

THE UNIVERSITY OF CALGARY

**Foraging and thermoregulatory behaviour of the long-eared bat (*Myotis evotis*)
roosting in natural habitat**

by

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ABSTRACT

I investigated the interaction between foraging, thermoregulation, and roost choice in reproductive female long-eared bats, *Myotis evotis*, roosting in natural habitat. I conducted my study in the badlands of the South Saskatchewan River Valley over two summers. The *M. evotis* in my study behaved unusually compared to other temperate insectivorous species studied previously. Individuals foraged all night every night regardless of ambient temperature or reproductive condition. A flexible foraging strategy may make this behaviour profitable for *M. evotis*. Individuals used torpor every day and the amount of time spent in torpor was mostly influenced by the amount of time available to do so. This suggests that torpor is not limited to energy emergencies. Pregnant and lactating females chose roosts that were different in structure and thermal characteristics. My results suggest that the *M. evotis* in my study area were on a tight energy budget. I discuss possible reasons.

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INTRODUCTION

The study of energy budgets is central to the understanding of life history strategies. To survive and reproduce, animals must balance energy use with energy accumulation. To maintain a balanced energy budget, energy accrued through foraging must account for energy spent in maintenance and production. Female mammals experience their highest energy demands during pregnancy and lactation (Gittleman and Thompson 1988). During these periods, in addition to normal maintenance costs, energy must be allocated to fetal growth and milk production (Gittleman and Thompson 1988, Speakman and Racey 1987). Furthermore, pregnant females must spend extra energy to transport unborn young.

Small mammals have high energy demands compared to large mammals. High surface area to volume ratios result in exacting heat loss and high metabolic rates (Schmidt-Nielsen 1990). In temperate-zone insectivorous bats, energy demands may be even more extreme because of their unique reproductive strategy, variable food source (Hickey and Fenton 1996), and expensive mode of locomotion (Kurta *et al.* 1989a). Females raise young without the assistance of males and juveniles must reach adult size before they are able to fly and forage for themselves (Barclay 1994). Furthermore, insects are only available as a source of prey for a few months each year. This means that there is a limited time for females to raise their young to self-sufficiency and prepare for hibernation (Kurta 1986). Furthermore, adverse conditions (low ambient

temperatures, precipitation) can reduce insect abundance below profitable levels within a season (Holloway 1998, Racey and Swift 1985, Rydell 1989).

Reproductive female bats may cope with high energy demands and a variable prey source by modifying their foraging, thermoregulatory, and/or roosting behaviour.

Foraging

Foraging behaviour is influenced by daily energy demand, prey availability, and foraging efficiency (Aldridge and Brigham 1991, Barclay 1989, Wilkinson and Barclay 1997). In female bats, daily energy demand is higher during lactation than during pregnancy (Kurta *et al.* 1987, Kurta *et al.* 1990, Studier *et al.* 1973). Furthermore, insect availability may be higher during lactation and females may be more maneuverable than during pregnancy (Barclay 1989). These differences correspond to changes in foraging behaviour, such as increased foraging time and food consumption, between pregnancy and lactation (Barclay 1989, Kunz 1974, McNab 1982, Racey 1982).

The profitability of foraging depends on the availability of prey (Rydell 1989). Taylor (1963) showed that insect flight occurs above a species-specific critical temperature. Below this temperature, the energy required for flight is not available. The dependence of insect activity on ambient temperature results in daily and seasonal fluctuations in insect abundance (Anthony and Kunz 1977, Audet and Fenton 1988, Barclay 1985, Holloway 1998, Racey and Swift 1985). Consequently, foraging strategies of aerial insectivorous bats may be affected.

Temperate-zone insectivorous bats often forage for one or two short bouts corresponding to peaks in insect abundance at dusk and dawn (Barclay 1993, Holloway 1998, Kunz 1974, Racey 1982, Racey and Swift 1985). These peaks correspond to thresholds of ambient temperature and light intensity (Lewis and Taylor 1964, Taylor 1963). Numerous authors have described the relationship between ambient conditions, insect availability, and foraging in insectivorous bats (Anthony *et al.* 1981, Audet and Fenton 1988, Aldridge and Brigham 1991, Grinevitch *et al.* 1995, Hamilton 1996, Racey and Swift 1985, Rydell 1989, Wilkinson and Barclay 1997). At low temperatures (often around 10°C) the density of flying insects is low, foraging is not profitable, and bats will often return to their roosts or fail to emerge at all (Grinevitch *et al.* 1995, Hamilton 1996, Rydell 1989).

The influence of ambient conditions on foraging behaviour may be less pronounced in species that are not dependent on aerial prey. The owlet-nightjar (*Aegotheles cristatus*), a nocturnal insectivorous bird, forages all night regardless of ambient conditions (Brigham *et al.* in press). This strategy is probably possible because owlet-nightjars can forage aerially as well as on the ground (Brigham *et al.* in press). When ambient conditions reduce aerial prey densities, *A. cristatus* can use ground-dwelling prey. Bats that can take prey in the air (hawking) as well as from surfaces (gleaning) are able to live in climates not available to strict aerial hawkers possibly because they have access to another source of prey (Barclay 1991).

Torpor

Torpor, a facultative energy-saving strategy in mammals and birds (Wang and Wolowyk 1988), has been viewed as a means of coping with energy emergencies (Kurta *et al.* 1987, Kurta and Kunz 1988, Pagels and Blem 1973). Poor ambient conditions (rain, low temperatures) and other circumstances that reduce foraging opportunities or food intake, frequently result in higher use of torpor (Anthony *et al.* 1981, Kissner and Brigham 1993, Körtner *et al.* in press, Kurta 1990, Racey and Swift 1981).

Torpid individuals accrue significant energy savings relative to individuals that maintain high T_b 's (Geiser 1993, Hosken 1997, Hosken and Withers 1997, Song and Geiser 1997, Studier and O'Farrell 1976, Webb *et al.* 1993). Daily energy demands may be less than 1% of those experienced by normothermic individuals (Webb *et al.* 1993). Considering the high energy demands of reproduction (Gittleman and Thompson 1988), it seems unusual that the use of torpor would be limited to energy emergencies. However, reduced body temperatures result in reduced rates of embryonic development, and prolonged gestation in some vespertilionid bats (Audet and Fenton 1988, Lewis 1993, Racey 1973). Milk production is also reduced at low body temperatures and may result in delayed weaning (Tuttle 1976, Wilde *et al.* 1995). Delays in parturition or weaning may result in delayed self-sufficiency of young. Consequently, mothers and young would have less time available to prepare for hibernation. This could be especially detrimental for temperate-latitude bats because the

foraging season is short and over-winter starvation is one of the highest sources of mortality (Kurta 1986).

A number of studies support the notion that the use of torpor is limited by its costs to fetal and juvenile development. In some species of birds known to use torpor, the use of torpor is infrequent during the breeding season (Brigham 1992, Brigham *et al.* in press, Casada and Brigham 1994). Outside the breeding season, the use of torpor is more common. In bats, males and nonreproductive females typically make more frequent use of torpor than do pregnant or lactating females (Grinevitch *et al.* 1995, Hamilton and Barclay 1994). In reproductive females the benefits of torpor may only outweigh the costs when ambient conditions reduce foraging opportunities.

Field studies of free-ranging *E. fuscus* have shown that the use of torpor is particularly limited during lactation (Audet and Fenton 1988, Grinevitch *et al.* 1995, Hamilton and Barclay 1994). Below the thermoneutral zone, the energy savings associated with torpor depend on the differential between ambient temperature (T_a) and body temperature (T_b) (Studier and O'Farrell 1976). Higher ambient temperatures during lactation may reduce the energetic benefits of torpor making it less profitable relative to the costs of slowed juvenile growth.

Even small reductions in body temperature may result in substantial energy savings. Studier (1981) showed that incremental reductions in body temperature result in diminishing returns in energy savings. In other words, initial reductions in body temperature result in higher energy savings than further reductions of the same increment. Webb *et al.* (1993) suggested that small

reductions in body temperature could produce significant energy savings while not compromising behavioural function (e.g. predator avoidance). Hamilton and Barclay (1994) suggested that reproductive female *E. fuscus* may use shallow torpor as a means of saving energy while avoiding the costs associated with excessively low body temperatures.

Roosts

Bats spend a significant proportion of their lives roosting (Kunz 1982, Lewis 1996). Roosts provide stable microclimates and protection from predation and adverse weather (Churchill *et al.* 1997, Hamilton and Barclay 1994, Kunz 1982, Lewis 1996). During reproduction, temperate-zone bats may spend up to 17 hours per day subjected to the microclimatic conditions of their roosts (Holloway 1998). Considering the energetic costs of reproduction, the influence of temperature on fetal and juvenile growth rates, and the thermal lability of temperate insectivorous bats, the importance of microclimate in roost choice is clear (Churchill *et al.* 1997, Hamilton and Barclay 1994, Kunz 1982, Lewis 1996, Tuttle and Stevenson 1982).

Reproductive females should choose warm roosts to reduce the energetic costs of maintaining high body temperatures while facilitating fetal and juvenile growth (Hamilton and Barclay 1994, McNab 1982). Maternity colonies are often located in warm sites and colonial roosting may influence roost microclimate and energy expenditure (Barclay 1993, Churchill *et al.* 1997, Kunz 1982). Metabolic heat produced by colonial bats may be trapped within their roosts improving

energy economy (Kunz 1982). Furthermore, colonial bats can cluster, reducing the exposed surface area of individual bats, and consequently reducing heat loss and evaporative water loss (Kunz 1982). Clustering may allow juvenile bats to maintain high body temperatures before they develop the ability to thermoregulate.

Colony size is variable in bats (Barclay 1993, Holloway 1998, Kunz 1982). Small colonies or solitary individuals are less able to take advantage of the benefits of metabolic heat accumulation and clustering behaviour. Therefore, the choice of roosts with appropriate microclimate may be particularly important for solitary-roosting bats or bats that roost in small colonies, especially during early lactation when juveniles are unable to thermoregulate.

Thermal variability in roosts permits behavioural thermoregulation (Hamilton and Barclay 1994, Vaughan and O'Shea 1976). Bats choose positions within their roosts corresponding to current energetic and reproductive requirements. Females can avoid high energetic demands while maintaining rapid fetal and juvenile growth rates by choosing positions that approximate their thermoneutral zone (Churchill *et al.* 1997, Vaughan and O'Shea 1976). As daytime temperatures change, bats change their positions accordingly. In mid-summer, pallid bats (*Antrozous pallidus*) roost in the entrance of deep crevices during the morning, but move deeper into the roosts as the day progresses to avoid overheating (Vaughan and O'Shea 1976). Behavioural thermoregulation also occurs at a seasonal level. Choice of roost microclimate changes as prey availability and energy requirements change during a season. For example, in

the spring and fall, pallid bats choose roosts that are sensitive to ambient temperatures to allow the use of torpor at a time when insect abundance is low (Vaughan and O'Shea 1976). During the summer, when insect abundance is high, pallid bats choose roosts with more stable temperature regimes (Vaughan and O'Shea 1976).

Objectives

Few studies have examined the interaction between foraging, thermoregulation, and roost choice in free-ranging bats roosting in their natural environment. Research has been limited to laboratory experiments (Kurta 1986, 1990, Kurta and Kunz 1988, Kurta *et al.* 1987, Studier and O'Farrell 1972, 1976) and studies of bats roosting in man-made structures (Audet and Fenton 1988, Grinevitch *et al.* 1995, Hamilton and Barclay 1994). The primary objective of my study was to provide a comprehensive account of foraging and thermoregulation in reproductive female bats roosting in their natural environment.

More specifically, my study addresses the following questions: (1) Do pregnant and lactating females have different foraging and thermoregulatory strategies? (2) Does ambient temperature influence foraging and thermoregulatory strategies? (3) Is the use of torpor limited to energy emergencies? (4) Does roosting behaviour differ between pregnant and lactating females? I used reproductive female long-eared bats, *Myotis evotis*, inhabiting the badlands of the South Saskatchewan River Valley to address these questions. I also addressed the question: (5) Does *M. evotis*, a

hawking/gleaning species, behave in a similar way to species that are strict aerial hawkers. By answering these questions I hope to provide insight into the energy budgets and life history strategies of naturally-roosting bats.

METHODS AND MATERIALS

Study Site

From May through August 1997 and 1998, I conducted my research in the badlands of the South Saskatchewan River Valley, about 30 kms southwest of its confluence with the Red Deer River. The site, known as the Old Ferry Crossing (in reference to an abandoned ferry crossing), is approximately 20 kms south of the town of Bindloss ($50^{\circ} 73'$, $110^{\circ} 56'$, elevation 700m) in southeastern Alberta. The river valley is bordered by steep sandstone cliffs inundated with drainage gullies (or coulees) eroded into the sandstone (Figure 1). Reproductive female *Myotis evotis* roosted in the coulees on either side of the river in cemented sandstone boulders that lay above the more permeable surrounding sandstone. Most foraging occurred in and around clusters of trees at the edge of the South Saskatchewan River (Figure 1). These clusters were dominated by a cottonwood species (likely *Populus deltoides* although the presence of two other species in the area, and the fact that they can hybridize made positive identification difficult; Stettler *et al.* 1996) with chokecherry (*Prunus virginiana*) and willow (*Salix* spp.) composing the understory. The cottonwoods were separated from the coulees

