterans (A. Yu pers. comm.). I found gleaning species in Fort Nelson had less diverse diets (relied on fewer insect orders) than non-gleaners; this did not occur in the interior wet-belt. The climate of the interior wet-belt would lead to lower insect abundance (Williams 1961). Foraging theory predicts that at times of food scarcity, individuals (e.g. gleaning wet-belt bats) have more generalist diets (Perry and Pianka 1997) and incorporate more food items (e.g. insect orders) in their diets.

The expected diet differences were not found because, unlike many other studies of temperate gleaning bats (Barclay 1991, Fenton and Bell 1979, Rydell et al. 1996, Swift and Racey 1983), the long-eared species did not rely heavily on Lepidoptera (moth). Moths made up under 30% of the long-eared diet in the interior wet-belt but over 60% of long-eared diets at Fort Nelson. Similarily, Barclay (1991) found moth made up 60% of *M. evotis* diets, and Yu (pers. comm.) found the diet of *M. septentrionalis* and *M. evotis* was 51% moth. Moths have a night-time activity peak later than other flying insects (Rydell et al. 1996). However, the long-eared bats in the interior wet-belt emerge as early as aerial hawking bats and thus may not be encountering moth activity peaks. The lower use of moths may also reflect a lower moth abundance in the interior wet-belt (although this was not examined).

Diet differences between species of bats have been attributed to temporal and spatial separation of gleaning bats from non-gleaning bats (Barclay 1991, Entwistle et al. 1996, Jones and Rydell 1994), as well as sensory system adaptations (Entwistle et al. 1996, Faure and Barclay 1992, Faure et al. 1993). Gleaning bats forage later than non-gleaning bats and prefer proximity to wooded habitat for foraging. Although there was little evidence of temporal partitioning between foraging guilds in the interior wet-belt, there was some spatial partitioning, as *M. lucifugus* was caught primarily over water and long-eared species were caught under or near a canopy. At the most successful bat capture sites, all species were present, partitioned into habitat types found in close proximity. Insects can be distributed patchily and bats opportunistically use aggregations of prey (Arlettaz 1996, de Jong 1994, Krull et al. 1991, Racey and Swift

1985). Thus, the sites with the highest capture rates could have the most abundant prey. The proximity of the habitat types, coupled with the lack of temporal separation, could result in all species sharing a similar insect fauna without competition (Rydell 1992).

The climate of the interior wet-belt could be contributing to the lack of diet differences between the two guilds in another way. Gleaning is thought to be an advantage in colder temperatures (Barclay 1991), but may not necessarily be so in wet conditions. During rain, insects may be hidden under foliage or the sound of raindrops on foliage may interfere with the ability of a gleaner to hear insects moving (Entwistle et al. 1996). Furthermore, a forest canopy collects water during a rainfall and continues to drop water from the canopy to the forest floor after the rainfall has ended. Thus, if gleaners rely on insects under a canopy, they could still be at a disadvantage immediately after a rainfall whereas aerial hawkers using more open habitat could forage. In the interior wet-belt short sudden rainstorms are common. It is possible that the long-eared bats of the region rely as much or more on aerial hawking as they do on gleaning for foraging because of the variable conditions they may encounter in each foraging bout. Therefore, gleaning bats of the interior wet-belt may often aerial hawk, and thus may depend on early peaks of flying insects and may occasionally forage in the same spatial location as strict aerial hawkers. The proximity of canopy and open habitats at the highly successful capture sites may facilitate a gleaner's ability to mix strategies as gleaners are flexible in their foraging behaviour (Arlettaz 1996, Krull et al. 1991).

Population Dynamics and Marginal Habitat

I suggest that the foraging and reproductive decisions of *Myotis* bats in the interior wet-belt are a reflection of low prey availability. Long-eared bats foraged at the same time as strict aerial hawking bats and were frequently caught at sites which all *Myotis* species used. These sites generally have a variety of foraging habitat within close proximity, perhaps making it easier for gleaning bats to switch between hawking and gleaning foraging strategies. The lack of temporal separation between guilds and the possibility of gleaners mixing strategies was reflected in the lack of diet differences between gleaning and non-gleaning bats. However, the proportion of reproductive females in the interior wet-belt was low and, despite the advantages gleaners were presumed to have, there was no difference in the proportion of reproductive females between guilds. Thus the question remains, why are bats, and especially *M. septentrionalis* using what appears to be marginal summer habitat?

I propose two hypotheses for the use of the interior wet-belt by *Myotis* bats. Firstly, non-reproductive bats may select cool environments to facilitate the use of torpor (Barclay 1991, Hamilton and Barclay 1994, Thomas 1988). If a female bat is old, young or otherwise unable to breed in a particular season, she may choose a summer home range with low ambient temperatures over a warm home range. Competition among females has been suggested to result in deferred reproduction in young females (Rydell 1993). Thus, marginal habitats with small non-reproductive populations may result in less competition and could act as refuges for non-reproducing individuals. This may result in more seasonal movement of individuals in and out of such areas although both male and female bats are thought to be highly philopatric (Barclay 1991, Palmeirim and Rodrigues 1995). Only one bat recapture between years occurred (although the interior wet-belt bat population is probably small) making it difficult to assess the annual fidelity the bats show to the wet-belt. Similar areas with low reproductive rates are often dominated by males, as they too can use torpor regularly (Barclay 1991, Thomas 1988). However, I captured approximately equal numbers of males and females in the interior wet-belt.

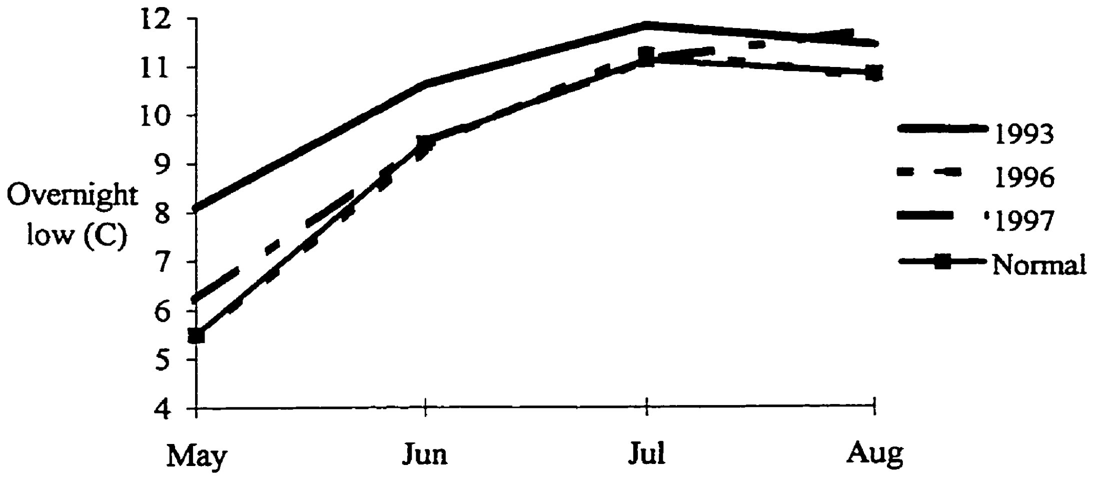
The suggestion that bats move from one home range to another depending on whether they reproduce in a particular year implies habitat suitable for reproductive bats is reasonably close to marginal habitats. Thomas (1988) found reproductive populations were within 100 km of non-reproductive populations, and maternity colonies of *M. lucifugus*, a species with non-reproductive bats in the Kananaskis valley (Barclay 1991), are located in the nearby prairies (<200 km, Schowalter et al. 1979). In the interior wet-belt, the closest known reproducing populations of *M. lucifugus*, *M. evotis* and *M. californicus* are in the Columbia valley south of Golden (<200 km south of my study area, Holroyd 1993), in the dry interior (~200 km west of study area, Holroyd et al. 1994) or in the Pend d'Oreille valley (~200 km south of study area, Vonhof 1997). Bats can travel on average, 200-300 km between hibernation sites and summer home ranges (Barbour and Davis 1969). There is no known reproducing population of *M. septentrionalis* within 300 km, although reproductive *M. septentrionalis* have been found in the Liard watershed, >900 km north of the study area (Wilkinson et al. 1995, Wilkinson pers. comm.) and hibernating (unknown reproductive status) at Cadomin Caves, Alberta (approximately 240 km north-east of Revelstoke, van Zyll de Jong et al. 1980). At present however, the population of *M. septentrionalis* in the interior wet-belt appears to be isolated and thus its population dynamics and viability are especially interesting.

A second hypothesis is that the bats of the interior wet-belt could rarely reproduce and form a sink population. Sink populations are those in which mortality is greater than reproductive output and the population requires immigration to be maintained (Dias 1996, Pulliam 1988). This would imply that the bats do reproduce when conditions are favourable but that reproduction may or may not be often enough to maintain the population. *Myotis* bats normally have only one young a year (van Zyll de Jong 1985), and have a long lifespan (Keen and Hitchcock 1980, van Zyll de Jong 1985). Thus, foregoing reproduction for one or two seasons may be the optimal strategy for an individual if conditions are poor, and may not have long-term consequences on population viability. However, if reproduction does not balance mortality, the population will display sink dynamics.

Holroyd (1993), working in my study area, captured 21 adult female bats, of which 17 (81%) were reproductive. The majority of the reproductive females were *M. septentrionalis* caught in Mount Revelstoke National Park (10 females); three reproductive *M. lucifugus*, three *M. californicus* and one *M. volans* were also caught. In that year, however, overnight temperatures were warmer than normal, especially during the spring (Fig. 2.8a). Summer rainfall was not abnormal (Fig. 2.8b). In contrast, conditions during my study (1996, 1997) were normal (Fig. 2.8). Studies of insect activity have shown that a few degrees of temperature change can have a strong influence on activity (Taylor 1963). Temperate bat activity is thought to be greatly reduced by temperatures below 10°C (e.g. Anthony et al. 1981, Rydell 1992). In northern Sweden, bat activity diminished between temperatures of 10°C and 6°C and did not occur at all below 6°C (Rydell 1989, Rydell 1992). In 1993, the springtime overnight lows were approximately 3°C above normal, and were above 6°C (May) and 10°C (June). Thus, the warmer overnight temperatures experienced in 1993 could have resulted in a higher abundance of flying insects or a longer peak of flying insect activity per night. This would lead to more foraging opportunities (either more nights with abundant insect activity or longer night-time insect activity) and thus could have allowed a higher proportion of reproductive females in that season.