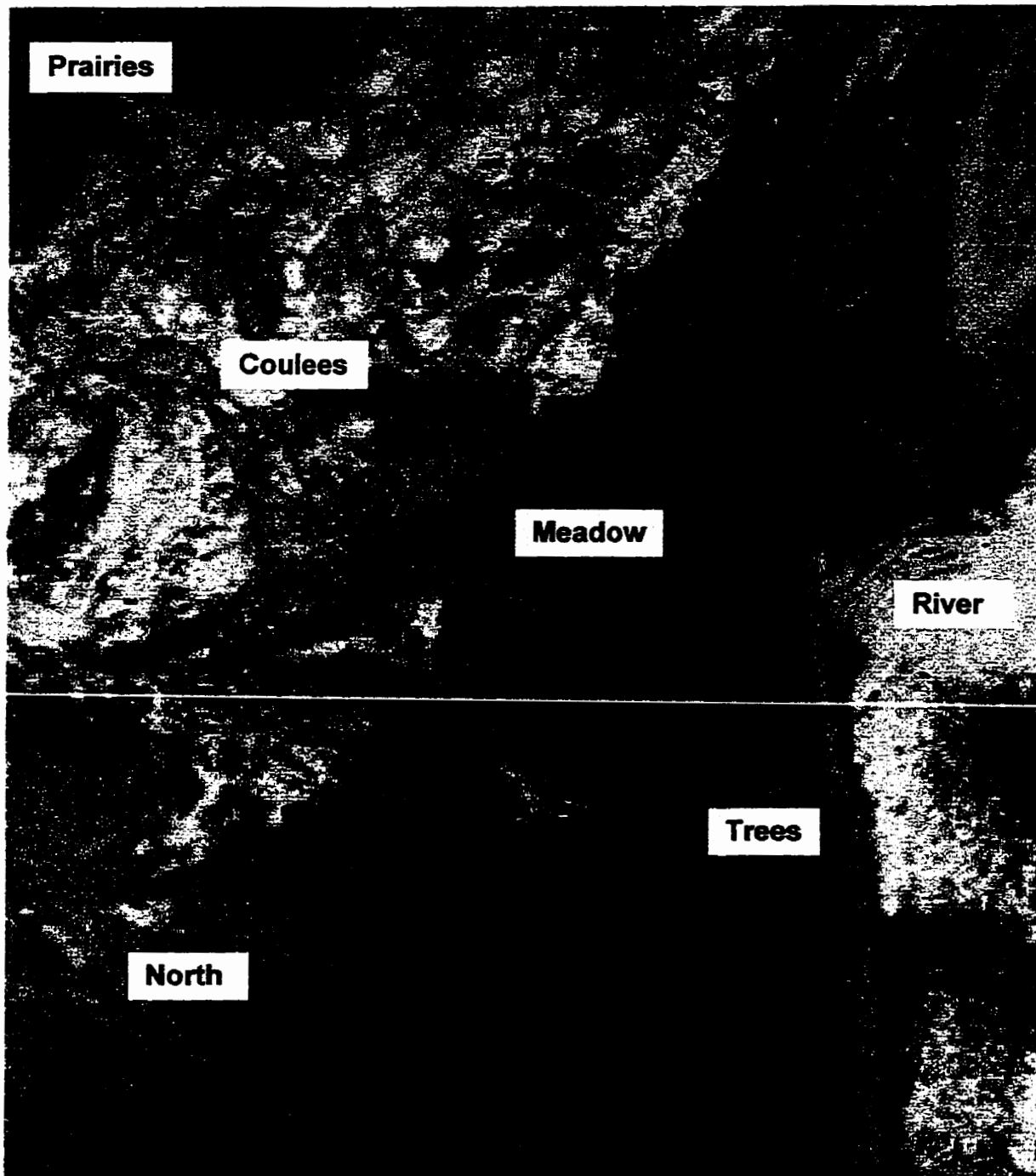


Figure 1. Aerial photo of study site showing the habitats where female *M. evotis* were found. Females roosted in the coulees and spent most of their foraging time in the trees (primarily Cottonwoods). The trees span a distance of approximately 200m.

by a meadow dominated by juniper (*Juniperus* spp.), sage (*Artemesia* spp.), prickly pear cactus (*Opuntia polyacantha*), ball cactus (*Coryphantha vivipara*), wild rose (*Rosa* spp.), spear grass (*Stipa comata*), and blue grama grass (*Bouteloua gracilis*).

Study Species

The long-eared bat, *Myotis evotis*, is a member of the Vespertilionidae. It is found throughout much of temperate western North America (Manning and Jones 1989). In my study area it is the second most abundant species, making up about 30% of all bats captured (Holloway 1998). As with most temperate species, *M. evotis* mates in the fall and this is the only investment males make to the reproductive effort. Females store sperm until the following spring when fertilization occurs (Manning and Jones 1989). In this study, all females captured before July 1 were pregnant and all but three of those captured after July 1 were lactating. Therefore, I will refer to May and June as the pregnancy period and to July and the beginning of August as the lactation period.

Lepidoptera make up a large component of the diet of *M. evotis* (Barclay 1991, Holloway 1998). Coleoptera and Diptera are also consumed in smaller amounts (Holloway 1998). The mixed diet of this species reflects the plasticity of its foraging strategy. *M. evotis* can take prey from vegetation (gleaning) as well as prey in flight (hawking) (Faure and Barclay 1992, 1994). The type of echolocation used by *M. evotis* depends on which foraging

strategy it uses. Gleaning bats use both passive hearing and low amplitude echolocation calls to detect prey. In contrast, hawking bats use higher amplitude echolocation calls to detect prey and do not rely on passive hearing (Faure and Barclay 1992, 1994). This plasticity in echolocation call behaviour, together with a slow, maneuverable mode of flight, allows *M. evotis* to obtain food through both gleaning and hawking. In my study area *M. evotis* is the only species that has been documented as a gleaner.

Capture

I captured bats by placing mist nets at various positions within the cottonwood stands (Figure 1). Reproductive condition of captured female bats was determined by gentle palpation of the abdomen for pregnancy, expression of milk or presence of bare patches around the nipples for lactation, and regrowth of fur around the nipples for post-lactation (Racey 1988). I determined the mass (Sartorius PT600 Electronic Precision Balance, ± 0.1 grams) and age (subadult or adult) of all captured bats. I determined age by examining the cartilaginous gap between the diaphysis of the metacarpal and proximal phalanx (Anthony 1988). I marked all captured females with numbered, coloured split-ring arm bands. I only used pregnant and lactating females in this study. Where palpation did not conclusively indicate the presence of a fetus (during early spring), I used subsequent captures to assess whether bats had been pregnant early on. Only one female used in

my analyses was not recaptured late enough in the season to confirm pregnancy.

Radio Transmitters

For the purposes of finding roosts, tracking foraging bats, and monitoring body temperatures, I attached temperature-sensitive radio transmitters (Holohil Systems, Carp, ON) weighing either 0.54g (1997) or 0.56g (1998) to reproductive female *Myotis evotis* (Audet and Fenton 1988, Grinevitch *et al.* 1995, Hamilton and Barclay 1994). To do this I trimmed the fur between the shoulder blades and glued the transmitters to the exposed skin using Skinbond® surgical adhesive (Smith & Nephew United, Inc.).

Aldridge and Brigham (1988) estimated that transmitters weighing 5% of an individual's mass would decrease their maneuverability by 5% leading to a reduction in foraging efficiency. They suggested that transmitters should be kept below 5% of an individual's mass to prevent this reduction. In 1998 I opportunistically attached 0.1g (less than 2.5% of the mass of the lightest bat) chemi-luminescent glow sticks (G. Pucci & Sons, Inc.) (Buchler 1976) to the backs of *M. evotis* to determine if they would behave in a way similar to bats carrying the heavier transmitters. I only light tagged one bat on any given night. One or two observers followed each light tagged bat for as long as it was visible noting where the bat was and whether it was foraging or roosting. Observations were recorded on hand held tape recorders (Realistic® Micro-14 Tape Recorder).

If added mass (e.g. the application of a transmitter or fetal production during pregnancy) influences behaviour, I would expect time spent foraging and time in torpor to change as females accumulate mass during pregnancy. I used a two-tailed t-test to determine if the mass of females changed between the first and second half of pregnancy. I used ANCOVAs to determine if time spent foraging or time in torpor differed between the first and second half of pregnancy. Period of pregnancy (first half or second half) was the categorical variable in these analyses. Night length was a covariate in the foraging time analysis and time available for torpor was a covariate in the torpor time analyses (see below).

Monitoring Ambient and Body Temperatures

Ambient Temperatures

I used a HOBO[®]-TEMP data logger (Model HTEA-37+46, Onset Computer Corporation) to keep a continuous record of ambient temperature in both 1997 and 1998. The logger recorded temperatures every 10 minutes. I placed the logger in a plastic bottle that had the bottom removed and vents cut into the sides to allow air to flow through the bottle. The bottle was painted white to avoid heating by direct sunlight. The bottle/logger was positioned about a meter and a half above the ground with the open end facing down. In 1997 I placed one logger in the cottonwoods by the South Saskatchewan River and one in the coulees where the bats roosted. Whenever possible I used temperatures from the coulee logger in my analyses. However, due to technical problems with the

logger in the coulees, I used temperatures from the logger in the cottonwoods in some of my analyses. I performed least square regressions of coulee temperatures on river temperatures at 01:00, 22:00, 08:00, 12:00 for the 1997 temperature data. None of the intercepts of these regressions were significantly different from zero ($p > 0.05$), none of the slopes were significantly different from one ($p > 0.05$), and all of the r^2 s were greater than 0.9. Therefore, the use of river temperatures in my analyses should not influence my results. In 1998 the bottle/logger was only placed in the coulees.

Use of Torpor and Deep Torpor

I monitored the body temperature of radio-tagged bats from the time they returned to their roost after foraging until they emerged again the following evening. I kept track of roosting bats manually using a Merlin 12 receiver (Custom Electronics, Urbana, IL) attached to a five-element Yagi antenna. I recorded the time taken for a transmitter to emit 10 pulses (averaged over 3 sets of 10) and compared these values to transmitter-specific calibration curves (provided by Holohil Systems Ltd) to determine skin temperatures. Skin temperature measured in this way accurately reflects core body temperature in active and torpid bats (Barclay *et al.* 1996, Audet and Thomas 1996). I also used a LOTEK SRX 400 scanning receiver to monitor body temperatures automatically while I was away from the study area each day.

I used the definitions of torpor and deep torpor described by Grinevitch *et al.* (1995) and Hamilton and Barclay (1994). An individual was in torpor if

its body temperature fell below its active temperature (i.e. the lowest body temperature of the individual immediately before it emerged to forage, from all of the days that it held its transmitter). It was in deep torpor if its body temperature fell below its active temperature by at least 10 °C. I defined the time available for the bat to use torpor as the amount of time when the ambient temperature was below the bat's active temperature (Figure 2).

I recorded the body temperatures of bats every ten to twenty minutes throughout the roosting period. Occasionally, the scanning receiver lost the signal, leaving gaps in the daily temperature profile of a roosting bat. In these cases I assumed that changes in body temperature occurred linearly with time, to determine entry or exit times for the use of torpor (Figure 3). I only did this for days where the existing portion of the temperature profile was sufficient to tell when the bat started entering or exiting torpor.

I analysed time in torpor using ANCOVA with minimum ambient temperature during torpor, foraging time the night before, and time available for torpor as covariates, and reproductive condition (i.e. pregnant or lactating) and individual nested within reproductive condition as class variables. I considered individual nested within reproductive condition to be a random effect. I included individual in the model to account for repeated measures (i.e. data taken over several days). Insufficient sample size prevented me from performing a similar analysis on time spent in deep torpor. I used a Fisher's exact test to look at differences in the frequency of use of deep torpor between pregnant and lactating females. This test was appropriate because

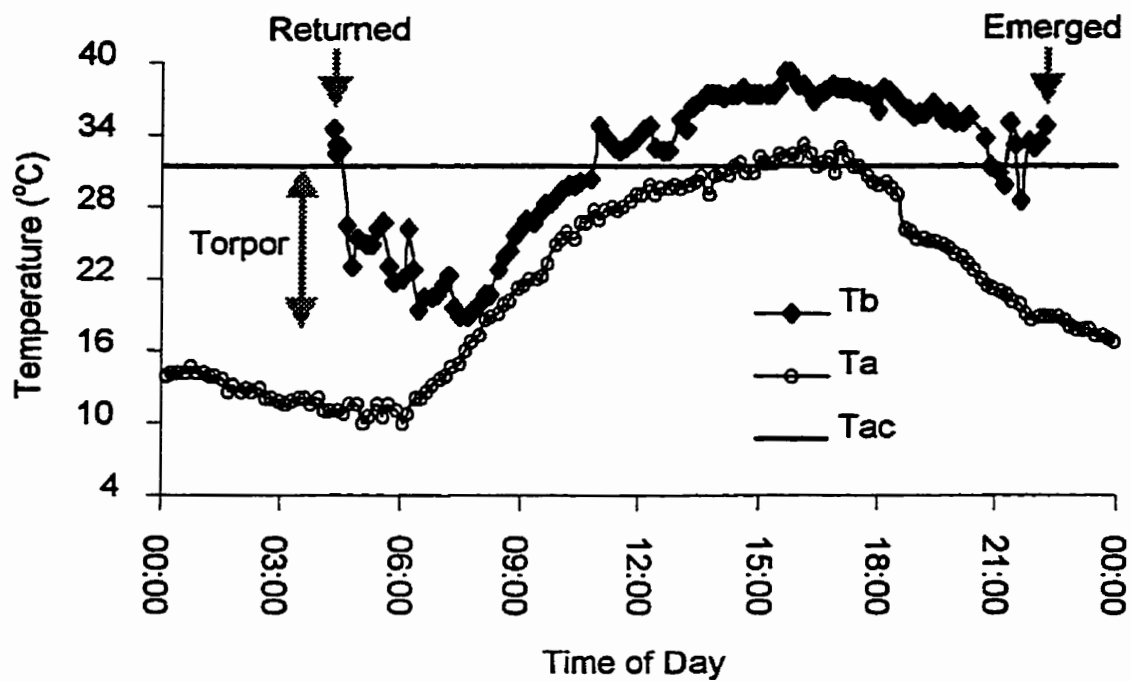
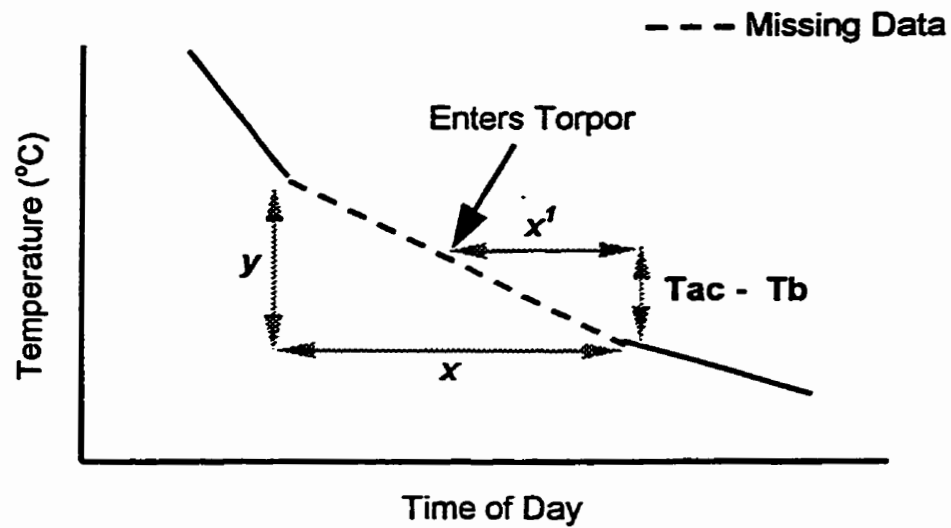


Figure 2. A typical daily temperature profile of a reproductive female *M. evotis*. This profile is from a pregnant bat on 25 May 1998. Tb is the body temperature of the bat. Ta is the ambient temperature. Tac is the active temperature of the bat. The female is in torpor when her body temperature is below the active temperature.