Keen and Hitchcock (1980) calculated the annual survival rate of female *M. lucifugus*, irrespective of age, to be 0.71. There have been no studies separating the over-winter survival of juveniles from adults. Records suggest all the studied *Myotis* have similar longevity (Barbour and Davis 1969) and thus I will use this value as representative for all *Myotis* species. At the start of the reproductive season (year 1), the bat population will be $0.71N_0$ where N_0 is the original female population size at year 0. For the population to be maintained, a proportion of the $0.71N_0$ females must reproduce so that the population is at pre-hibernation level (N_0) after reproduction.

2.8a. Overnight temperature



2.8b. Monthly precipitation (Ppt)

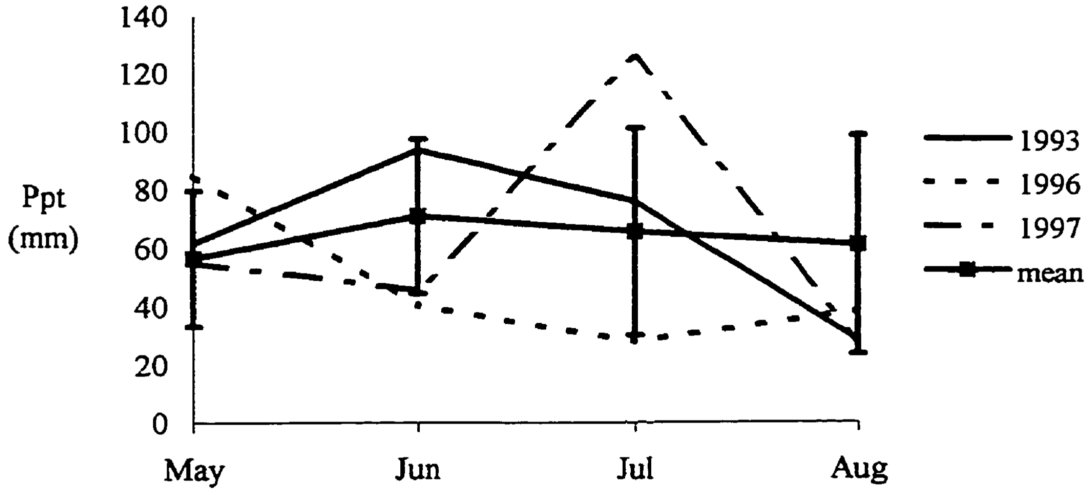


Figure 2.8. The monthly mean overnight low temperature (°C) and the monthly precipitation (mm) at Revelstoke, B.C. for 1993, 1996 and 1997. Figure 2.8a shows the normal temperature as calculated from 1970-1990 (provided by Environment Canada). Figure 2.8b includes the mean precipitation (± S.D.) from 1970-1990.

(Equation 2.3) $$0.71N_0 + X(0.71N_0) = N_0$$

where N_0 = population of females at year 0

0.71 is the annual survival of juveniles and females

X = the proportion of females which reproduce (assuming all offspring are female)

Solving for X, we find an average of 0.41 females must reproduce (and have female offspring) for the population to be self-sustaining. If half the offspring are male, then 0.8 of all adult females must reproduce every year.

As 1996 and 1997 appear to be climatically normal years, I expect the proportion of female *Myotis* normally reproducing in the interior wet-belt is up to 0.17. In a climatically "good" year (1993), the proportion of reproductive females was 0.81 (Holroyd 1993). Thus the interior wet-belt population is likely not self-sustaining and would become extinct without immigration. "Good" years would need to be the norm in order for the population to be maintained. However, the occurrence of warm spring temperatures is rare.

Other surveys in the study area have found reproductive (lactating and post-lactating) long-eared bats at Giant Cedars (Fenton et al. 1983, van Zyll de Jong 1980, M. Vonhof pers. comm.). However, these surveys all occurred in late summer and do not clearly demonstrate whether bats were present at the site for the entire season (although see van Zyll de Jong et al. 1980). My study represents the first full summer investigation of the bats of the region. I found the activity under the canopy at Giant Cedars boardwalk showed a marked change between early and late summer in 1996 and 1997. It appears as if the bats move into Giant Cedars only in the late summer. These bats may have moved a short distance from forest around Giant Cedars or may be migrating from another home range to hibernacula. Whether this pattern is common or only occurred in 1996 and 1997 is unknown.

In 1996, I caught significantly more females earlier in the summer than later. Reproductive females may arrive at a summer home range early to establish maternity colonies (Barclay 1984, Davis and Hitchcock 1965). If females find the climatic conditions are not suitable for reproduction, some may choose to move to another, unknown breeding home range. However, there is no documented movement between summer home ranges of female bats, rather females are considered to be highly philopatric (Barclay 1991, Fenton and Barclay 1980, Palmeirim and Rodrigues 1995). There was little reproduction in the study area in 1996. In 1997 there was no sex bias in the distribution of bat captures and there was an overall drop (approximately 50%) in capture rate. If reproduction normally does occur in the study area, the low reproduction in 1996 could have affected the 1997 population size. However, as 1996 and 1997 were climatically "normal" years, it is unlikely reproduction is common in the interior wet-belt.

Thus, I suggest that the interior wet-belt *Myotis* populations display sink dynamics. However, regarding *M. septentrionalis*, no nearby reproducing population which can act as a source to maintain the population is known. Knowing the frequency of reproduction in the study area would allow for a more accurate assessment of the viability of the interior wet-belt population. More summer-long surveys of the study area (especially the National Parks) would address this as well as confirming the fidelity of bats to the interior wet-belt and clarifying the causes of seasonal variation in activity.

CHAPTER THREE

Roosting behaviour of long-eared *Myotis* species in the interior wet-belt, B.C.

INTRODUCTION

Choice of summer day-roosts by bats has consequences for survival and successful reproduction (Kunz 1982). Roosts which maintain a relatively constant temperature and humidity minimize energetic costs to bats. Moreover, fetal development and juvenile growth is delayed in colder roosts, especially if a female bat relies heavily on torpor (Barclay 1982, Kunz 1982, Racey and Swift 1981). The microclimate of a cavity is important in determining its suitability as a roost. There is a considerable literature on bats roosting in man-made structures and caves in temperate climates (e.g. Brigham and Fenton 1986, Hamilton and Barclay 1994, Kunz 1982, Lewis 1995, Vaughan and O'Shea 1976). However, relatively few studies on roost selection in forest-dwelling bats have occurred (Betts 1996, Brigham et al. 1997, Crampton 1995, Lunney et al. 1988, Sasse and Pekins 1996, Taylor and Savva 1988, Vonhof and Barclay 1996).

A pattern of tree-roost selection is emerging from recent studies of forest bats. Roosts located in trees of great height or diameter, containing cavities which may be above the forest canopy, and having uncluttered entrances are preferred (Betts 1996, Brigham et al. 1997, Crampton 1995, Sasse and Pekins 1996, Taylor and Savva 1988, Vonhof and Barclay 1996). These types of roosts may be exposed to more solar radiation and may be spacious enough to hold more than one bat; clustering is another manner in which bats can regulate roost temperature (Kurta 1986). Large trees are also easier to find which could be important as individuals frequently (sometimes daily) switch between roost sites (Kunz 1982, Lewis 1995, Vonhof 1995). Travel time between foraging and roosting sites and between different roost trees could also affect bats' selection of roosting areas.

Standing dead or live but injured trees with cavities, cracks or bark peeling in large sheets are commonly selected by bats for roost trees. These types of trees are more often found in older forest stands (Cline et al. 1980, Tyrrell and Crow 1994) suggesting that forest age is also important for bats (Crampton 1995, Gellman and Zielinski 1996, Taylor and Savva 1988). Competition for suitable roost sites may affect bat diversity and distribution within managed forests (Perkins 1996). Thus, many of the recent studies of forest-dwelling bats have made explicit or implied reference to forest management (Brigham et al. 1997, Crampton 1995, Law 1996, Lunney et al. 1988, Rasheed and Holroyd 1995, Sasse and Pekins 1996, Vonhof 1997, Vonhof and Barclay 1996). My study area contains both old-growth cedar-hemlock forest and fragmented, managed forest. Thus my goal was to compare the roosts selected by long-eared bats within these two forest types.

In North America, studies of forest roost selection have specifically examined the requirements of reproductive females. Reproductive females are hypothesized to need warm roosts to minimize the use of torpor, and females may show more roost fidelity than males do, especially during lactation (Audet and Fenton 1988, Grinevitch et al. 1995, Kurta et al. 1996, Lewis 1995, Vonhof and Barclay 1996). Thus warm roosts which allow a female to maintain a constant body temperature at little cost, and larger roosts which allow for maternity colonies to form, should be important. Males and non-reproductive females are presumed to select cooler roosts to facilitate the use of torpor (Hamilton and Barclay 1994). Male and non-reproductive female forest-dwelling bats roost alone or in small groups away from maternity colonies (Kalcounis and Hecker 1996, Rydell 1989, L. Lumsden pers. comm.). They are more flexible in their roost selection, occasionally using younger trees, isolated (not canopy) trees or artificial structures (Law 1996, B. Law pers. comm, J. Sedgeley pers. comm.). The population of bats I studied in the interior wet-belt is primarily a non-reproductive one. Thus, I would expect tree roosts and group sizes may be selected based on maximizing the efficient use of torpor. However, studies have found males occasionally do not use torpor (Kalcounis and Hecker 1996, Vonhof and Barclay 1997) and may lessen energetic costs by using passive warming. Re-warming is the most costly phase of torpor and it may be an advantage to avoid this cost (Prothero and Jurgens 1986, Vaughan and O'Shea 1976). In this case, the roosts used by non-reproductive bats may be selected to be warm, especially towards late day, to allow for passive re-warming (Vaughan and O'Shea 1976, Vonhof and Barclay 1997).

I investigated roost selection by the gleaning species, *M. septentrionalis* and *M. evotis*. I focused on *M. septentrionalis* as it is a red-listed species whose roosting requirements in British Columbia are unknown. I also examined the day-roosting behaviour of *M. evotis*, an ecologically similar species whose roosting behaviour has been documented in other areas. Previous research has found *M. evotis* to be flexible in its choice of roost sites. It has commonly been found using cracks in the ground, rock crevices, wildlife trees (dead or dying trees), and even tree stumps left in clear-cuts (Manning and Knox Jones 1989, Vonhof and Barclay 1997, B. Chruszcz pers. comm.). I wanted to determine whether *M. evotis* is as flexible in the interior wet-belt and whether or not *M. septentrionalis* behaves similarly.