A) Schematic Temperature Profile

B) Determining x^1

$$\frac{y}{x} = \frac{T_{ac} - T_b}{x^1}$$

$$\therefore x^1 = \frac{x(T_{ac} - T_b)}{y}$$

Figure 3. The method used to calculate the time of entry into torpor when data points were missing from the temperature profile. (A) T_{ac} is the bat's active temperature. T_b is the first recorded body temperature after the missing data. x and y are both known quantities. x^1 is the amount of time before the first new data point that the bat entered torpor. (B) The calculations used to determine x^1 . These calculations assume that temperature is changing in a linear fashion.

more than half of the cells contained expected values that were less than five. Finally, I used least square regressions to investigate the influence of ambient temperature on minimum body temperature during both pregnancy and lactation.

Foraging

Time Spent Foraging

I monitored tagged bats from the time they emerged until they finished foraging at the end of the night. Observations were typically made every ten to twenty minutes. On some nights when we were occupied with other tasks the intervals were longer, and on other nights we kept a continuous record of a bat's activity. I calculated foraging time as the amount of time between emergence from the roost at dusk and return to the roost at dawn because bats did not spend long periods of time roosting (i.e. not in flight) during the night (see Results).

I analysed foraging time using ANCOVA with night length (defined as the time between sunset and sunrise), time spent in torpor the day before, and ambient temperature at return (T_a) as covariates, and reproductive condition and individual nested within reproductive condition as class variables. I considered individual nested within reproductive condition to be a random effect. I included individual in the model to account for repeated measures (i.e. data taken over several days).

Habitat Use

I examined the pattern of nighttime activity in reproductive females during the 1998 field season. Radio tracking observations from 1997 were not sufficiently detailed (i.e. the intervals between observations were longer and they were not categorized into specific habitats) to include them in this analyses. In 1998 I kept track of whether bats were foraging (moving) or roosting (sedentary) and whether they were in the coulees, meadow, prairie, trees, or across the river. Because bats never roosted in the meadow or coulees, I performed two analyses on these data. First for each night, I determined the proportion of the tracking time (while the bat was within range of the radio receiver) that a bat spent foraging in each of the five habitats. I used a four-factor ANOVA for this analysis (factors: habitat, reproductive condition, individual nested within reproductive condition, and night nested within both individual and reproductive condition). Second, for each night, I determined the proportion of the tracking time (while the bat was within range) that an individual spent foraging or roosting in the prairies, trees, or across the river. I used a five-factor ANOVA for this analysis (factors: activity, habitat, reproductive condition, individual nested within reproductive condition, and night nested within both individual and reproductive condition). Within each day, for each individual, the calculated proportions always added to one. Because the data for each day were bounded in this way, I transformed the data for both analyses using a logodds transformation (Neter *et al.* 1985),

$$LN\left(\frac{proportion}{1-proportion}\right)$$

and variances were weighted according to:

$$\frac{1}{proportion^3(1-proportion)^3}$$

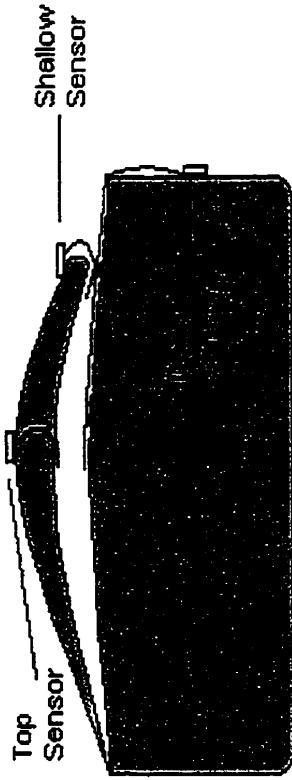
Means and SE's of logodds-transformed data were back-transformed, resulting in asymmetrical SE's. Individual was considered to be a random variable and was included in the model to account for repeated measures (i.e. data taken over several days).

Characterization of Roosts

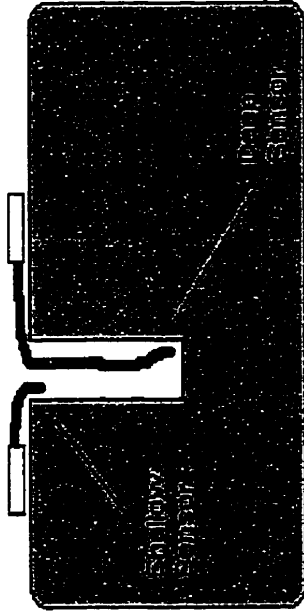
Roost Structure

During the 1997 field season I found that pregnant and lactating females chose roosts that were structurally different (Figure 4). I quantified these differences in a number of ways. First, I grouped roosts as having the longest dimension either vertical or horizontal to the ground. I used a two-tailed Fisher's exact test to examine differences in the use of vertical or horizontal roosts by pregnant and lactating females. This test was appropriate because more than half of the expected values were less than five. Second, I measured the minimum width of the rock on either side the roost chamber. This provided two measures: one of the larger bounding piece of rock and one of the smaller bounding piece of rock. Because the data were non-normal, I

A) Schematic Diagram of a Horizontal Roost



B) Schematic Diagram of a Vertical Roost



C) Horizontal Roost



D) Vertical Roost

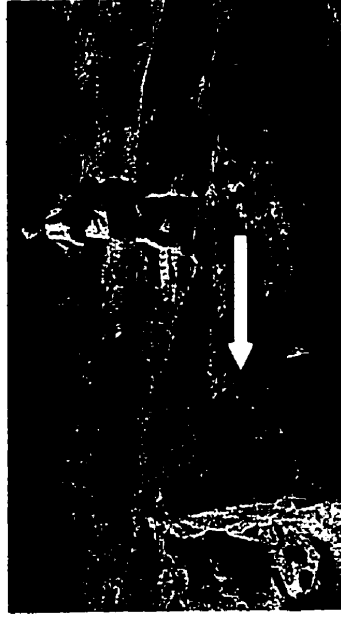


Figure 4. Types of roosts chosen by pregnant and lactating *M. evotis*. (A, C) Pregnant females roosted in horizontal crevices under flakes of rock that weathered off the surface of cemented sandstone boulders. (B, D) Lactating females roosted in vertical crevices where the cemented sandstone boulder had split in two. (A, B) Show the various positions where I placed HOBO-TEMP[®] data loggers. (C, D) The arrows indicate the location of the roost in the two photographs.

used Mann-Whitney U tests to compare these measures between roosts chosen by pregnant and lactating females.

Roost Temperatures

In 1998 I placed HOBO[®]-TEMP data loggers (Model HTEA-37+46) into pregnancy (horizontal) and lactation (vertical) roosts at the same time. I monitored six horizontal/vertical pairs consecutively throughout the summer (Table 1). Loggers remained in each pair of roosts for ten to twelve days. The loggers recorded roost temperatures every 10 minutes. I placed two loggers in each roost. In vertical roosts, loggers were always in both a deep position (~15 to 30 cm from the roost opening) and a shallow position (~ 3 cm from the roost opening) (Figure 4). In horizontal roosts, one logger was always placed in the deep position (~15 to 30 cm from the roost opening on the lower surface of rock), but the second alternated between placement in the shallow position (~ 3 cm from the roost opening on the lower surface) and the top position (immediately above the deep position, but on the upper rock surface) (Figure 4). In both types of roosts, the deep position corresponded to the position of bats when I could actually see them in the roosts. Bats were not necessarily in the roosts that I had sensors in at the time when the sensors were there, although all roosts had been used previously.

I determined mean daytime and mean nighttime temperatures for both types of roosts at each position. Mean daytime temperatures were calculated as the mean of all temperatures between the average return time and average

Table 1. Position of HOBO®-TEMP data loggers in roosts chosen by pregnant and lactating *M. evotis*. Data loggers were in horizontal and vertical roosts at the same time for the dates specified. See Figure 4 for a description of the positions.

Pair	Period	Position of Sensors		Dates
		Horizontal Roost	Vertical Roost	
1	Pregnancy	Shallow, Top	Shallow, Deep	26 May -6 June
2	Pregnancy	Shallow, Top	Shallow, Deep	11 Jun -21 Jun
3	Pregnancy	Shallow, Deep	Shallow, Deep	23 Jun -2 Jul
4	Lactation	Shallow, Deep	Shallow, Deep	7 Jul -16 Jul
5	Lactation	Shallow, Deep	Shallow, Deep	17 Jul -25 Jul
6	Lactation	Shallow, Top	Shallow, Deep	31 Jul - 9 Aug

emergence time of all bats during the period in question (i.e. pregnancy or lactation). Similarly, mean nighttime temperatures were calculated as the mean of all temperatures between the average emergence time and the average return time of all bats during the period in question. I also determined daily (24 h) maximum temperatures, minimum temperatures, and temperature ranges for each of the roosts.

Thermal Regimes of Horizontal vs. Vertical Roosts

I examined the temperature regimes of roosts chosen by pregnant (horizontal roosts) and lactating (vertical roosts) females during the pregnancy and lactation periods (Table 1). This information may explain why females switch roost-types when they start lactating. I used the deep position in this analysis because it was the position where I actually saw females within the roosts. I analysed mean daytime temperatures, mean nighttime temperatures, daily maximum temperatures, daily minimum temperatures, and daily temperature ranges separately using ANCOVA, with the appropriate measure of ambient temperature (i.e. mean daytime temperatures, mean nighttime temperatures, maximum temperatures, minimum temperatures, or temperature ranges) as a covariate. Period of the season (i.e. pregnancy or lactation), roost-type (i.e. horizontal or vertical) and roost-pair (i.e. 1 – 6) were class variables (Table 1). Roost-pair was included in the models to account for repeated measures (i.e. data taken over several days). I did not include a random variable in this analysis because bats reused many of the same roosts within and between years. Therefore, I assumed that these roosts

corresponded to a large and representative portion of the population of roosts chosen by reproductive female *M. evotis*.

Thermal Conditions Within Roosts

To assess the range of conditions available to bats within roosts, I analysed horizontal and vertical roosts separately. For horizontal roosts I divided the data further and analysed roosts that had loggers in the top position separately from those that had loggers in the shallow position (Figure 4). I used two-factor ANOVAs to analyse mean daytime temperatures, mean nighttime temperatures, and daily maximum temperatures, minimum temperatures, and temperature ranges for each set of analyses (deep vs. shallow in vertical roosts, deep vs. shallow in horizontal roosts, and deep vs. top in horizontal roosts). The two factors included in each analysis were position of the sensor within the roosts and individual roost. Individual roost was included in the models to account for repeated measures (i.e. data taken over several days).

Analyses

All ANCOVAs and regressions were performed on SAS Version 7.0. Other analyses were performed on Statistix for Windows and Systat Version 5.0. I present means \pm SE unless otherwise stated. I used an alpha value of 0.05 except for pairwise comparisons where I corrected alpha values using the sequential Bonferroni procedure (Rice 1989).

RESULTS

Captures

In 1997 I captured a total of 13 adult female *M. evotis*. Three of these were recaptured once and three were recaptured twice, for a total of 22 captures. Eight of the captures (seven females) involved females that were not obviously pregnant, seven (seven females) involved females that were obviously pregnant, six (five females) involved females that were lactating, and one involved a female that was post lactating.

In 1998 I captured a total of 17 adult female *M. evotis*. Seven of these were recaptures from 1997. Within 1998, three bats were recaptured once and one was recaptured three times, for a total of 23 captures. Four of the captures (four females) involved females that were not obviously pregnant, five (four females) involved females that were obviously pregnant, nine (seven females) involved females that were lactating, and five (five females) involved females that were non-reproductive.

Subsets of females were used in the analyses of foraging and torpor. Which females were used depended on whether I had obtained radio-tracking data for the individuals and whether the data were suitable for the particular test. Post-lactating and non-reproductive females were not used in the analyses. Only one not-obviously-pregnant female used in the analyses was not captured late enough in the season to reassess her reproductive state. Removing this bat from the analyses did not influence any results.

Effect of Radio Transmitters

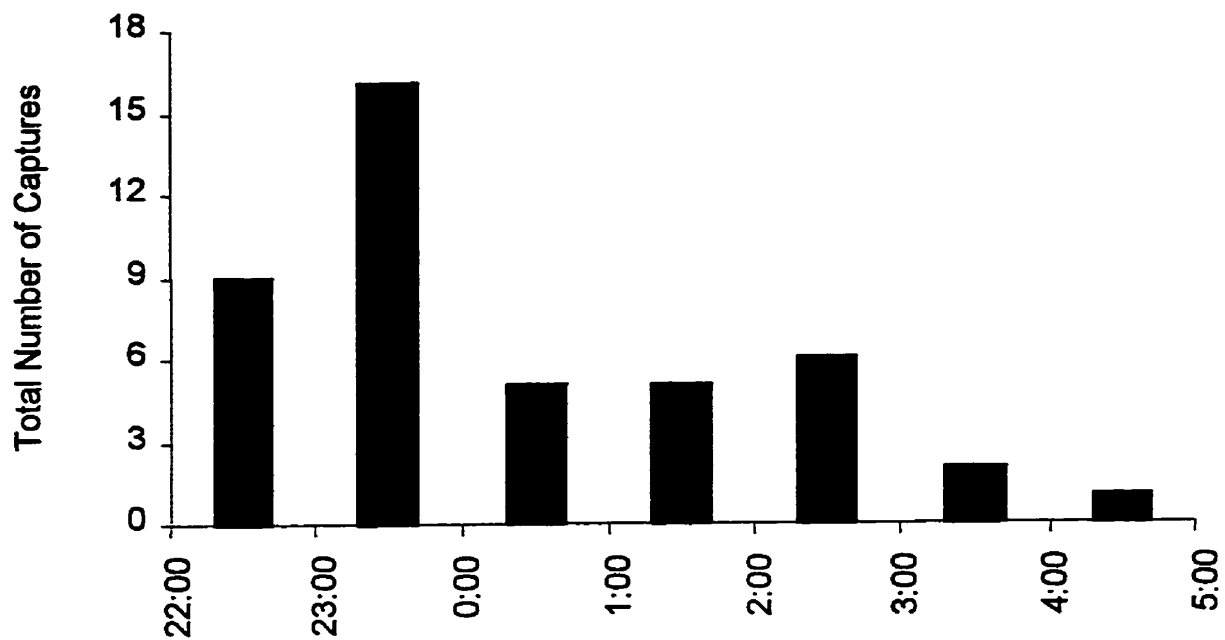
Aldridge and Brigham (1988) suggested that transmitters should be kept below 5% of an individual's body mass. In this study, using the smallest transmitters available, transmitter mass ranged from 5.9% to 8.9% of bat mass, with a mean of $7.3 \pm 0.1\%$ of bat mass (N=34).