METHODS

I examined the roost preference of the long-eared species using radio telemetry. Originally I focused on female *M. evotis* and *M. septentrionalis* as I had hoped to examine the roosts of reproductive females. However, males and non-reproductive females were also used once it became evident that reproductive females were scarce. The transmitters used (LB-2 transmitters, Holohil Systems Ltd., Carp, Ontario) weigh 0.45 grams. A minimum bat weight of 5 grams was required for radio-tagging (transmitter was a maximum of 9% of the bat's mass) and the heaviest captured bats were preferred. Previous studies have used radio-tags between 5 -10% of a bat's mass to locate roosts and found no detrimental effect (Aldridge and Brigham 1988, Bradbury et al. 1979, Brigham et al. 1997). Once a suitable bat was captured, I trimmed a small patch of hair away from between the shoulder blades. I then affixed the transmitter to the bat using Skin-Bond® adhesive (Canadian Howmedica, Guelph, Ontario). The bat was released from the capture site on the same night the transmitter was affixed to it. On the following day, I returned to the release site and located the signal. I followed the signal until the roost was located (or it was no longer possible to follow the signal). The roost tree was marked with flagging tape and left undisturbed. A bat was followed every day the signal was detectable.

At dusk, I returned to the roost tree to watch for bat emergence. I watched the roost tree until the tagged bat emerged and there was no subsequent bat emergence for 20 minutes. The numbers of bats using the roost and the aspect and height of the roost entrance were noted when possible. I measured distance between roosts when an individual switched roosts and I estimated the distance between the capture site and roost site for all roosts.

Once I found a roost tree and the bat had vacated that roost, I measured diameter at breast height (DBH), tree height with a clinometer (Suunto clinometer PM-5/360 PC), and percent canopy closure with a spherical densiometer (Forest densiometers model-C). I also visually estimated percent bark remaining (Table 3.1), identified the tree to species, and classified it by decay stage (Table 3.2). I established a 17m-radius plot around the roost tree (Fig. 3.1) and measured canopy height within the plot and site slope with the clinometer. I noted site aspect and determined site elevation from topographical maps of the region. I also measured DBH of all trees with DBH greater than 15cm to calculate tree basal area as a measure of tree density. All the trees in the plot were visually examined and classified by decay stage (Table 3.2, Vonhof and Barclay 1996). Of those trees in decay stage 2-7, I randomly selected (using a random number table) two trees within the plot and measured the same characteristics measured for the roost tree. I then established two other 17m radius plots around randomly

Table 3.1. Measurements made on roost and random trees as well as stand characteristics measured.

Tree Characteristics	**17m Diameter Plot Characteristics**
Diameter at Breast height (cm) (DBH)	Number of trees in the plot (DBH>15cm)
Tree height (m)	Total basal area of trees in plot (DBH >15cm)
Percent bark remaining (%)	Canopy height (m)
Percent canopy closure around the tree (%)	Site slope
	Site aspect
	Site elevation
Roost Tree Characteristics	
Tree species	
Date(s) used	
Colony size (if known)	
Entrance height	
Entrance aspect	
Distance from previous roost (if known)	
Distance to capture site (approximated)	

Table 3.2. Decay stage classification (from Vonhof and Barclay 1996).

Stage	Description
2	Live; usually unhealthy; obvious defects such as broken tops, cracks or hollows present
3	Recently dead; needles still present; little decay; heartwood hard
4	Dead; no needles, few twigs; top often broken; <50% branches lost; bark loose; heartwood hard; sapwood spongy
5	Dead; most branches and bark lost; top broken; heartwood spongy; sapwood soft
6	Dead; no branches or bark; broken midtrunk; sapwood sloughing from upper bole; heartwood soft
7	Dead; stubs <3m in height; heartwood soft; extensive internal decay; shell may be hard

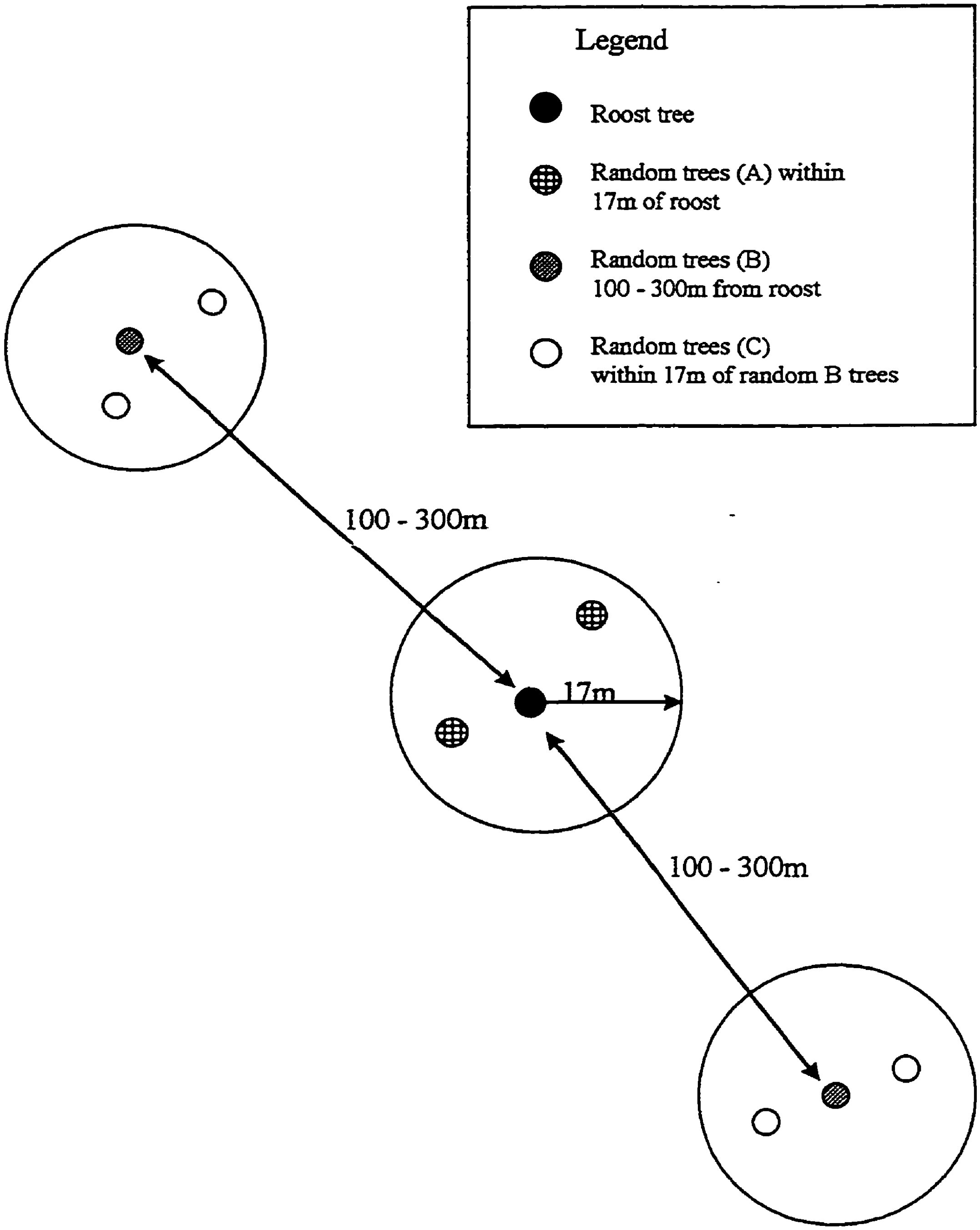


Figure 3.1. Schematic representation of the methodology for roost tree characterization.

selected wildlife trees (decay stages 2-7) at 100-300 m from the roost tree (Fig. 3.1). The distance was based on Vonhof (1995) who found the distance between roosts of an individual was generally less than 100m. These trees were at two random directions with a minimum of 90° between the directions. The same protocol used at the roost tree plot was used at these two random plots.

RESULTS

Tree Roosting

My success in finding roost trees was limited, particularly because so few long-eared bats were captured. In 1996, I radio-tagged six bats (2 females, 4 males), three of which led to the identification of eight roost trees. In 1997, I radio-tagged 10 bats (7 females, 3 males), eight of which led to six roost trees as well as three roosts in tree stumps and two in rock crevices (Table 3.3). I analyzed the characteristics of roost trees for roosts used by *M. evotis* and *M. septentrionalis* together as in most cases, too few roosts were found to compare these species independently.

Most roosts (16 / 19) were within 500m of where the bat was released. Yet, two male bats moved over 1km from capture to roost site (Table 3.3). The average distance (and standard error) between sequentially used roosts was 277 ± 107m (n = 9). However, male 022 traveled over 1000m between roosts, too far for accurate measurement. Excluding male 022, the average (± S.E.) distance between roosts was 186 ± 48m. The largest number of bats occupying a roost in one night was two.

Table 3.3. Characteristics of 14 tree roosts, 2 rock crevice roosts and 3 tree stump roosts. Roost ID is based on radio tag number and sequential use of roosts; all ID's starting with the same three digits are roosts used by one radio-tagged individual.

Roost ID	Species	Sex	Date found	Type of Roost	Colony size	Distance (m) from previous roost	Distance (m) from capture site to roost (approximated)
177B	*M. septentrionalis*	F	21 Jun 96	W. Hemlock	1		150
177C	*M. septentrionalis*		22 Jun 96	W. Hemlock	1	88	200
177D	*M. septentrionalis*		23 Jun 96	W. Hemlock	1	71.2	150
177E	*M. septentrionalis*		25 Jun 96	W. Hemlock	1	400	500
185A	*M. septentrionalis*	M	18 Aug 96	W. Hemlock			400
185B	*M. septentrionalis*		24 Aug 96	R. Cedar		200	150
189A	*M. evotis*	F	23 Jul 96	W. Hemlock	2		300
189B	*M. evotis*		24 Jul 96	W. Hemlock		75	300
079A	*M. evotis*	F	18 Jun 97	W. Hemlock			300
079B	*M. evotis*		10 Jun 97	R. Cedar		400	800
091A	*M. evotis*	F	29 Jun 97	W. Pine	2		20
091B	*M. evotis*		30 Jun 97	Rock Crevice	2	200	200
022A	*M. septentrionalis*	M	8 Aug 97	R. Cedar			300
022B	*M. septentrionalis*		9 Aug 97	W. Pine		>1000	>1000
029A	*M. septentrionalis*	F[1]	22 Aug 97	W. Hemlock			300
087A	*M. evotis*	M	18 Jun 97	Rock Crevice	1		>1000
080A	*M. evotis*	F	13 Jun 97	Stump	1		400
080B[2]	*M. evotis*		29 Jul 97	Stump	2	55	400
088A[2]	*M. evotis*	F					
093A	*M. evotis*	F	28 Jul 97	Stump	1		400