In 1998 I opportunistically attached 0.1g chemi-luminescent glow sticks to the backs of *M. evotis* to determine if they would behave in a manner similar to bats carrying transmitters. Light tagged bats were difficult to keep track of because they spent much of their time within or above the canopy of the cottonwoods. The cottonwoods spanned a distance of about 200m. This made it difficult to monitor even one side of the trees because there were typically only one or two observers at a given time. Furthermore, the bats foraged over a wide range of heights (from ~ 1m above the ground to > 14.5 m – the height of the tallest cottonwood). The light tags were hard to see when the bats were high, in or above the trees. In spite of these limitations, our light tagging observations indicate that at least some bats forage for most of the night, and bats seem to spend the majority of their foraging time in or around the cottonwoods, as did radio tagged bats (see below). For example, on one night, a light tagged bat was observed periodically for almost four hours. On another, a bat was observed for almost six hours.

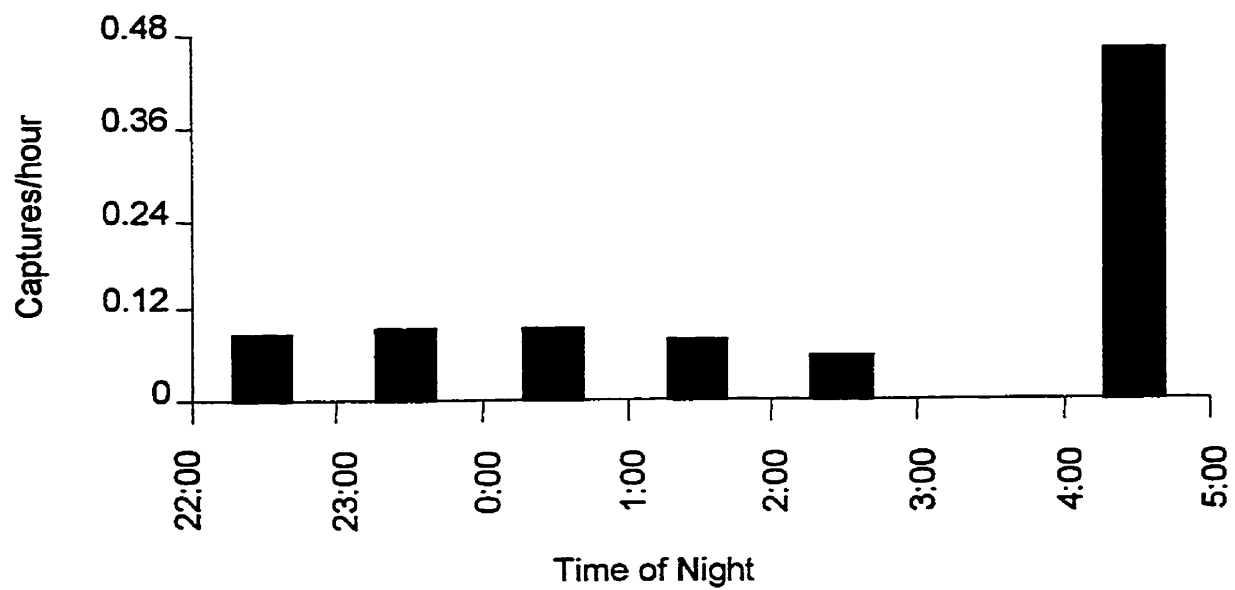
Data from mist netting show that *M. evotis* were captured during every hour of the night (earliest capture was 22:15 and latest capture was 4:08) and capture rates were consistent throughout the night (Figure 5). The peak in

Figure 5. (A) The total number of captures of female *M. evotis* relative to time of night. The data are pooled for 1997 and 1998. N=44 captures. (B) The capture rate (i.e. captures/hour) relative to time of night. The time spent netting was not recorded in 1997. Therefore, capture rates were only calculated with 1998 data.

A) Total Captures



B) Capture Rate



capture rate in the 4:00 to 5:00 category (Figure 5B) results from a single capture during a short period of time spent netting (i.e. 130 min over the entire season). I used chi-square to determine if the observed frequency of captures during the first two hours, second two hours, or third two hours of the night differed from the expected frequency during these periods based on time spent netting. They did not ($X^2=1.92$, $df=2$, $p>0.05$). This suggests that I was equally likely to capture female *M. evotis* at any time of night. Radio tagged bats also foraged for most of the night every night (see below).

The mass of pregnant females increased significantly between the first half and second half of pregnancy (mean increase=1.4g or 20.3%, $N=19$, $t=4.43$, $df=17$, $p<0.001$), but not between the first half and second half of lactation (mean decrease=0.1g or 1.2%, $N=16$, $t=0.35$, $df=14$, $p>0.7$). I used ANCOVAs to see if the change in mass during pregnancy corresponded to a change in time spent foraging or time spent in torpor. The model describing time spent foraging explained a significant proportion of the variation in the data ($F_{2,42}=9.34$, $r^2=0.31$, $p<0.001$). However, neither night length ($F_{1,42}=3.28$, $p>0.077$) nor period of pregnancy (first half or second half, $F_{1,42}=0.70$, $p>0.4$) significantly influenced the amount of time spent foraging during the pregnancy period. The model describing the time spent in torpor did not describe a significant proportion of the variation in the data ($F_{2,23}=2.70$, $r^2=0.19$, $p>0.088$). The use of habitat was also similar between the first half and second half of pregnancy (Table 2). The bats used the trees most frequently, the meadow and river moderately frequently, and the coulees and prairies least frequently during both the first and second half of pregnancy.

Table 2. The percentage of the total foraging time that was spent in each habitat during the first half (2670 min) and second half of pregnancy (1203 min).

	Coulees	Meadow	Trees	River	Prairies
First Half	8.2 %	17.2 %	58.4 %	16.3 %	0 %
Second Half	3.7%	11.6 %	54.4 %	26.3 %	4.0 %

Myotis evotis that had transmitters attached previously, had consistently increased in body mass upon recapture (Table 3). The only loss in mass occurred because the female (*M. evotis* 10) gave birth between two successive captures three days apart. On average bats that were captured more than once were recaptured 26.8 ± 12.3 days after a previous capture, after wearing a transmitter for from one to eight days (mean 3.3 ± 2.0 days). On average these bats had gained 12.6 ± 6.4 % of their initial body mass. This result is partly a consequence of differences in reproductive stage between recaptures, but there was a similar trend for both pregnant and lactating bats. *M. evotis* 6 is a striking example. *M. evotis* 6, a pregnant female, gained 20.6 % of her initial body mass over 15 days while wearing a transmitter for at least six of those days. Similarly, *M. evotis* 20, a lactating female, gained 11.3 % of her initial body mass over eight days while wearing a transmitter for three of those days. These results suggest that foraging was not hampered by the application of a radio-transmitter.

There was no evidence that the application of transmitters resulted in prolonged gestation or aborted pregnancy. The earliest date that I caught a lactating female that had carried a transmitter during pregnancy was July 11; the earliest date that I caught a lactating female that had not carried a transmitter during pregnancy was July 7. When recaptured, all individuals initially recorded as not obviously pregnant or pregnant were reproductive (pregnant or lactating). This indicates that the application of transmitters did not cause females to abort.

Table 3. Mass changes in recaptured adult female *M. evotis* after carrying radio-transmitters for different lengths of time. + indicates an increase in mass and - indicates a decrease in mass. N.O.P. indicates a female that was not obviously pregnant.

Bat	Date	Reproductive Condition	Transmitter Applied	Transmitter Mass	Bat Mass	# of Days with Transmitter	Change in Mass Since Last Capture
M. evotis 1	1-June-97	N.O.P.	Yes	0.54 g	7.1 g	3 days	-----
M. evotis 1	23-July-97	Lactating	-----	-----	9.1 g	-----	+ 29.6 %
M. evotis 2	1-June-97	N.O.P.	Yes	0.54 g	7.1 g	2 day	-----
M. evotis 2	25-June97	Pregnant	Yes	0.54 g	8.4 g	3 days	+ 18.3 %
M. evotis 2	2-August-97	Post Lactating	-----	-----	8.7 g	-----	+ 3.6 %
M. evotis 6	4-June-97	N.O.P	Yes	0.54 g	6.3 g	≥ 6 days	-----
M. evotis 6	19-June-97	Pregnant	-----	-----	7.6 g	-----	+ 20.6 %
M. evotis 12	18July-97	Lactating	Yes	0.54 g	8.0 g	1 day	-----
M. evotis 12	26-July97	Lactating	-----	-----	8.0 g	-----	0 %
M. evotis 10	19-May-98	Pregnant	Yes	0.56 g	6.8 g	7 days	-----
M. evotis 10	11-July-98	Pregnant	No	-----	9.9 g	-----	+ 45.6 %
M. evotis 10	13-July-98	Lactating	No	-----	7.7 g	-----	- 22.2 %
M. evotis 10	29-July-98	Lactating	-----	-----	8.2 g	-----	+ 6.5 %
M. evotis 20	13-July-98	Lactating	Yes	0.56 g	7.1 g	3 days	-----
M. evotis 20	21-July-98	Lactating	-----	-----	7.9 g	-----	+ 11.3%

Foraging

Habitat Use

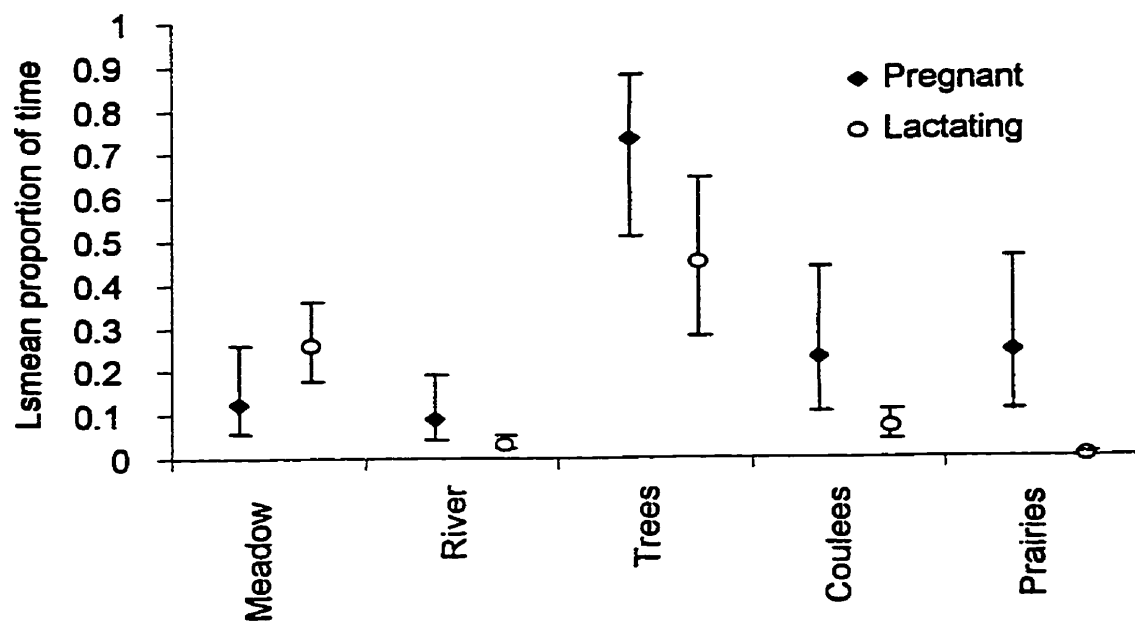
I examined the pattern of nighttime activity in reproductive females during the 1998 field season. I radio tracked four pregnant (N=20 bat-nights) and six lactating females (N=27 bat-nights). Of the total time spent tracking, bats were only out of range 16.8% of the time. I kept track of whether bats were foraging (moving) or roosting (sedentary) and whether they were in the coulees, meadow, prairie, trees, or across the river.

The ANOVA with four factors (habitat, reproductive condition, night and individual) explained a significant amount of the variation in the pattern of habitat use of foraging bats ($F_{51,39}=202.53$, $p<0.001$). Night ($F_{21,39}=6.57$, $p<0.001$) and habitat ($F_{4,39}=5.90$, $p<0.001$) both had significant effects. Significant interactions between habitat and reproductive condition ($F_{4,39}=8.34$, $p<0.001$, Figure 6A) and habitat and individual ($F_{14,39}=3.92$, $p<0.001$) also explained variation in the pattern of habitat use. Pregnant bats spent a significantly greater proportion of their nights foraging in the trees than in any other habitat (Figure 6A). Lactating females also spent a significantly greater proportion of their time foraging in the trees than in any habitat other than the meadow (Figure 6A).

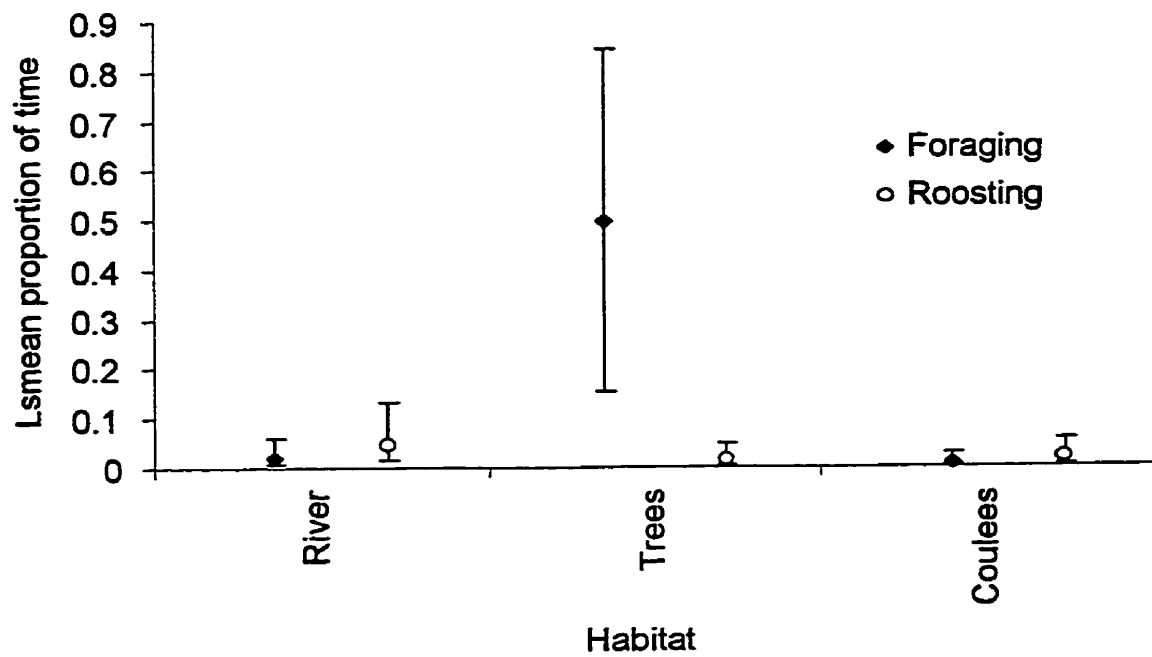
The ANOVA with five factors (habitat without meadow or prairie as levels, activity, reproductive condition, night, and individual) explained a significant amount of the variation in the pattern of activity and habitat use ($F_{97,14}=2626.34$, $p<0.001$). Habitat ($F_{2,14}=6.39$, $p=0.011$) and activity ($F_{1,14}=24.99$, $p<0.001$) had significant effects. There were also significant interactions between habitat and

Figure 6. Interactions from two ANOVA's describing the foraging activity of reproductive female *M. evotis*. x represents an interaction. (A) Pregnant females spent significantly more time foraging in the trees than in any other habitat ($p < 0.03$ for each comparison). Similarly, lactating females spent significantly more time foraging in the trees than in any other habitat except for the meadow ($p < 0.005$ for each comparison). (B) Females spent significantly more time foraging in the trees than roosting in the trees or performing either activity in either of the other two habitats ($p < 0.04$ for each comparison). Nine females were used in these analyses (N=30 bat-nights).

A) Reproductive Condition x Habitat



B) Habitat x Activity



individual ($F_{9,14}=6.54$, $p<0.001$), habitat and reproductive condition ($F_{2,14}=8.83$, $p=0.003$), habitat and night ($F_{28,14}=2.75$, $p=0.025$), and habitat and activity ($F_{2,14}=11.35$, $p<0.001$, Figure 6B). Females spent significantly more time foraging in the trees than roosting in the trees or performing either activity in either of the other two habitats (Figure 6B). There was also a significant interaction between activity and night ($F_{24,14}=3.69$, $p=0.007$).

Time Spent Foraging

Bats only spent a small proportion of the night roosting (see above). On average females stopped flying 5.1 ± 0.8 times per night for a total of 32.3 ± 4.8 minutes ($N=37$ bat-nights). These short breaks were likely used to consume large prey (Faure and Barclay 1992, 1994) so I consider them to be a part of the foraging bout. Therefore, I calculated foraging time as the time between a female's emergence from her roost at dusk and her return at dawn. I examined foraging time using data from 1997 and 1998 in a five-factor ANCOVA with reproductive condition, individual nested within reproductive condition, night length, ambient temperature at the time of return to the roost, and time spent in torpor the day before, as main effects. Five pregnant ($N=16$ bat-nights) and five lactating females ($N=14$ bat-nights) were used in this analysis. Variances were homogeneous, but foraging times for pregnant females were not normally distributed. Attempts to produce a normal distribution through transformations were unsuccessful so I treat marginal results with caution. Rain altered the

behaviour of one female producing an outlier. I removed this data point from the foraging time and torpor time analyses.

The model explained a significant proportion of the variation in foraging time ($F_{12,16}=18.1$, $r^2=0.93$, $p<0.001$). Only night length ($F_{1,16}=8.85$, $p<0.009$, Figure 7) had a significant effect. The longer the night, the longer the bats spent foraging, although foraging time was always less than night length (Figure 7).

Torpor

Use of Torpor and Deep Torpor

I monitored daytime body temperatures of 10 pregnant and seven lactating females over the 1997 and 1998 field seasons. Mean minimum body temperatures of pregnant and lactating females were 18.36 ± 0.88 °C and 23.92 ± 0.82 °C, respectively; mean maximum body temperatures of pregnant and lactating females were 36.22 ± 0.50 °C and 37.25 ± 0.42 °C, respectively; and mean active temperatures of pregnant and lactating females were 27.61 ± 0.53 °C and 31.25 ± 0.43 °C, respectively. Every bat used torpor every day.

However, pregnant females used deep torpor more frequently (71% of bat-days, N=38 bat-days) than lactating females (37% of bat-days, N=27 bat-days, Fisher's exact test, $p=0.011$, Figure 8).

I examined time in torpor using a five-factor ANCOVA with reproductive condition, individual nested within reproductive condition, time possible for the use of torpor, minimum ambient temperature during torpor, and time spent foraging the night before, as main effects. Six pregnant (N=15 bat-days) and six lactating (N=19 bat-days) females were used in this analysis. The model

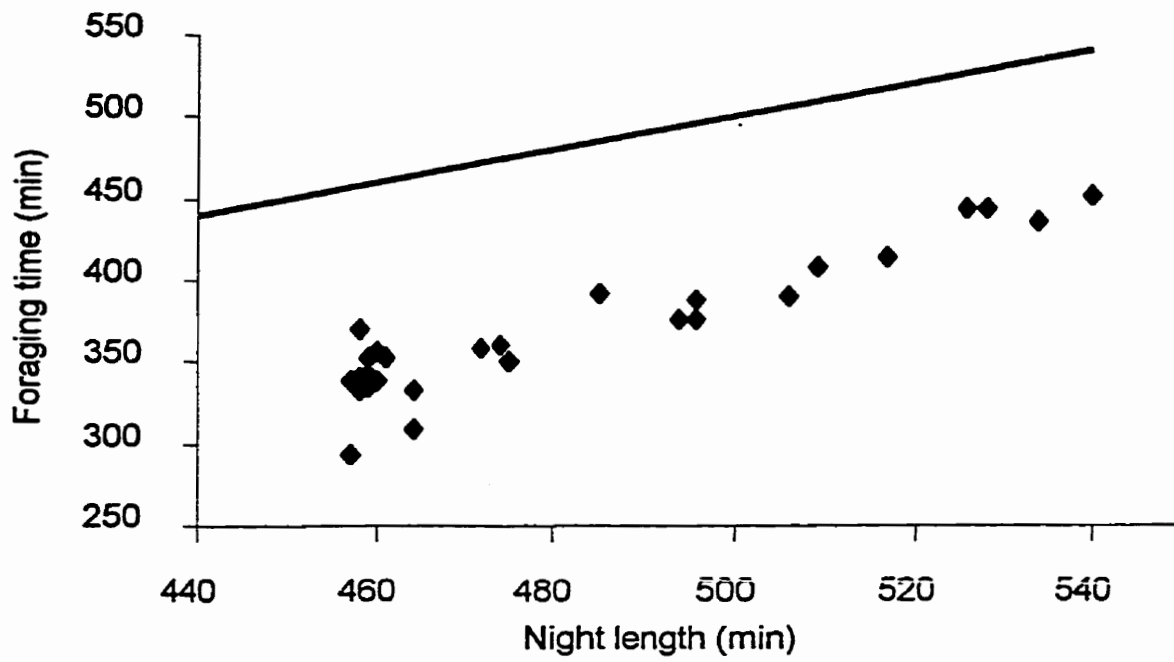


Figure 7. The significant effect from the ANCOVA describing the foraging time of reproductive *M. evotis*. Ten females were used in this analysis (N=29 bat-nights). The solid line indicates foraging time=night length. The regression line for the relationship is foraging time=0.99night length-108.5.

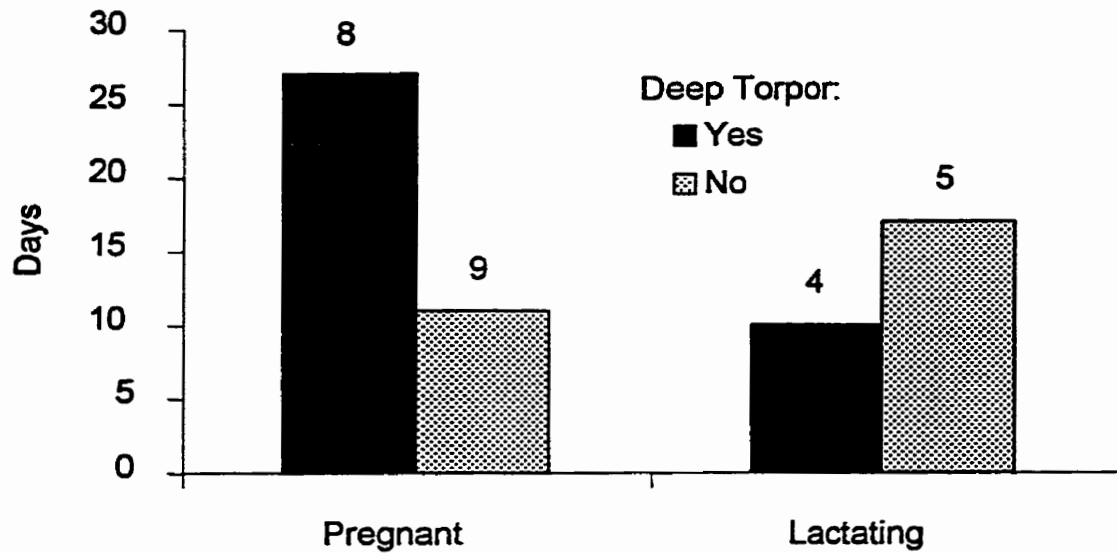


Figure 8. The number of days in which pregnant and lactating *M. evotis* entered or did not enter deep torpor. The numbers above the bars represent the number of bats observed in each category.

explained a significant proportion of the variation in torpor time ($F_{21,12}=4.08$, $r^2=0.88$, $p<0.008$). There was significant variation between individual females within a reproductive class ($F_{6,12}=3.58$, $p=0.029$), but the main factor influencing torpor time was the time available for the use of torpor ($F_{1,12}=21.96$, $p<0.001$, Figure 9). The relationship between torpor time and the time available for torpor was positive and the data (other than two points) fell below the one to one line (i.e. the time spent in torpor was less than the time available for torpor, Figure 9). There was also a significant interaction between foraging time the night before and individual ($F_{7,12}=3.96$, $p=0.018$).

Influence of Ta on Minimum Tb

I used least squares regressions to examine the influence of Ta on the minimum Tb of roosting females. I considered pregnant and lactating females separately. Ten pregnant (N=29 bat-days) and six lactating (N=24 bat-days) females were used in the respective regressions. There was no significant relationship between Ta and minimum Tb for pregnant females ($F_{1,27}=1.12$, $r^2=0.04$, $p>0.2$, Figure 10A). However, examination of the data showed two distinct groups of points (Figure 10A, regulators and conformers). The regulator group consisted of data from five of the ten females, with two bats represented on two different days (N=7 bat-days). Three of the five regulating females also had data points in the conformers group. The data in the regulators group came from 1997 and 1998 and span most of the pregnancy period, occurring from June 4 through June 28. The mean \pm SE minimum Tb of the regulators was 25.03 ± 0.29 °C. Because of the limited sample size, I did not perform a separate

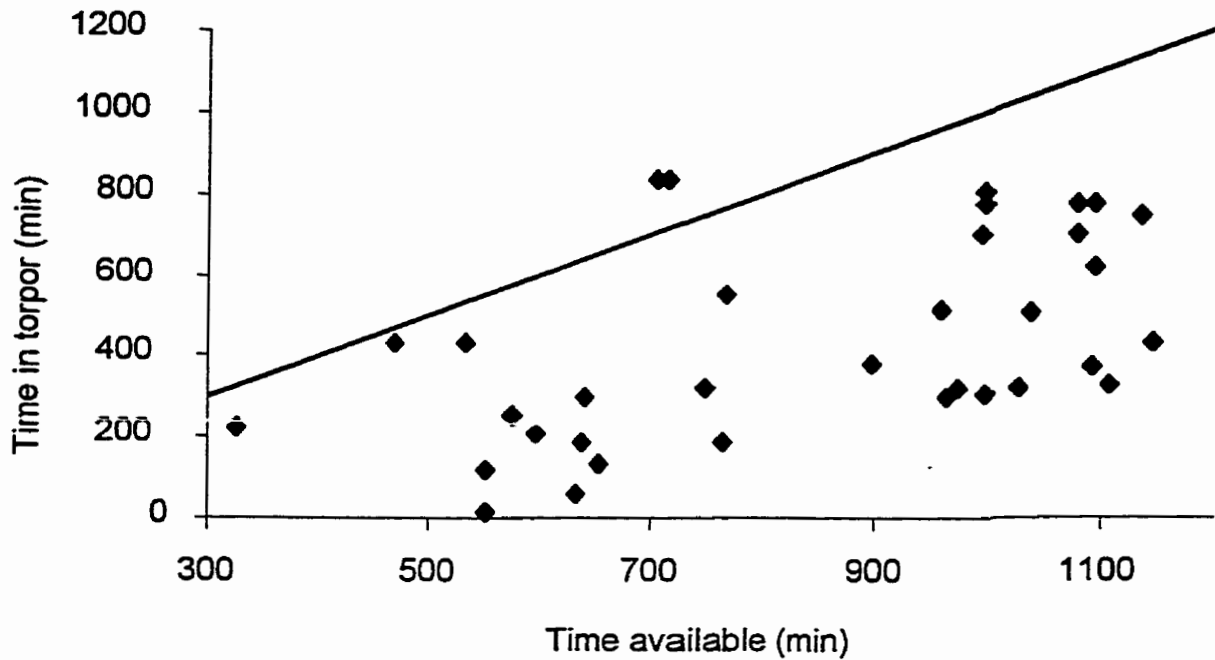
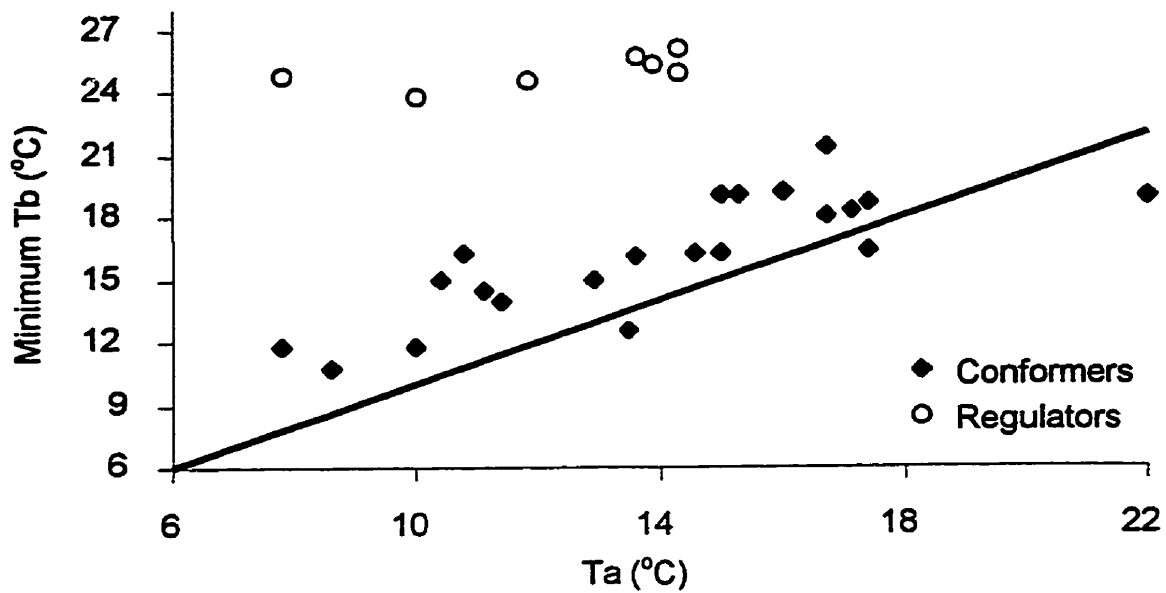