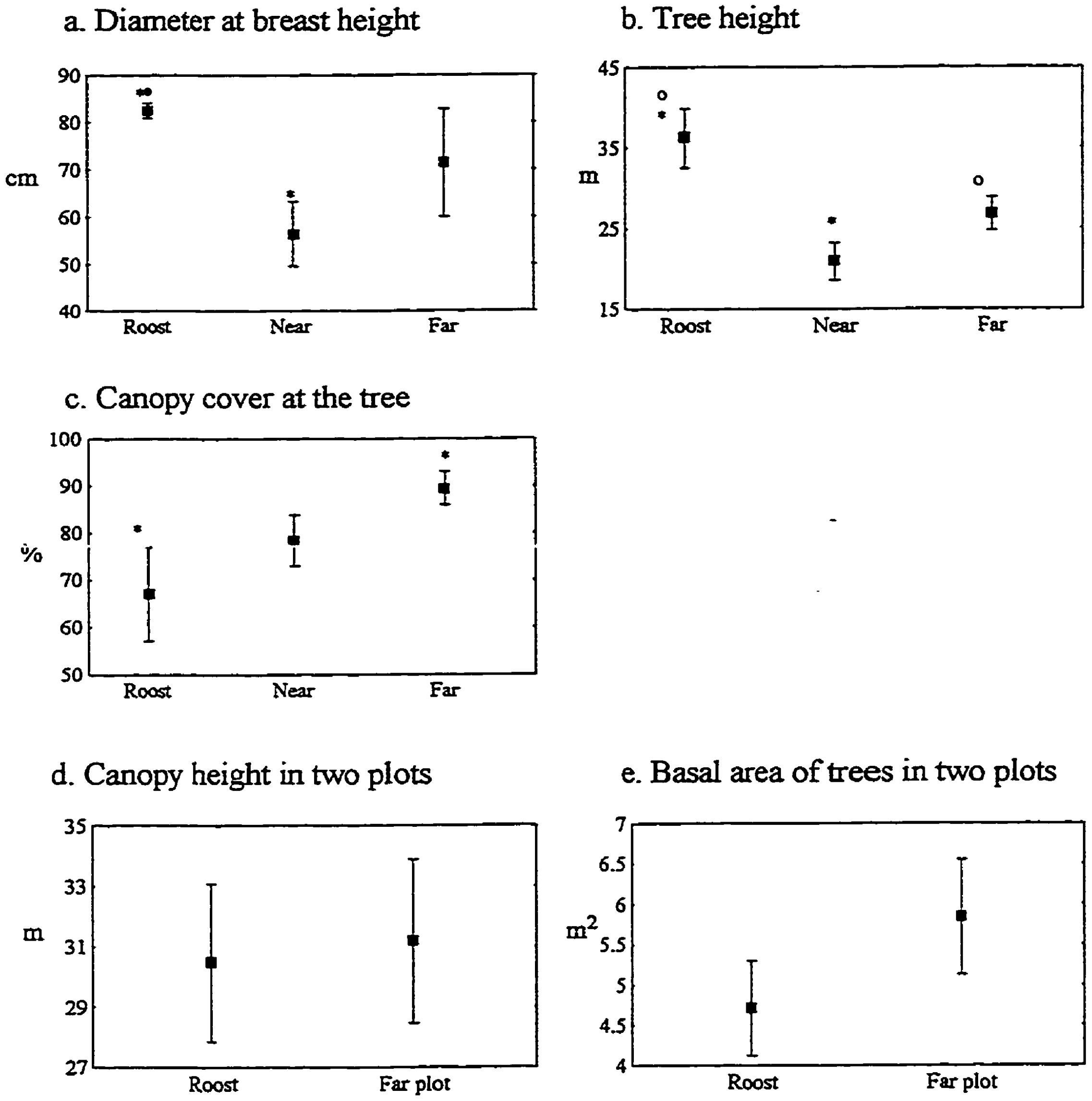
[1] This was a post-lactating female, the only known reproductive female radio-tagged.

[2] These individuals shared a roost.

I compared tree characteristics (DBH, tree height, canopy cover, bark remaining) and plot characteristics using 2-factor MANOVA with roost ID and tree (roost or random) or roost ID and plot (roost or random) as main effects. Roost trees were taller ($F_{2,38}$ =8.14, p =0.001, Fig. 3.2) and wider (larger DBH, $F_{2,38}$ =4.47 p =0.02, Fig. 3.2) than randomly available nearby trees (random trees "A", Fig. 3.1) within 17m of the roost (Wilks' lambda =0.610, $F_{8,70}$=2.45, p =0.02). Stand characteristics (canopy height, number of trees, average DBH, total basal area occupied by trees of DBH>15cm) of plots centred around a roost tree and those centred around randomly chosen trees within the forest stand were not significantly different (Wilks' lambda = 0.5889, $F_{4,32}$=1.00, p =0.42, Fig. 3.2). However, roost trees differed from the randomly selected trees 100 - 300m from the roost (random trees "B", Fig. 3.1, Wilks' lambda =0.7458, $F_{4,33}$=2.81, p =0.04). Roost trees were taller and had less canopy closure around them (height: $F_{1,36}$ =7.54, p =0.009, canopy cover: $F_{1,36}$=6.75, p =0.01, Fig. 3.2). Bats chose trees in decay-stage 2 (live with a defect, Table 3.2) significantly more often than randomly available (Fisher exact probability test, p =0.03, Fig. 3.3), but did not significantly select particular species of tree (Fisher exact probability test, p =0.08, Fig 3.4).

Stump and Rock Crevice Roosting.

I found two *M. evotis* roosts in rock crevices. One was used by a male captured in the vicinity of Giant Cedars Boardwalk. This roost was located approximately 1.3 km east and across the Illecillewaet river from where the bat was captured. A second crevice used by a female *M. evotis* was found in the side of a rock face 14 km north of



a. Diameter at breast height

b. Tree height

c. Canopy cover at the tree

d. Canopy height in two plots

e. Basal area of trees in two plots

Figure 3.2. Characteristics (± S.E.) of roost trees (n=14), random trees within 17m of the roost (n=26, Near) and random trees (or plots) located 100-300m from the roost tree (n=23, Far). Means denoted by the same symbol (* or °) are significantly different.

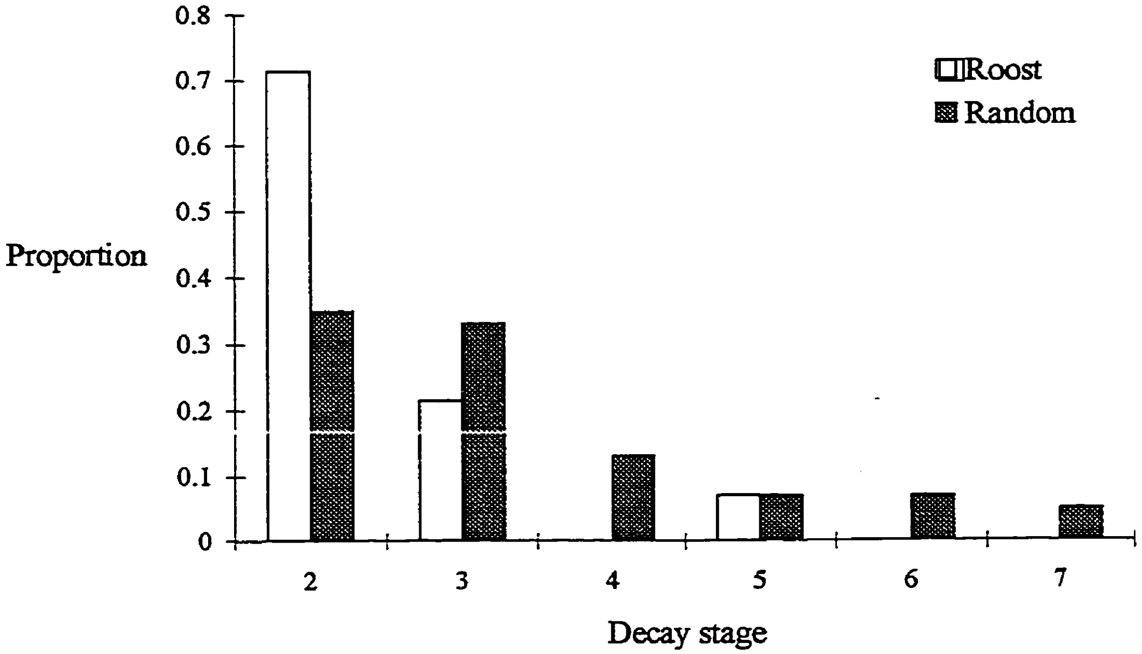


Figure 3.3. Proportion of all roost trees (n=14) and random trees (n=100) in decay stages 2-7 (Vonhof and Barclay 1996, Table 3.2).

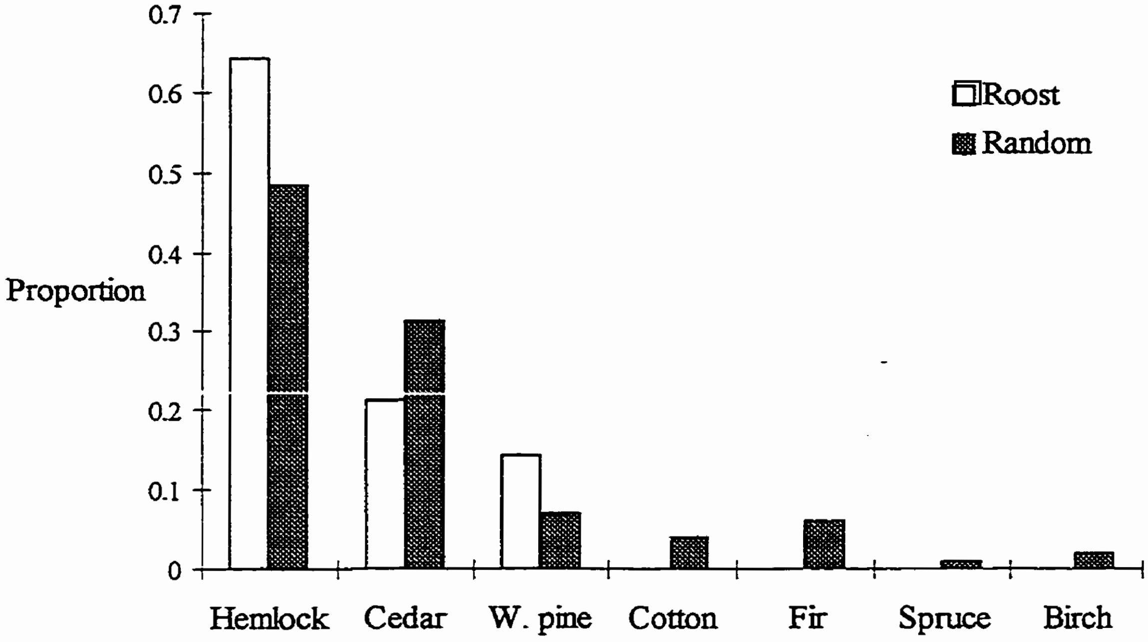


Figure 3.4. Proportion of all roost trees (n=14) and random trees (n=99) which were western hemlock (Hemlock), western red-cedar (Cedar), western white pine (W. pine), black cottonwood (Cotton), Douglas-fir (Fir), Engelmann spruce (Spruce) and paper birch (Birch).