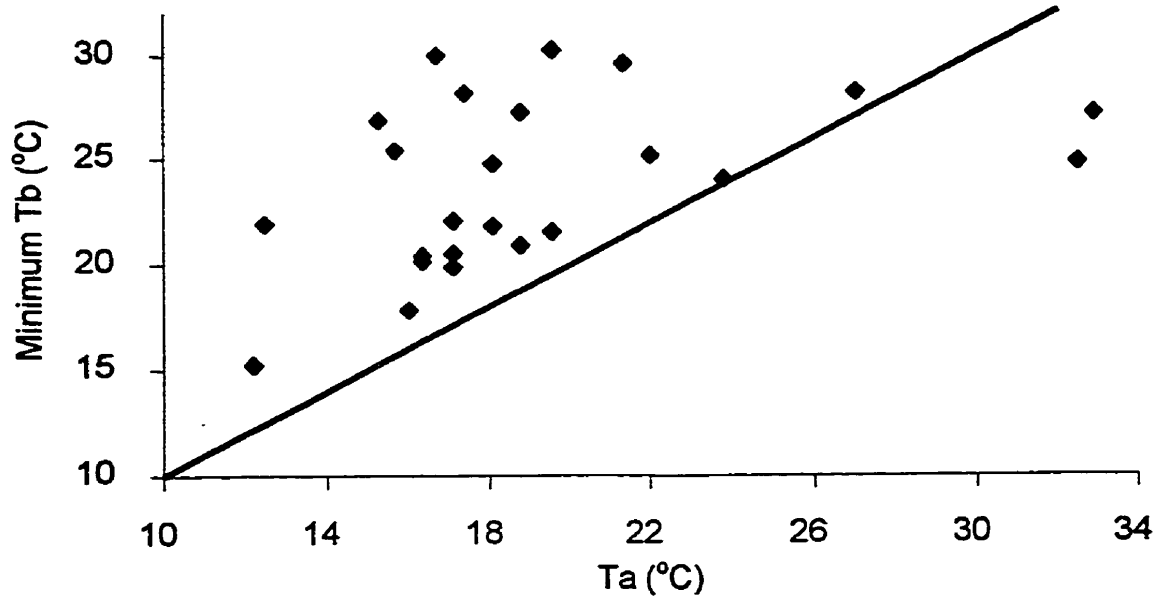
Figure 9. One significant effect from the ANCOVA describing the amount of time spent in torpor by reproductive female *M. evotis*. Twelve females were used in this analysis (N=34 bat-days). The solid line indicates torpor time=time available. The regression line for these data is $\text{Torpor time} = 0.65\text{Time available} - 202.3$.

Figure 10. The relationship between ambient temperature (T_a) and minimum body temperature (T_b) in (A) Pregnant and (B) Lactating female *M. evotis*. Ten pregnant females (N=28 bat-days) and six lactating females (N=24 bat-days) were used in these analyses. The solid lines indicate where minimum $T_b=T_a$. In (A) the regression is significant only when regulators are removed from the data set. The corresponding regression equation is $T_b=0.66T_a+6.93$. In (B) the regression is also significant and has a regression equation of $T_b=0.32T_a+17.81$.

A) Pregnancy



B) Lactation



regression on the regulator data points. However, it appears that these females maintained body temperature independent of ambient conditions, at least on the days in question (Figure 10A). Nevertheless, the mean minimum Tb for this group was still below the corresponding mean active temperature (27.34 ± 1.00 °C), and each minimum Tb was below the active temperature of the individual that it was obtained from.

The conforming group included data from eight of the ten pregnant females, with seven bats represented more than once (N=22 bat-days). The mean \pm SE minimum Tb of the conformers was 16.13 ± 0.60 °C. I performed a separate regression on the data from the conforming group. Ta had a significant, positive influence on minimum Tb for conformers ($F_{1,19} = 33.13$, $r^2 = 0.64$, $p < 0.001$).

Finally, there was also a significant positive relationship between Ta and minimum Tb for lactating females ($F_{1,23} = 4.56$, $r^2 = 0.17$, $p = 0.044$, Figure 10B). There was no obvious dichotomy in the data for lactating females.

Characterization of Roosts

Roost Structure

I tested for differences in the orientation of roosts chosen by pregnant and lactating females using two-tailed Fisher's exact tests. Pregnant females tended to use roosts that were in a horizontal plane (85% of roosts, N=13 roosts) whereas lactating females tended to use roosts that were in a vertical plane relative to the ground (88% of roosts, N=8 roosts, $p < 0.005$, Figure 11).

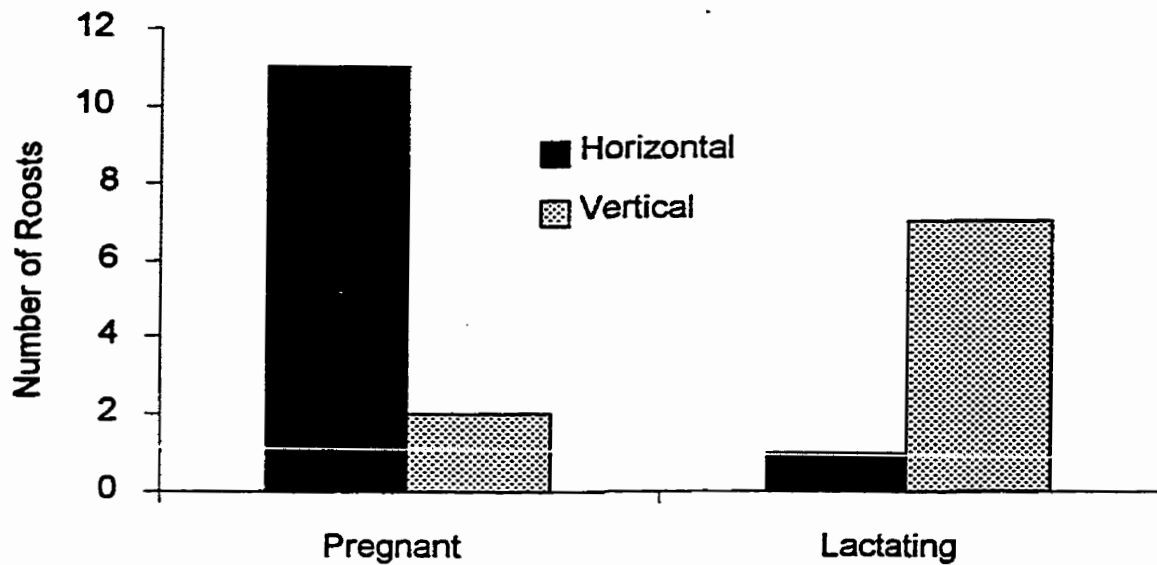


Figure 11. Choice of roosts by pregnant and lactating *M. evotis*. The roost chambers chosen by pregnant and lactating females were readily categorized as being in either a horizontal or a vertical plane relative to the ground (see Figure 4). N=21 roosts.

I measured the minimum width of rock on either side of the roost chamber. I compared the width of the smaller and larger bounding pieces of rock between roosts used by pregnant and lactating females using Mann-Whitney U tests. The width of the smaller bounding piece of rock was significantly smaller in roosts chosen by pregnant compared to those chosen by lactating females (Mann-Whitney $U=99$, $N_1=13$ pregnancy roosts, $N_2=8$ lactation roosts, $p<0.001$, Figure 12A). However, the width of the larger bounding piece of rock did not differ between roosts chosen by pregnant and lactating females (Mann-Whitney $U= 63$, $N_1=13$ pregnancy roosts , $N_2=8$ lactation roosts, $p>0.4$, Figure 12B). Because the smaller bounding rock layer was thinner in roosts used by pregnant females, pregnant females had less rock buffering them against the surrounding ambient conditions than lactating females.

Thermal Regimes of Horizontal vs. Vertical Roosts

I used four-factor ANCOVAs to examine differences in mean daytime temperatures, mean nighttime temperatures, and daily maximum temperatures, minimum temperatures, and temperature ranges (in the deep position, Figure 4) between roosts chosen by pregnant (horizontal roosts) and lactating (vertical roosts) females. Roost-type (vertical or horizontal), period of the season (pregnancy or lactation, see methods), ambient temperature (T_a), and roost-pair were the main effects in each of the five models. Each analysis involved six pairs of roosts ($N=63$ nights for nighttime means and $N=62$ days for the other four analyses).

The model describing mean daytime roost temperature explained a

A) Smaller bounding rock



B) Larger bounding rock

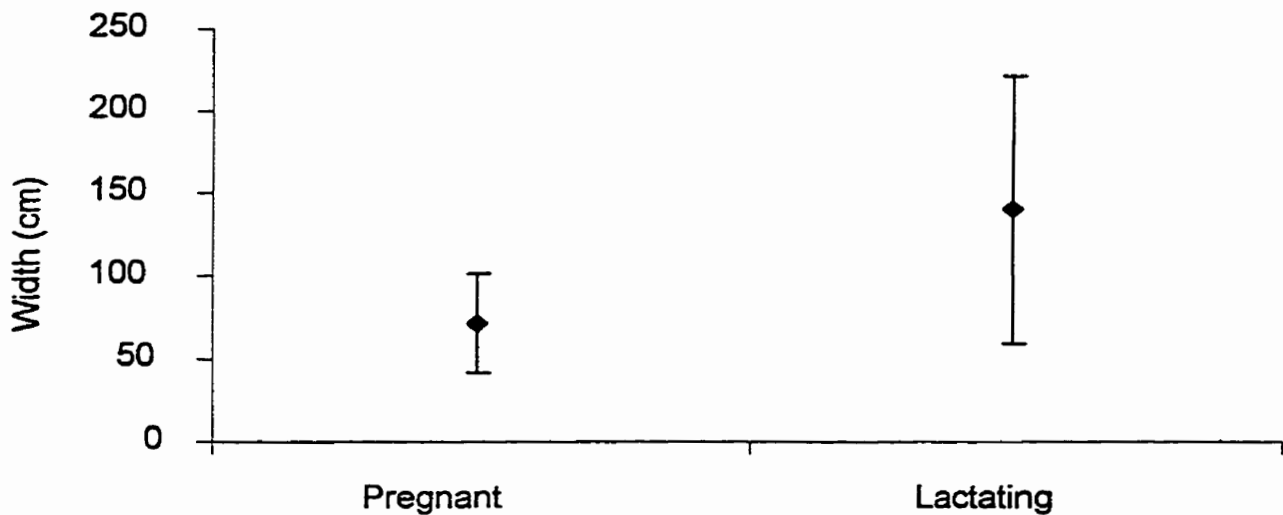


Figure 12. Comparison between the structure of roosts chosen by pregnant and lactating *M. evotis*. Differences in the widths of the (A) smaller and (B) larger bounding pieces of rock surrounding roosts chosen by pregnant and lactating *M. evotis*. Values are mean \pm SE.

significant proportion of the variation in the data (Table 4A). Period of the season, roost-pair, and mean daytime ambient temperature all significantly influenced mean daytime roost temperature (Table 4A), although these results must be interpreted with caution due to a number of significant interactions. There were significant interactions between roost-type and period of the season (Table 4A, Figure 13A), and roost-type and roost-pair (Table 4A). During the pregnancy period, horizontal roosts were significantly warmer than vertical roosts (Figure 13A). However, during the lactation period there was no significant difference between roost-types (Figure 13A).

Mean daytime ambient temperature is an important determinant of mean daytime roost temperature, although this relationship is influenced by period of the season, roost-pair, and roost-type (Table 4A, Figure 13B). Although these interactions are statistically significant, they are not visually obvious (e.g. Figure 13B), and their biological relevance is questionable. Considering all of the mean daytime temperature data together, the regression equation is $T_r = 0.79T_a + 6.03$.

The model describing mean nighttime roost temperature explained a significant proportion of the variation in the data (Table 4B). Period of the season, roost-pair, roost-type, and mean nighttime ambient temperature all significantly influenced mean nighttime roost temperature, although again there were a number of significant interactions (Table 4B). At night, vertical roosts were significantly warmer than horizontal roosts (Figure 14A). There was a significant interaction between roost-type and roost-pair (Table 4B).

Mean nighttime ambient temperature significantly influenced mean nighttime roost temperature, although this relationship was influenced by roost-

Table 4. Results of ANCOVA's testing the effects of period of the season, roost-pair, roost-type, and Ta on the temperature regime at the deep position of roosts chosen by reproductive female *M. evotis*. Type=roost-type, Pair=roost-pair, and Period=period of the season. x represents an interaction between factors.

Pair(Period) means that Pair is nested within Period.

A) Mean Daytime Temperature

	r^2	df	F	p<	Figure
Model	0.96	18, 105	126.7	0.001	
Period		1, 105	12.51	0.001	
Pair (Period)		4, 105	6.10	0.001	
Type		1, 105	3.63	0.060	
Ta		1, 105	544.6	0.001	
Period x Type		1, 105	4.80	0.031	13A
Type x Pair(Period)		4, 105	14.17	0.001	
Ta x Period		1, 105	7.64	0.007	
Ta x Pair(Period)		4, 105	3.69	0.009	
Ta x Type		1, 105	518	0.025	13B

B) Mean Nighttime Temperature

	r^2	df	F	p<	Figure
Model	0.92	17, 108	75.90	0.001	
Period		1, 108	35.24	0.001	
Pair (Period)		4, 108	18.26	0.001	
Type		1, 108	27.92	0.001	14A
Ta		1, 108	293.0	0.001	
Type x Pair(Period)		5, 108	22.96	0.001	
Ta x Period		1, 108	26.62	0.001	14B
Ta x Pair(Period)		4, 108	11.72	0.001	

C) Temperature Range

	r^2	df	F	p<	Figure
Model	0.88	14, 109	54.84	0.001	
Period		1, 109	1.53	0.220	
Pair (Period)		4, 109	2.41	0.054	
Rsttype		1, 109	13.84	0.001	
Ta		1, 109	137.3	0.001	
Period x Type		1, 109	58.52	0.001	15A
Ta x Pair(Period)		5, 109	5.08	0.003	
Ta x Type		1, 109	57.66	0.001	15B

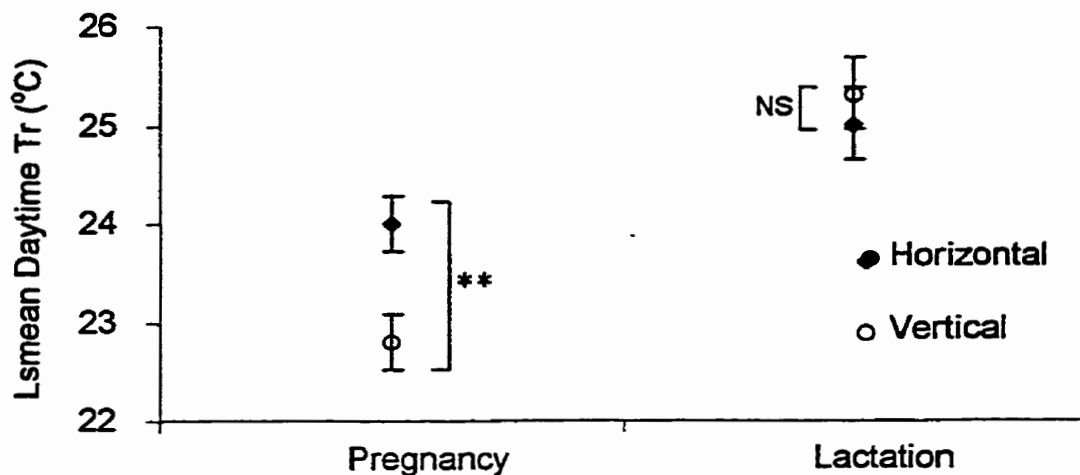
D) Maximum Temperature

	r^2	df	F	p<	Figure
Model	0.90	13, 110	78.72	0.001	
Period		1, 110	28.84	0.001	
Pair (Period)		4, 110	0.17	0.952	
Type		1, 110	12.81	0.001	
Ta		1, 110	382.7	0.001	
Period x Type		1, 110	23.03	0.001	16A
Type x Pair(Period)		4, 110	7.88	0.001	
Tax Type		1, 110	22.95	0.001	16B

E) Minimum Temperature

	R^2	df	F	p<	Figure
Model	0.88	12, 111	65.10	0.001	
Period		1, 111	35.88	0.001	
Pair (Period)		4, 111	22.08	0.001	
Type		1, 111	17.51	0.001	17A
Ta		1, 111	171.4	0.001	17B
Type x Pair(Period)		5, 111	12.88	0.001	

A) Period x Roost-type



B) Ta x Roost-type

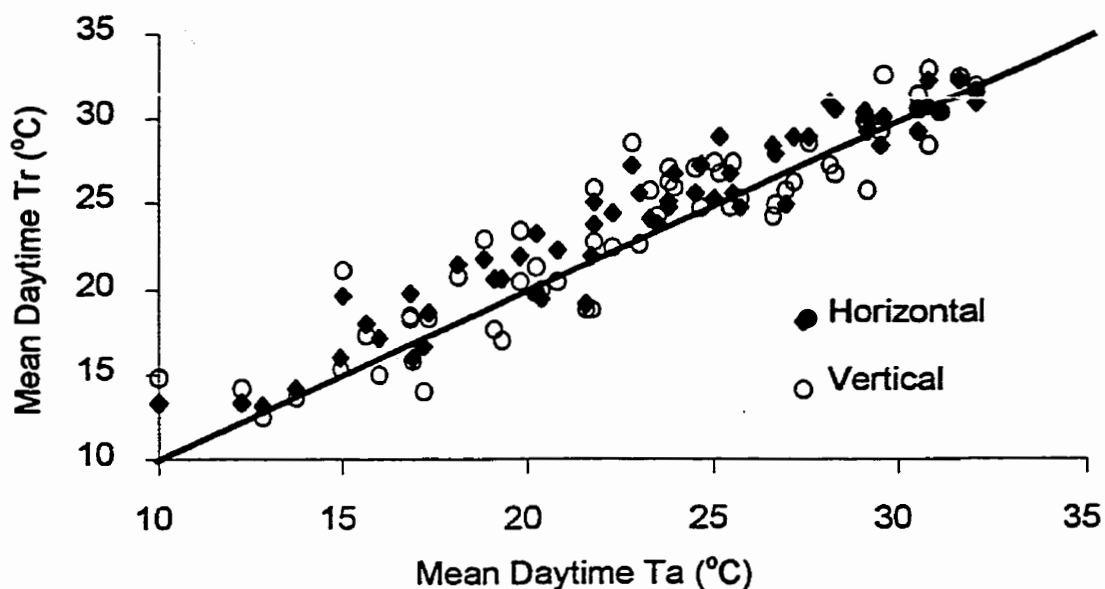
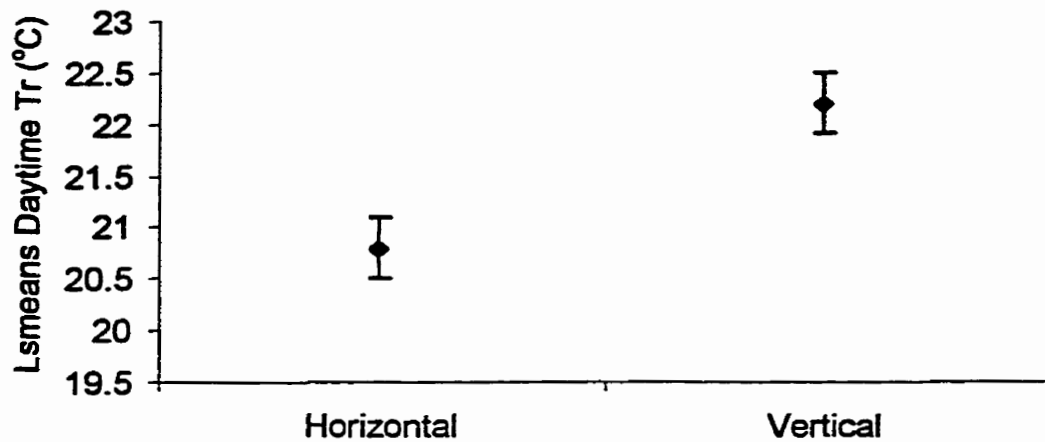


Figure 13. Significant effects from the ANCOVA describing the mean daytime temperatures of roosts chosen by pregnant and lactating *M. evotis* (see Table 4A). Ta=ambient temperature. Tr=roost temperature. The solid line in (B) indicates Ta=Tr. x represents an interaction between factors. ** = p<0.003. NS=not significant.

A) Roost-type



B) Ta x Period

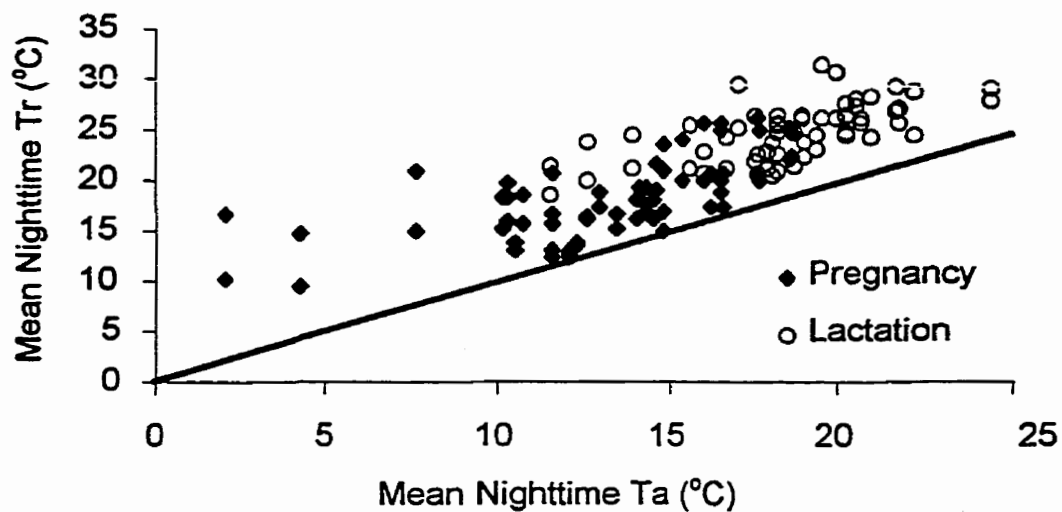


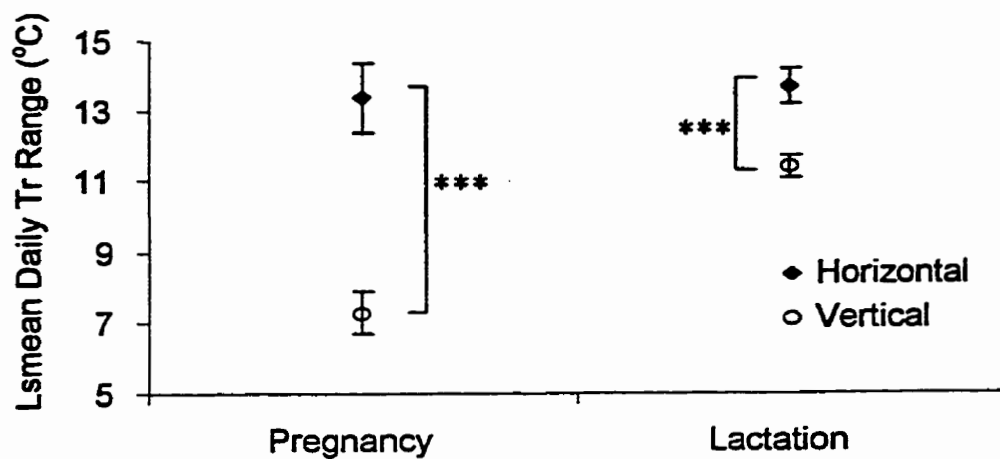
Figure 14. Significant effects from the ANCOVA describing the mean nighttime temperatures of roosts chosen by pregnant and lactating *M. evotis* (see Table 4B). Ta=ambient temperature. Tb=roost temperature. The solid line in (B) indicates Ta=Tr. x represents an interaction between factors.

pair (Table 4B) and period of the season (Table 4B, Figure 14B). Again, the biological relevance of these interactions is not obvious. Considering all of the data together, the regression equation is $T_r=1.03T_a+5.31$. All of the data lie above $T_a=T_r$ (Figure 14B) suggesting that the roosts are buffered against low ambient temperatures at night (i.e. they remain warmer than ambient conditions).

Data for daily roost temperature range were not homoscedastic and attempts to transform the data did not correct the problem. Therefore, these results should be considered with caution. The model describing daily roost temperature range explained a significant proportion of the variation in the data (Table 4C). Roost-type and ambient temperature range significantly influenced roost temperature range, but again there were a number of significant interactions. There was a significant interaction between roost-type and period of the season (Table 4C, Figure 15A). Horizontal roosts had significantly greater temperature ranges than vertical roosts did during both periods, although the difference between roost-types was reduced during the lactation period (Figure 15A). This suggests that vertical roosts are more buffered against ambient temperatures than horizontal roosts.

Daily ambient temperature range significantly influenced daily roost temperature range, although this relationship was influenced by roost-type and roost-pair (Table 4C). Considering all of the data together, the regression equation is $T_r=0.53T_a+0.99$. All but two of the data points lie below $T_a=T_r$ indicating that the roosts are buffered from the environment and fluctuate in temperature less than ambient temperature (Figure 15B). The slope of the relationship between roost temperature range and ambient temperature range is

A) Period x Roost-type



B) Ta x Roost-type

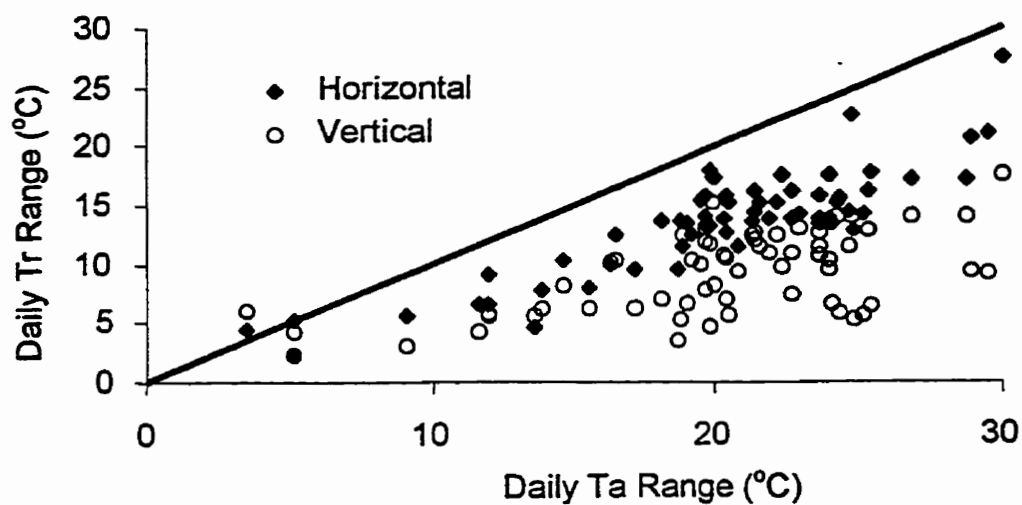


Figure 15. Significant effects from the ANCOVA describing the daily temperature range of roosts chosen by pregnant and lactating *M. evotis* (see Table 4C).

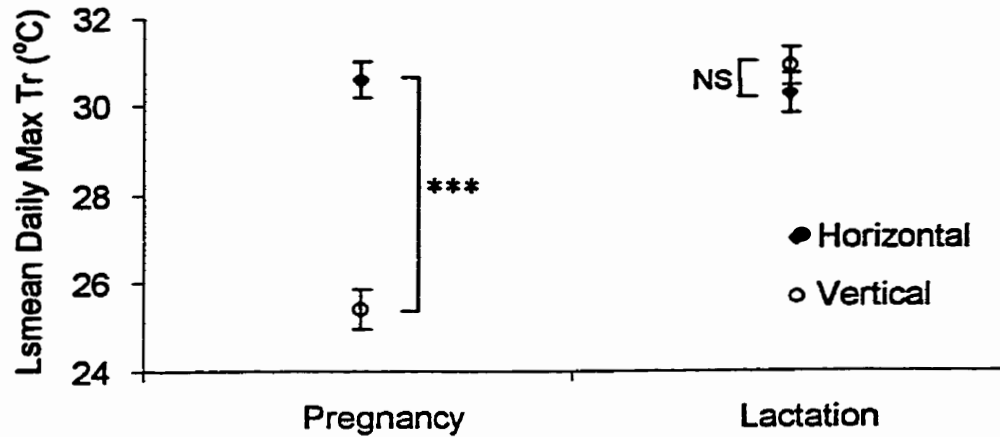
Ta=ambient temperature. Tr=roost temperature. The solid line in (B) indicates Ta=Tr. x represents an interaction between factors. *** = $p < 0.001$.

closer to one in horizontal ($Tr=0.74Ta-1.19$) compared to vertical roosts ($Tr=0.32Ta+3.18$, Figure 15B). Again, this suggests that vertical roosts are more buffered against ambient temperatures than horizontal roosts.