Revelstoke, bordering the highway. On the first day after capture, the female was found in a western white pine. On the following three evenings and then three days later, she was found in the rock crevice.

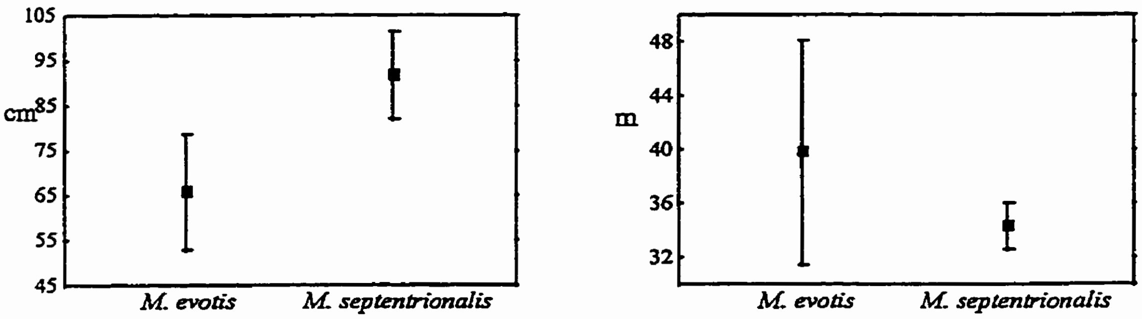
In 1997, three different western hemlock tree stumps in the same small clear-cut were used by three female *M. evotis*. Bat 080 (identified by radio-tag number) used two of the stumps, one of which was shared with bat 088. Bat 093 used the third stump. The clear-cut was along the French Creek road at km 7 and was less than 700m long and 500m wide. The bats switched between stump roosts and other roosts as, on the second and subsequent days after capture, two of the bats (088 and 093) were tracked into the higher elevation uncut forest bordering the clear-cut. This forest was quite steep and either the signal was not detectable from the forest or led to the base of a cliff. Triangulation of the signal suggested the roosts were located in the steep exposed rock, 420 - 580m above the clear-cut. Bat 080 was first located in the clear-cut on 13 June and then found in the same clear-cut, but in a different tree stump, on 29 July. At this time, she was sharing the stump with bat 088. The tree stumps had all been burnt and the bats used cavities under bark peeling away from the stump. The stumps were 1- 2m tall and were clear of vegetation (Table 3.4).

Species Differences in Roosts

The limited data suggest that there may be differences in the roosts preferred by *M. evotis* and *M. septentrionalis*. *M. septentrionalis* tended to use trees of a larger diameter than *M. evotis* (Mann Whitney U-test, $U_{9,5} = 35$, $p<0.2$, Fig. 3.5). The roosts

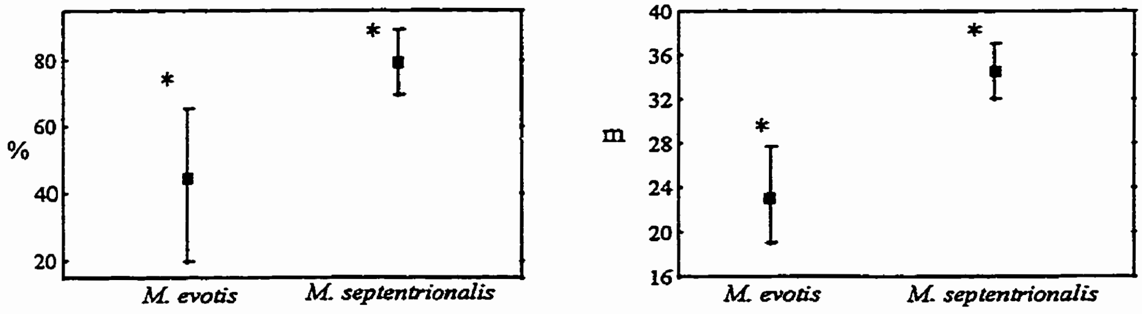
Table 3.4. Characteristics of three roost stumps used by female *M. evotis* in one clear-cut at km 7, French Creek Road. All roosts were located in hemlock stumps which had been burnt. Roosts were located behind loose flaps of bark. Roost 080B/088A was shared by two bats. Roost is identified by the number of the radio placed on the bat.

Roost	Stump diameter (cm)	Stump height (m)	Entrance height above ground (m)	Roost Aspect	Entrance width (cm)	Roost depth (cm)
080A	118.1	1.5	1.4	SW	3	28
080B/ 088A	80.6	2	1.9	SE	2	25
093A	79.8	2	1.7	W	4	



a. Diameter at breast height of roost

b. Roost tree height



c. Canopy cover at the roost tree

d. Canopy height in the plot

Figure 3.5. Selected characteristics of roost trees (± S.E.) used by *M. septentrionalis* (n=9) and *M. evotis* (n=5). 3 *M. evotis* and 4 *M. septentrionalis* individuals led to 14 roost trees in total. Asterisks indicate significant differences.

used by *M. septentrionalis* had significantly more canopy closure ($U_{9,5}$ =39, $p<0.05$, Fig. 3.5) around them and a significantly higher canopy in the roost plot ($U_{9,5}$ =38, p =0.05, Fig. 3.5). The trees used by *M. septentrionalis* were usually (6 out of 9 trees) within a forest canopy whereas *M. evotis* roost trees were generally along forest-opening edges such as beside a river or highway (4/5). This pattern was not significant, however (Fisher exact probability test, p =0.12). *M. septentrionalis* was only found roosting in trees whereas *M. evotis* used trees, rock crevices and tree stumps.

DISCUSSION

Long-eared bats in interior cedar-hemlock forests appear to select for the same basic criteria in a roost as bats in other forest studies (Brigham et al. 1997, Crampton 1995, Lunney et al. 1988, Rasheed and Holroyd 1995, Sasse and Pekins 1996, Vonhof and Barclay 1996). The long-eared bats of my study area rely on taller trees with less canopy closure than what is randomly available. Roosts in trees with these characteristics may be easier to access. With less canopy cover there is less foliage clutter for a bat to maneuver through when entering or departing a roost. Tall, uncluttered (by foliage) trees may also be prominent landmarks. Thus bats switching between roosts could easily identify a particular roost tree (Lewis 1995). These characteristics would be important to bats regardless of reproductive status.

To date there are numerous hypotheses as to when and why roost switching occurs (Lewis 1995) but none are fully satisfactory. In North America, roost selection and roost switching has been primarily examined for reproductive females (Betts 1996, Brigham 1991, Brigham et al. 1997, Crampton 1995, Ormsbee 1996, Sasse and Pekins 1996, Vonhof 1995). However, roost switching occurs as commonly in non-reproductive bats of the interior wet-belt as has been documented for reproductive bats in forest habitats. Thus, roost switching is not solely a characteristic of reproductive bats (see also Lunney et al. 1988, Taylor and Savva 1988). The distances traveled by bats in my study between capture site and roost site, and between successive roosts, was variable but similar to those reported by others (Crampton 1995, Entwistle et al. 1996, Taylor and Savva 1988, Vonhof and Barclay 1996).

Only one or two bats occupied a roost in my study. Colonies are an advantage for increasing ambient temperature in a roost. This is important for reproductive females attempting to avoid using torpor (Barclay 1982, Kunz 1982, Racey and Swift 1981). Increasing the ambient temperature of a roost with collective body heat allows females to maintain a high body temperature at minimal cost (Kurta 1986). However, in my study area there were few reproductive females with the above requirements and using torpor does not incur the same costs for males and non-reproductive females as reproductive females experience. Roosting singly is one way in which bats may facilitate the use of torpor (Kurta 1986).

The national parks in the study area contained mature climax cedar-hemlock forest. Older forests provide the largest diameter, tallest standing-dead trees as well as greater snag longevity (Cline et al. 1980, Crampton 1995, Thomas 1988, Tyrrell and Crow 1994). These forests also have proportionally more dead or dying trees than managed forests (Tyrrell and Crow 1994). It is possible that the interior cedar-hemlock forests of the national parks provide a large number of potential roosts, and thus there may be less competition for roosts between individuals (Perkins 1996), especially if non-reproductive bats do not have to compete for roosts with reproductive individuals.

In the northern portion of the study area the low-elevation cedar-hemlock forest is being fragmented and removed. In this region, I found five roosts. Three roosts were in tree stumps, one in a cliff crevice and one in a western white pine in a riparian strip. The bats roosting in the stumps did leave the clear-cut and roost in nearby uncut forest. However, these roosts appeared to be located in cliff faces above the clear cut, although this was not confirmed. The type of tree (tall, uncluttered) favoured for roosts may not be as readily available in the northern forests and other roost types may provide the best alternative.

It has been suggested (Vonhof and Barclay 1996) that species' differences in roost-tree selection are minimal as all temperate-zone bats are under the same selective pressures in choosing tree roost-sites. While similar constraints may result in general similarities between roost trees, there could also be species specific roost requirements. These may be important, especially in assessing habitat associations for rare bat species. *M. septentrionalis* used roosts primarily found under the forest canopy and having more canopy closure and a higher canopy than *M. evotis* roost trees. *M. evotis* also showed greater flexibility in the types of roosts used (Manning and Knox Jones 1989, Vonhof and Barclay 1997) as I found it throughout the study area in trees, crevices and tree stumps. I found *M. septentrionalis* only in the vicinity of the parks and only roosting in trees. The fact that one *M. evotis* captured in Mount Revelstoke National Park used a rock crevice roost suggests that rock crevices are available to bats in the vicinity of the parks, where *M. septentrionalis* was exclusively caught. Similarly, in the vicinity of the parks logging does occur and there are clear-cuts present in the southern study area. It is thus possible that *M. septentrionalis* is more dependent on trees and forests than is *M. evotis*. The range of *M. septentrionalis* in western Canada encompasses generally forested environments whereas *M. evotis* is also found on the prairies (van Zyll de Jong 1985) where it roosts in rock crevices (G. Holloway pers. comm.). The sample sizes I had were quite small, and it is not possible to make definite conclusions on the specific roost requirements of these species. However, the data suggest that further research, especially into the rarer species, is merited.

CHAPTER FOUR

Conclusions

The results of my study lead me to conclude that the interior wet-belt is a marginal habitat for bats and as such influences the behavioural decisions of the resident bats. The populations using this habitat are small and the frequency of reproduction appears to be low. In the two climatically "normal" years I studied, the proportion of reproductive *Myotis* females was only 11%. This does not appear to be sufficient for the *Myotis* populations to be self-sustaining and I conclude the populations are showing sink dynamics (Pulliam 1988). While there are nearby (within 200km) populations of the more common *Myotis* species present in the study area, there are no known nearby *Myotis septentrionalis* populations to act as a source. More extensive surveys of the surrounding areas are necessary to confirm this.

Theories on populations in marginal habitats, particularly those on the edge of the species' range, suggest that individuals in these populations are more adapted to unfavourable conditions than individuals in the centre of the species' range (Hoffman and Blows 1994). These populations tend to be more isolated and variable in size than those found at the centre of the geographic range (Lomolino and Channell 1995, Schoener 1987). Thus, theory suggests the geographic range of a species will collapse from the periphery inward and remnant populations may be found in the centre of the species' historical range (Lomolino and Channell 1995). However, Lomolino and

Channell (1995) found that in 23 of 31 mammal species whose current range has been reduced, remaining populations were usually those historically inhabiting the edge (presumably marginal habitat) of their previous range. Isolated populations may develop behavioural responses to contend with unfavourable conditions so as to be self-sustaining. An example would be Alberta kangaroo rats (*Dipodomys ordii*) who use torpor during winter unlike southern desert populations (Gummer 1997). The ability to adjust to novel conditions will have implications on population survival. Although it is not known whether or not the interior wet-belt is the edge of the range for the resident *Myotis* (for the long-eared species in particular), it is apparent that this habitat is marginal.

In agreement with the above, I found the long-eared bats of the interior wet-belt do not behave in ways expected of them based on studies from other, more benign areas. The long-eared species did not display the typical patterns of temporal segregation (from non-gleaners) of foraging activity found in other studies (e.g. Entwistle et al. 1996, Jones and Rydell 1994, Rydell et al. 1996). The long-eared bats foraged for short periods of time early in the evening. Long-eared bats did appear to segregate spatially from non-gleaners but were commonly caught within a few hundred meters of habitats (e.g. ponds) favoured for foraging by strict aerial hawkers. The diets of the foraging guilds did not significantly differ and long-eared species did not consume a high proportion of moths, as has been found in other studies (Barclay 1991, Fenton and Bell 1979, Rydell et al. 1996, Swift and Racey 1983). In poor climatic conditions, gleaning may not always be the most profitable foraging strategy and the gleaning species may use both gleaning and aerial hawking to maximize energetic intake. In doing so, the diets of individuals of the two foraging guilds in the interior wet-belt are more similar than has been found in other areas. In this way both *M. septentrionalis* and *M. evotis* are adjusting their foraging patterns to the marginal conditions of the wet-belt.

I also examined the roosting preferences of the long-eared species and found that roost trees had similar characteristics to those selected by other forest-dwelling bats in other areas (Brigham et al. 1997, Crampton 1995, Lunney et al. 1988, Rasheed and Holroyd 1995, Sasse and Pekins 1996, Vonhof and Barclay 1996). However, I found *M. septentrionalis*, the red-listed species, used only trees for roosting whereas *M. evotis* also used stumps and rock crevices. Preliminary evidence suggests that the types of forest stands selected by *M. septentrionalis* differ from those used by *M. evotis* in canopy height and closure. *M. septentrionalis* was only caught in or near the national parks, which provide a large area of mature-climax cedar-hemlock forest. Most *M. septentrionalis* roost trees were found within these forests. Mature forests contain a greater proportion of trees with characteristics selected by bats (Cline et al. 1980, Crampton 1995, Thomas 1988, Tyrrell and Crow 1994). In the fragmented forests north of the parks, *M. evotis* used stumps and crevices more often than trees, suggesting that suitable roost trees were less available, although a larger sample size is needed to substantiate this. Unlike *M. evotis*, *M. septentrionalis* does not appear to exploit novel roosts or adjust its roost preferences to what is available. Similarly, the range of *M. septentrionalis* in Canada (and especially western Canada) coincides with forested regions whereas the range of *M. evotis* includes prairie zones where it relies on rock crevices for roosting (B. Chruszcz, G. Holloway pers. comm.). Thus, *M. septentrionalis* in British Columbia may not be as flexible in its roosting selection as *M. evotis* is. An abundance of tree roosts in the national parks may be especially significant to *M. septentrionali*,, particularly as more forests are fragmented and old stands are removed from other parts of British Columbia.

In summary, the patterns of bat foraging behaviour are flexible and responsive to environmental fluctuations (Arlettaz 1996, de Jong 1994, Krull et al. 1991, Racey and Swift 1985). However, flexibility in roosting behaviour may not be as great and may vary between species. I suggest that roosting, more so than foraging opportunities, may influence a bat's choice of summer habitat (see also Crampton 1995). Consequently, existing mature cedar-hemlock forests may be attracting *M. septentrionalis* to the interior wet-belt study area despite climatic drawbacks. However, further research into the ecology of *M. septentrionalis* in British Columbia is necessary to test this hypothesis.

The potential reliance of *M. septentrionalis* on mature forest may influence the long-term viability of the species in British Columbia. Studies of species' rarity suggest that if a species depends on a diminishing resource, the species is more likely to become extinct (Rosenzweig and Lomolino 1997). The Revelstoke forest district, which includes wet-belt cedar-hemlock forests, has been intensively logged since the early 1960's. This district is approximately 750 000 ha and the maximum annual cut is 230 000 m^3. Thus, on average 0.31 m^3 of timber is removed per hectare per year. In contrast, the Fort Nelson forest district is larger (8.2 million ha), has been logged actively since the mid-1970's, and has a greater maximum allowable cut (1.2 million m^3 /

year). This becomes about 0.15 m^3 removed per hectare per year (B.C. Ministry of Forests, Revelstoke and Fort Nelson District Office, Regional Information Officer, pers. comm.). Forestry is a dominant industry in the Revelstoke forest district. Potentially, the diminishing mature-climax wet-belt forests has led the wet-belt *M. septentrionalis* population to occupy remnant, relatively undisturbed habitat. Thus, the impacts of forestry could be greater for *M. septentrionalis* in the wet-belt than in the Fort Nelson area boreal forest. However, more needs to be known about the population dynamics of *M. septentrionalis* before definitive conclusions on its population viability can be drawn.

LITERATURE CITED

Achuff, P. L., W. D. Holland, G. M. Coen, and K. Van Tighem (eds). 1984. Ecological land classification of Mount Revelstoke and Glacier National Parks, British Columbia. Publication M-84-11. Alberta Institute of Pedology, University of Alberta, Edmonton, Alberta. 261 pp.

Aldridge, H. D. J. N., and R. M. Brigham. 1988. Load carrying and maneuverablility in an insectivorous bat: a test of the 5% "rule" of radio-telemetry. J. Mammal. 69: 379-382.

Anthony, E. L. P., and T. H. Kunz. 1977. Feeding strategies of the little brown bat, *Myotis lucifugus*, in southern New Hampshire. Ecology 58: 775-786.

Anthony, E. L. P., M. H. Stack, and T. H. Kunz. 1981. Night roosting and the nocturnal time budget of the little brown bat, *Myotis lucifugus*: effects of reproductive status, prey density and environmental conditions. Oecologia 51: 151-156.

Arlettaz, R. 1996. Feeding behaviour and foraging strategy of free-living mouse-eared bats, *Myotis myotis* and *Myotis blythii*. Anim. Behav. 51: 1-11.

Audet, D. 1990. Foraging behavior and habitat use by a gleaning bat, *Myotis myotis* (Chiroptera: Vespertilionidae). J. Mammal. 71: 420-427.

Audet, D., and M. B. Fenton. 1988. Heterothermy and the use of torpor by the bat *Eptesicus fuscus* (Chiroptera: Vespertilionidae): A field study. Physiol. Zool. 61: 197-204.

Barbour, R. W., and W. H. Davis. 1969. Bats of America. University of Kentucky Press, Lexington, Kentucky. 286pp.

Barclay, R. M. R. 1982. Night roosting behavior of the little brown bat, *Myotis lucifugus*. J. Mammal. 63: 464-474.

Barclay, R. M. R. 1984. Observations on the migration, ecology and behaviour of bats at Delta Marsh, Manitoba. Can. Field-Nat. 98: 331-336.

Barclay, R. M. R. 1989. The effect of reproductive condition on the foraging behaviour of female hoary bats. Behav. Ecol. Sociobiol. 24: 31-37.

Barclay, R. M. R. 1991. Population structure of temperate zone insectivorous bats in relation to foraging behaviour and energy demand. J. Anim. Ecol. 60: 165-178.

Betts, B. J. 1996. Roosting behaviour of silver-haired bats (*Lasionycteris noctivagans*) and big brown bats (*Eptesicus fuscus*) in northeast Oregon. Pp. 55-61. *In* Bats and Forest Symposium. R. M. R. Barclay and R. M. Brigham (eds). B.C. Ministry of Forests, Victoria, British Columbia. Working Paper 23/1996. 292pp.

Brigham, R. M. 1991. Flexibility in foraging and roosting behaviour by the big brown bat (*Eptesicus fuscus*). Can. J. Zool. 69: 117-121.

Brigham, R. M., and M. B. Fenton. 1986. The influences of roost closure on the roosting and foraging behaviour of *Eptesicus fuscus* (Chiroptera: Vespertilionidae). Can. J. Zool. 64: 1128-1133.

Brigham, R. M., M. J. Vonhof, R. M. R. Barclay, and J. C. Gwilliam. 1997. Roosting behaviour and roost-site preferences of forest-dwelling Californica bats (*Myotis californicus*). J. Mammal. 78: 1231-1239.

Bradbury, J. W., D. Morrison, E. Stashko, and R. Heithaus. 1979. Radio-tracking methods for bats. Bat Res. News 20: 9-17.

Braumandl, T. F., and M. P. Curran. 1992. A field guide for site identification and interpretation for the Nelson Forest Region. B.C. Ministry of Forests, Nelson, British Columbia. 311pp.

Cline, S. P., A. B. Berg, and H. M. Wight. 1980. Snag characteristics and dynamics in Douglas-fir forests, western Oregon. J. Wildl. Manage. 44: 773-786.

Crampton, L. H. 1995. Habitat selection and the potential impacts of forest fragmentation on bat populations in aspen mixedwood forests in northern Alberta. M.Sc. Thesis. University of Calgary, Calgary, Alberta. 114 pp.

Davis, W. H., and H. B. Hitchcock. 1965. Biology and migration of the bat, *Myotis lucifugus*, in New England. J. Mammal. 46: 296-313.

deJong, J. 1994. Habitat use, home-range and activity pattern of the northern bat, *Eptesicus nilssoni*, in a hemiboreal coniferous forest. Mammalia 58: 535-548.

Dias, P. C. 1996. Sources and sinks in population biology. TREE 11: 326-330.

Ekman, M., and J. de Jong. 1996. Local patterns of distribution and resource utilization of four bat species (*Myotis brandti, Eptesicus nilssoni, Plecotus auritus* and *Pipistrellus pipistrellus*) in patchy and continuous environments. J. Zool. Lond. 238: 571-580.

Entwistle, A. C., P. A. Racey, and J. R. Speakman. 1996. Habitat exploitation by a gleaning bat, *Plecotus auritus*. Phil. Trans. R. Soc. Lond. B 351: 921-931.

Erkert, H.G. 1982. Ecological aspects of bat activity rhythms. Pp. 201-242. *In* Ecology of bats. T. H. Kunz (ed). Plenum Press, New York, New York. 425 pp.

Faure, P.A., and R. M. R. Barclay. 1992. The sensory basis of prey detection by the long-eared bat, *Myotis evotis*, and the consequences for prey selection. Anim. Behav. 44: 31-39.

Faure, P.A., and R. M. R. Barclay. 1994. Substrate-gleaning versus aerial-hawking: plasticity in the foraging and echolocation behaviour of the long-eared bat, *Myotis evotis*. J. Comp. Physiol. A 174: 651-660.

Faure, P.A., J. H. Fullard, and J. W. Dawson. 1993. The gleaning attacks of the Northern Long-eared Bat, *Myotis septentrionalis*, are relatively inaudible to moths. J. exp. Biol. 178: 173-189.

Fenton, M. B. 1990. The foraging behaviour and ecology of animal-eating bats. Can. J. Zool. 68: 411-422.

Fenton, M. B., and R. M. R. Barclay. 1980. Myotis lucifugus. Mammal. Species 142: 1-8.

Fenton, M. B., and G. P. Bell. 1979. Echolocation and feeding behaviour in four species of *Myotis* (Chiroptera). Can. J. Zool. 57: 1271-1277.

Fenton, M. B., and J. H. Fullard. 1979. The influence of moth hearing on bat echolocation strategies. J. Comp. Physiol. 132: 77-86.

Fenton, M. B., H. G. Merriam, and G. L. Holroyd. 1983. Bats of Kootenay, Glacier, and Mount Revelstoke national parks in Canada: identification by echolocation calls, distribution, and biology. Can. J. Zool. 61: 2503-2508.

Gellman, S. T., and W. J. Zielinski. 1996. Use by bats of old-growth redwood hollows on the north coast of California. J. Mammal. 77: 255-265.

Grindal, S. D., T. S. Collard, R. M. Brigham, and R. M. R. Barclay. 1992. The influence of precipitation on reproduction by *Myotis* bats in British Columbia. Am. Midl. Nat. 128: 339-344.

Grinevitch, L., S. L. Holroyd, and R. M. R. Barclay. 1995. Sex differences in the use of daily torpor and foraging time by big brown bats (*Eptesicus fuscus*) during the reproductive season. J. Zool. 235: 301-309.

Gummer, D. 1997. Effects of latitude and long-term isolation on the ecology of northern Ord's Kangaroo Rats (*Dipodomys ordii*). MSc. Thesis. University of Calgary, Calgary, Alberta. 111pp.

Hamilton, I. M. 1996. Age-related influences on foraging by bats. MSc. Thesis. University of Calgary, Calgary, Alberta. 136 pp.

Hamilton, I. M., and R. M. R. Barclay. 1994. Patterns of daily torpor and day-roost selection by male and female big brown bats (*Eptesicus fuscus*). Can. J. Zool. 72: 744-749.

Hoffmann, A. A., and M. W. Blows. 1994. Species borders: ecological and evolutionary perspectives. TREE 9:223-227.

Holroyd, S. L. 1993. Inventory and habitat assessment of bats in the MICA Wildlife Compensation area. Prepared for B.C. Hydro, B.C. Environment, Lands and Parks, Nelson B.C., B.C. Environment, Lands and Parks, Prince George, B.C., and Parks Canada. 96 pp.

Holroyd, S. L., R. M. R. Barclay, L. M. Merk, and R. M. Brigham. 1994. A survey of the bat fauna of the dry interior of British Columbia. Prepared for Ministry of Environment, Lands and Parks, Wildlife Branch, Victoria, British Columbia. Wildlife Working Report No. WR-63. 73 pp.

Hurlbert, S. H. 1978. The measurement of niche overlap and some relatives. Ecology 59: 67-77.

Jones, G., and J. Rydell. 1994. Foraging strategy and predation risk as factors influencing emergence time in echolocating bats. Phil. Trans. R. Soc. Lond. B. 346: 445-455.

Kalcounis, M. C., and K. R. Hecker. 1996. Intraspecific variation in roost-site selection by little brown bats (*Myotis lucifugus*). Pp. 81-90. *In* Bats and Forest Symposium. R. M. R. Barclay and R. M. Brigham (eds). B.C. Ministry of Forests, Victoria, British Columbia. Working Paper 23/1996. 292pp.

Keen, R., and H. B. Hitchock. 1980. Survival and longevity of the little brown bat (*Myotis lucifugus*) in southeastern Ontario. J. Mammal. 61: 1-7.

Ketcheson, M. V., T. F. Braumandl, D. Meidinger, G. Utzig, D. A. Demarchi, and B. M. Wikeem. 1991. Interior Cedar-Hemlock Zone. Pp. 167-180. *In* Ecosystems of British Columbia. D. Meidinger and J. Pojar (eds). B.C. Ministry of Forests, Victoria, British Columbia. Special Report Series 6. 330pp.

Krull, D., A. Schumm, W. Metzner, and G. Neuweiler. 1991. Foraging areas and foraging behavior in the notch-eared bat, *Myotis emarginatus* (Vespertilionidae). Behav. Ecol. Sociobiol. 28: 247-253.

Kunz, T. H. 1973. Resource utilization: temporal and spatial components of bat activity in central Iowa. J. Mammal. 54: 14-32.

Kunz, T. H. 1982. Roosting ecology of bats. Pp. 1-55. *In* Ecology of Bats. T. H. Kunz (ed). Plenum Press, New York, New York. 425 pp.

Kunz, T. H., and E. L. P. Anthony. 1982. Age estimation and post-natal growth in the bat *Myotis lucifugus*. J. Mammal. 63: 23-32.

Kunz, T. H., and C. E. Brock. 1975. A comparison of mist nest and ultrasonic detectors for monitoring flight activity of bats. J. Mammal. 56: 907-911.

Kunz, T. H., and J. O. Whitaker Jr. 1983. An evaluation of fecal analysis for determining food habits of insectivorous bats. Can. J. Zool. 61: 1317-1321.

Kurta, A. 1986. Factors affecting the resting and postflight body temperature of little brown bats, *Myotis lucifugus*. Physiol. Zool. 59: 429-438.

Kurta, A., K. J. Williams, and R. Mies. 1996. Ecological, behavioural and thermal observations of a peripheral population of Indiana bats (*Myotis sodalis*). Pp. 102-117. *In* Bats and Forest Symposium. R. M. R. Barclay and R. M. Brigham (eds). B.C. Ministry of Forests, Victoria, British Columbia. Working Paper 23/1996. 292pp.

Law, B. S. 1996. The ecology of bats in south-east Australian forests and potential impacts of forestry practices: a review. Pacific Cons. Biol. 2: 363-374.

Levins, R. 1968. Evolution in changing environments: some theoretical explorations. Princeton University Press, Princeton, New Jersey. 120pp.

Lewis, S. E. 1993. Effect of climatic variation on reproduction by pallid bats (*Antrozous pallidus*). Can. J. Zool. 71: 1429-1433.

Lewis, S. E. 1995. Roost fidelity of bats: a review. J. Mammal. 76: 481-496

Lewis, T., and L. R. Taylor. 1965. Diurnal periodicity of flight by insects. Trans. R. Ent. Soc. Lond. 116: 393-479.

Lomolino, M. V., and R. Channell. 1995. Splendid isolation: patterns of geographic range collapse in endangered mammals. J. Mammal. 76: 335-347.

Lunney, D., J. Barker, D. Priddel, and M. O'Connell. 1988. Roost selection by Gould's Long-eared Bat, *Nyctophilus gouldi* Tomes (Chiroptera: Vespertilionidae), in logged forest on the south east coast of New South Wales. Aust. Wild. Res. 15: 375-384.

Manning, R. W., and J. Knox Jones Jr. 1989. Myotis evotis. Mammal. Species 329: 1-5.

McAney, C., C. Shiel, C. Sullivan, and J. Fairley. 1991. The analysis of bat droppings. Occasional Publication No. 14. Mammal Society, London. 48pp.

McNab, B. K. 1982. Evolutionary alternatives in the physiological ecology of bats. Pp. 151-200. *In* Ecology of bats. T. H. Kunz (ed). Plenum Press, New York, New York. 425 pp.

Meidinger, D., and J. Pojar. 1991. Ecosystems of British Columbia. B.C. Ministry of Forests, Victoria, British Columbia. Special Report Series 6. 330pp.

Miller, L. A. 1975. The behaviour of flying green lacewings *Chrysopa carnea*, in the presence of ultrasound. J. Insect Physiol. 21: 205-219.

Nagorsen, D. W., and R. M. Brigham. 1993. Bats of British Columbia. UBC Press, Vancouver, British Columbia. 164 pp.

Norberg, U. M., and J. M. V. Rayner. 1987. Ecological morphology and flight in bats (Mammalia; Chiroptera): wing adaptations, flight performance, foraging strategy and ecolocation. Phil. Trans. R. Soc. Lond. B. 316: 335-427.

Ormsbee P. 1996. Characteristics, use and distribution of day roosts selected by female *Myotis volans* (long-legged myotis) in forested habitat of the central Oregon Cascades. Pp. 124-131. *In* Bats and Forest Symposium. R. M. R. Barclay and R. M. Brigham (eds). B.C. Ministry of Forests, Victoria, British Columbia. Working Paper 23/1996. 292pp.

Palmeirim, J. M., and L. Rodrigues. 1995. Dispersal and philopatry in colonial animals: the case of *Miniopterus schreibersii*. Symp. Zool. Soc. Lond. 67: 219-231.

Perkins, J. M. 1996. Does competition for roosts influence bat distribution in a managed forest? Pp. 164-172. *In* Bats and Forest Symposium. R. M. R. Barclay and R. M. Brigham (eds). B.C. Ministry of Forests, Victoria, British Columbia. Working Paper 23/1996. 292pp.

Perry, G., and E. R. Pianka. 1997. Animal foraging: past, present and future. TREE 12: 360-364.

Prothero J., and K. D. Jurgens. 1986. An energetic model of daily torpor in endotherms. J. Theor. Biol. 121: 403-415.

Pulliam, H. R. 1988. Sources, sinks and population regulation. Am. Nat. 132: 652-661.

Racey, P. A. 1974. Aging and assessment of reproductive status of Pipistrelle bats, *Pipistrellus pipistrellus*. J. Zool. (Lond.) 173: 264-271.

Racey, P. A. 1982. Ecology of bat reproduction. Pp. 57-104. *In* Ecology of bats. T. H. Kunz (ed). Plenum Press, New York, New York. 425 pp.

Racey, P. A., and S. M. Swift. 1981. Variations in gestation length in a colony of pipistrelle bats (*Pipistrellus pipistrellus*) from year to year. J. Reprod. Fertil. 61: 123-129.

Racey, P. A., and S. M. Swift. 1985. Feeding ecology of *Pipistrellus pipistrellus* (Chiroptera: Vespertilionidae) during pregnancy and lactation. I. Foraging behaviour. J. Anim. Ecol. 54: 205-215.

Rasheed, S. A., and S. L. Holroyd. 1995. Roosting habitat assessment and inventory of bats in the MICA Wildlife Compensation area. Prepared for B.C. Hydro, B.C. Environment, Lands and Parks Nelson B.C., B.C. Environment, Lands and Parks, Prince George, B.C. and Parks Canada. 77pp.

Rosenzweig, M. L. and M. V. Lomolino. 1997. Who gets the short bits of the broken stick? Pp. 63-90. *In* The biology of rarity: causes and consequences of rare-common differences. W. E. Kunin and K. J. Gaston (eds). Chapman and Hall, London, UK. 280pp.

Rydell, J. 1989. Feeding activity of the northern bat *Eptesicus nilssonii* during pregnancy and lactation. Oecologia 80: 562-565.

Rydell, J. 1992. Occurrence of bats in northernmost Sweden (65°N) and their feeding ecology in summer. J. Zool. Lond. 227: 517-529.

Rydell, J. 1993. Variation in foraging activity of an aerial insectivorous bat during reproduction. J. Mammal. 74: 503-509.

Rydell, J., A. Entwistle, and P. A. Racey. 1996. Timing of foraging flights of three species of bats in relation to insect activity and predation risk. Oikos 76: 243-252.

Sasse, D. B., and P. J. Pekins. 1996. Summer roosting ecology of Northern Long-eared Bats (*Myotis septentrionalis*) in the White Mountain National Forest. Pp. 91-101. *In* Bats and Forest Symposium. R. M. R. Barclay and R. M. Brigham (eds). B.C. Ministry of Forests, Victoria, British Columbia. Working Paper 23/1996. 292pp.

Saunders, M. B., and R. M. R. Barclay. 1992. Ecomorphology of insectivorous bats: a test of predictions using two morphologically similar species. Ecology 73: 1335-1345.

Schoener, T. W. 1987. The geographical distribution of rarity. Oecologia 74: 161-173.

Schowalter, D. B., J. R. Gunson, and L. D. Harder. 1979. Life history characteristics of little brown bats (*Myotis lucifugus*) in Alberta. Can. Field-Nat. 93: 243-251.

Stevens, V. 1995. Wildlife diversity in British Columbia: distribution and habitat use of amphibians, reptiles, birds, and mammals in biogeoclimatic zones. Research Branch, B.C. Ministry of Forests., Wildlife Branch, B.C. Ministry of Environment, Lands and Parks. Victoria, British Columbia. Working Paper 04/1995. 288pp.

Swift, S. M. 1980. Activity patterns of Pipistrelle bats in north-east Scotland. J. Zool. 190: 285-295.

Swift, S. M., and P. A. Racey. 1983. Resource partitioning in two species of vespertilionid bats (Chiroptera) occupying the same roost. J. Zool. 200: 249-259.

Taylor, L. R. 1963. Analysis of the effect of temperature on insects in flight. J. Anim. Ecol. 32: 99-117.

Taylor, L. R., and C. I. Carter. 1961. The analysis of numbers and distribution in an aerial population of macrolepidoptera. Trans. R. Ent. Soc. Lond. 113: 369-386.

Taylor, R. J., and M. G. O'Neill. 1988. Summer activity patterns in insectivorous bats and their prey in Tasmania. Aust. Wild. Res. 15: 533-539.

Taylor, R. J., and N. M. Savva. 1988. Use of roost sites by four species of bats in state forest in south-eastern Tasmania. Aust. Wild. Res. 15: 637-645.

Thomas, D. W. 1988. The distribution of bats in different ages of Douglas-Fir forests. J. Wildl. Manage. 52: 619-626.

Thomas, D. W., G. P. Bell, and M. B. Fenton. 1987. Variation in echolocation call frequencies recorded from North American vespertilionid bats: a cautionary note. J. Mammal. 68: 842-847.

Tuttle, M. D. 1974. An improved trap for bats. J. Mammal. 71: 475-479.

Tyrrell, L. E., and T. R. Crow. 1994. Structural characteristics of old-growth hemlock-hardwood forests in relation to age. Ecology 75: 370-386.

van Zyll de Jong, C. G. 1985. Handbook of Canadian Mammals 2. Bats. National Museum of Natural Sciences, National Museums of Canada, Ottawa, Ontario. 212pp.

van Zyll de Jong, C. G., M. B. Fenton, and J. G. Woods. 1980. Occurrence of *Myotis californicus* at Revelstoke and a second record of *Myotis septentrionalis* for British Columbia. Can. Field-Nat. 94: 455-456.

Vaughan, N., G. Jones, and S. Harris. 1997. Habitat use by bats (Chiroptera) assessed by means of a broad-band acoustic method. J. Appl. Ecol. 34: 716-730.

Vaughan, T. A., and T. J. O'Shea. 1976. Roosting ecology of the pallid bat, *Antrozous pallidus*. J. Mammal. 57: 19-41.

Vonhof, M. J. 1995. Roosting ecology of forest-dwelling bats. MSc. Thesis. University of Calgary, Calgary, Alberta. 101pp.

Vonhof, M. J. 1997. A survey of the abundance, diversity and roost-site preferences of bats in the Pend d'Oreille Valley, British Columbia. Prepared for the Columbia Basin Fish and Wildlife Compensation Program. 72pp.

Vonhof, M. J., and R. M. R. Barclay. 1996. Roost-site selection and roosting ecology of forest-dwelling bats in southern British Columbia. Can. J. Zool. 74: 1797-1805.

Vonhof, M. J., and R. M. R. Barclay. 1997. Use of tree stumps as roosts by the Western Long-eared Bat. J. Wildl. Manage. 61: 674-684.

Whitaker, J. O. Jr. 1989. Food habits analysis of insectivorous bats. Pp. 171-189. *In* Ecological and behavioural methods for the study of bats. T. H. Kunz (ed). Smithsonian Institution, Washington D.C. 533pp.

Wilkinson, L. C., P. F. J. Garcia, and R. M. R. Barclay. 1995. Bat survey of the Liard river watershed in northern British Columbia. Prepared for Ministry of Environment, Lands and Parks, Wildlife Branch, Victoria, British Columbia. 39pp.

Williams, C. B. 1961. Studies on the effect of weather conditions on the activity and abundance of insect populations. Phil. Trans. R. Soc. Lond. B. 244: 331-378.

Zar, J. H. 1984. Biostatistical analysis, 2nd ed. Prentice-Hall. Englewood Cliffs, NJ. 718pp.

Appendix 1. The location of trapping sites. The number of bats captured and the netting effort (nights and net-nights) at each site is shown.

Trapping Sites	East (UTM)	North (UTM)	No. Captures	No. Nights	No. Net-nights
Parks Sites					
Skunk Cabbage	435400	5659500	23	12	53
Giant Cedars boardwalk	436650	5661900	15	14	49
Giant Cedars Pit	436750	5661900	4	12	34
GC pond A	436600	5661800	7	3	8
GC pond B (along highway)	436750	5661750	2	2	6
Beaver valley at Copperstein	469700	5690200	10	12	38
On Copperstein trail	470200	5690000	2	5	14
Pond in Beaver valley	468100	5693700		1	1
Old campground in Beaver valley	466500	5699600	2	2	10
Hemlock Grove	458000	5677900		2	6
Flat Creek	453200	5674800		2	6
Highway					
Tangier Creek	441400	5669600	1	2	7
Woosley Creek	436600	5665000	1	3	9
Echo Lake	South of Revelstoke		1	1	3
Canyon Pond	438400	5664800	3	4	12
Jumping Creek	446500	5669800	1	2	7

Appendix 1. continued

Trapping sites	East (UTM)	North (UTM)	No. Captures	No. Nights	No. Net-nights
North					
Cairnes Creek	411000	5683700	2	2	4
Downie Km 22	420400	5699550	1	2	7
Downie Km 2	406000	5707000		3	9
Downie Km 4.5	408000	5708000	1	1	3
Downie Km 9	409500	5708200		1	2
Goldstream Rd. Km 5	394000	5722000		2	5
French Creek Km 6.5	394300	5724100	3	3	8
French Creek Km 7	394700	5723700	16	5	15
French Creek Km 10	397500	5723200	1	1	1
French Creek Km 7.5 cut	394900	5724100	1	Bat captured in stump roost	
Pitt Creek campground	North of Goldstream			1	4
Key Road Km. 5	between Cairnes Creek and Downie			1	2
Laforme Road	416600	5674500		1	3
"Leech" Pond	388000	5725200	1	1	3
Old Downie Prov. Park	398000	5703000		1	3