Daily maximum temperatures were not homoscedastic and attempts to transform the data did not correct the problem. Therefore, these results should be considered with caution. The model describing daily maximum roost temperature explained a significant proportion of the variation in the data (Table 4D). Period of the season, roost-type and maximum ambient temperature significantly influenced maximum roost temperature, and again there were a number of significant interactions. There were significant interactions between roost-type and period of the season (Table 4D, Figure 16A), and roost-type and maximum ambient temperature (Table 4D, Figure 16B). Horizontal roosts had significantly greater maximum temperatures than vertical roosts during the pregnancy period, but there was no significant difference between roost-types during lactation (Figure 16A).

Daily maximum ambient temperature significantly influenced daily maximum roost temperature, although this relationship was influenced by roost-type (Table 4D, Figure 16B). Considering all of the data together, the regression equation is $Tr=0.75Ta+4.77$. Most of the data lie below $Ta=Tr$ indicating that the roosts tend to maintain low maximum temperatures relative to ambient conditions (Figure 16B). The slope of the relationship between maximum roost temperature and maximum ambient temperature is closer to one in horizontal ($Tr=0.94Ta+0.19$) compared to vertical roosts ($Tr=0.57Ta+9.34$, Figure 16B). Again this suggests that vertical roosts are more buffered against ambient

A) Roost-type x Period



B) Ta x Roost-type

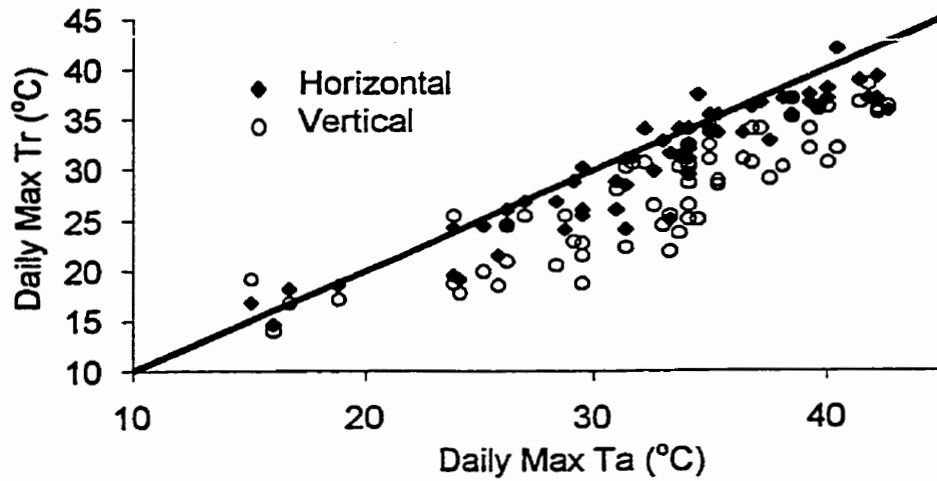


Figure 16. Significant effects from the ANCOVA describing the daily maximum temperature of roosts chosen by pregnant and lactating *M. evotis* (see Table 4D). Ta=ambient temperature. Tr=roost temperature. The solid line in (B) indicates Ta=Tr. x represents an interaction between factors. ***=p<0.001.

temperatures than horizontal roosts.

The model describing daily minimum roost temperature explained a significant proportion of the variation in the data (Table 4E). Period of the season, roost-pair, roost-type, daily minimum ambient temperature, and the interaction between roost-type and roost-pair all significantly influenced daily minimum roost temperature (Table 4E). Daily minimum roost temperature was significantly greater during the lactation period than during the pregnancy period (Table 4E,). Similarly, daily minimum roost temperature was significantly greater in vertical roosts than in horizontal roosts (Table 4E, Figure 17A). There was a significant positive relationship between daily minimum roost temperature and daily minimum ambient temperature described by the equation $T_r = 0.73T_a + 8.70$ (Table 4E, Figure 17B). All of the data lie above $T_a = T_r$ again indicating that the roosts act to moderate microclimatic conditions relative to the ambient.

Thermal Conditions Within Roosts

I examined variation in thermal conditions within roosts chosen by pregnant (i. e. horizontal roosts) and lactating females (i. e. vertical roosts). I compared mean daytime temperatures, mean nighttime temperatures, and daily maximum roost temperatures, minimum roost temperatures , and temperature ranges between the deep and top position of horizontal roosts (3 roosts, N=28 days), between the deep and shallow position of horizontal roosts (3 roosts, N=28 days) and between the deep and shallow position of vertical roosts (6 roosts, N=62 days) (Figure 4). I used two-factor ANOVA's for these analyses. Position of the sensor within the roost and individual roost were the main effects

A) Roost-type

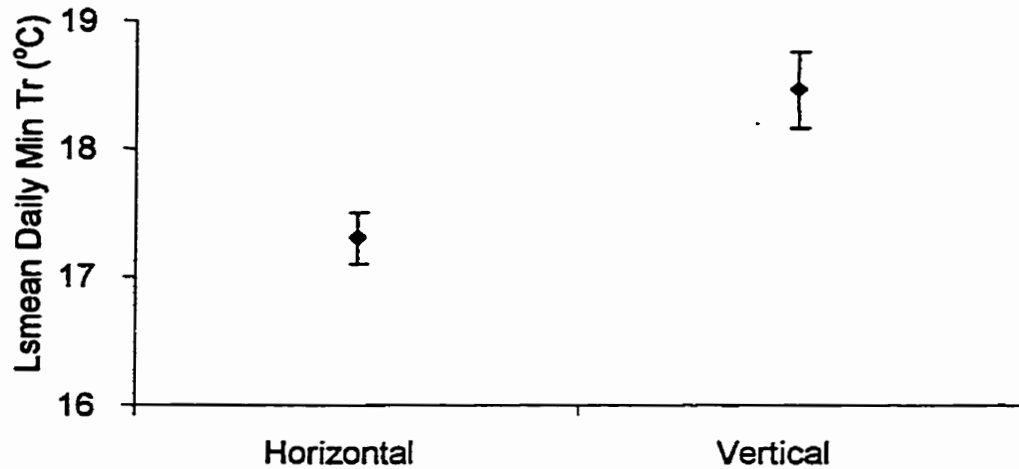
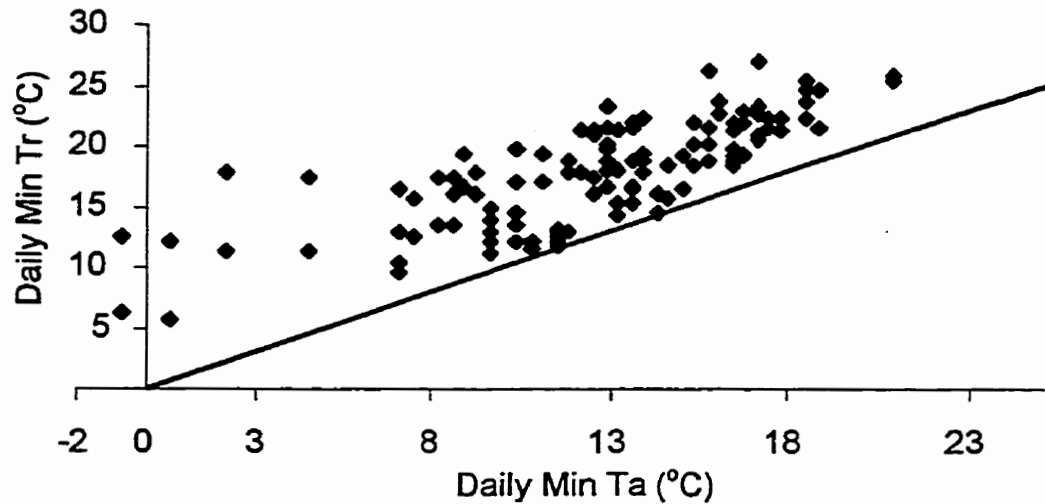
B) T_a 

Figure 17. Significant effects from the ANCOVA describing the daily minimum temperature of roosts chosen by pregnant and lactating *M. evotis* (see Table 4E).

T_a =ambient temperature. T_r =roost temperature. The solid line in (B) indicates

$T_a=T_r$.

of the ANOVA's. Data used in two of the fifteen ANOVA's (temperature range top versus bottom in horizontal roosts, and temperature range deep versus shallow in horizontal roosts) did not conform to the assumptions of normality and heterogeneity of variances. Transforming these data did not correct the problem. Therefore, the results of these two analyses should be interpreted cautiously.

In all fifteen ANOVA's, individual roost significantly influenced the dependent variable, indicating that the thermal regimes of some roosts differed from other roosts. Position within the roost played a significant role in four of the five ANOVA's comparing the top and deep position of horizontal roosts (Figure 18). Mean nighttime temperature was significantly higher in the deep position than in the top position ($F_{1,52}=13.88$, $p<0.001$, Figure 18B), as was daily minimum temperature ($F_{1,52}=17.03$, $p<0.001$, Figure 18D). Conversely, daily maximum temperature was higher in the top position ($F_{1,52}=10.25$, $p<0.001$, Figure 18C) as was daily temperature range ($F_{1,52}=25.07$, $p<0.001$, Figure 18E). Position did not play a significant role in any of the five ANOVA's comparing the deep and shallow positions of horizontal roosts (Figure 19).

Position played a significant role in four of the five ANOVA's comparing the deep and shallow position of vertical roosts (Figure 20). Mean nighttime temperature was significantly higher in the deep position than in the shallow position ($F_{1,112}=75.07$, $p<0.001$, Figure 20B), as was daily minimum temperature ($F_{1,112}=93.60$, $p<0.001$, Figure 20D). Conversely, daily maximum temperature was higher in the shallow position ($F_{1,112}=62.38$, $p<0.001$, Figure 20C), as was daily temperature range ($F_{1,112}=224.71$, $p<0.001$, Figure 20E).

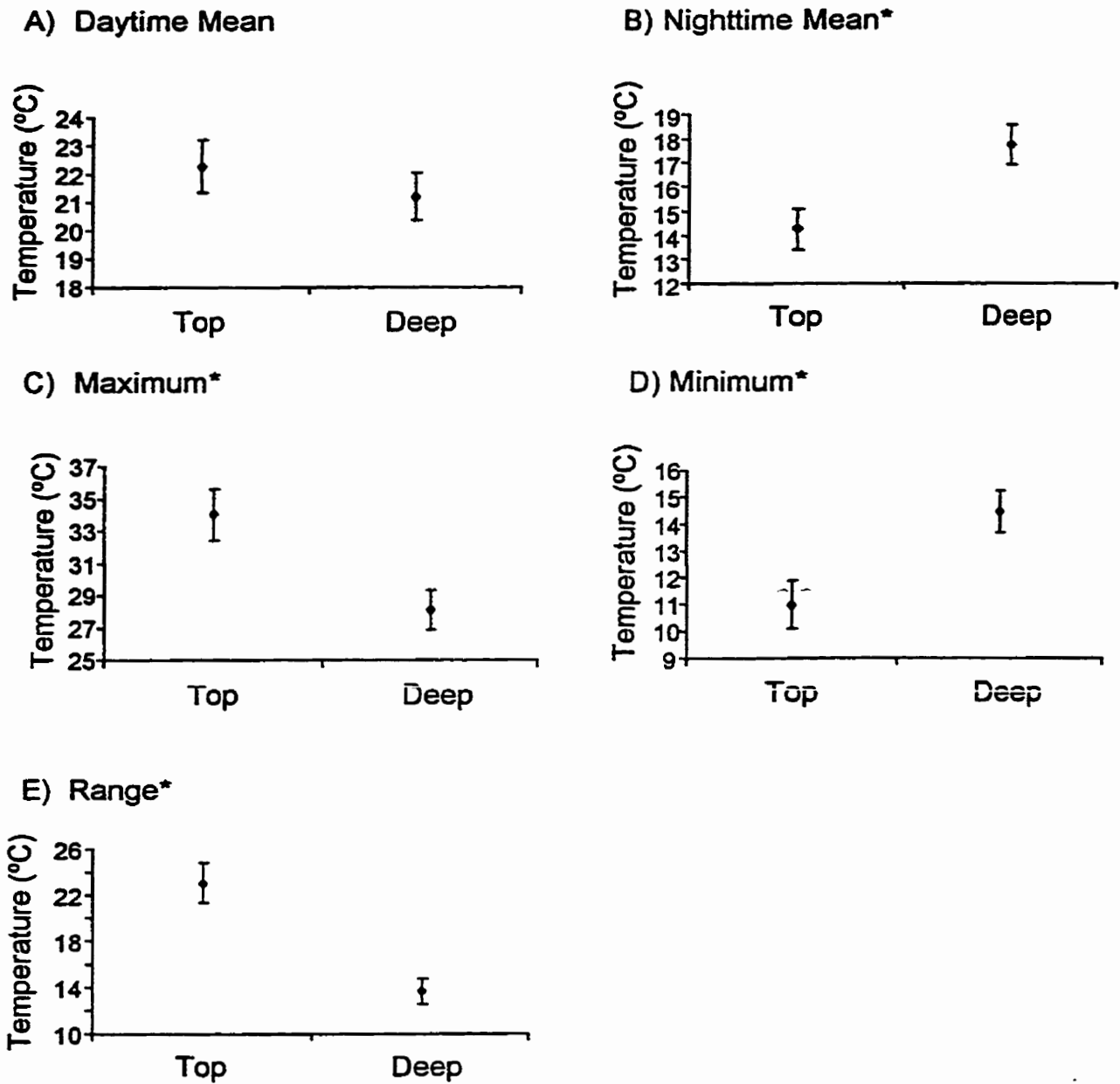


Figure 18. Thermal characteristics at two positions within roosts chosen by pregnant *Myotis evotis* (i. e. horizontal roosts) during the 1998 field season. * indicates a significant result. In this case all significant results have $P \leq 0.003$ (see Figure 4 for meaning of positions). The data are from three roosts (N=28 bat-days).

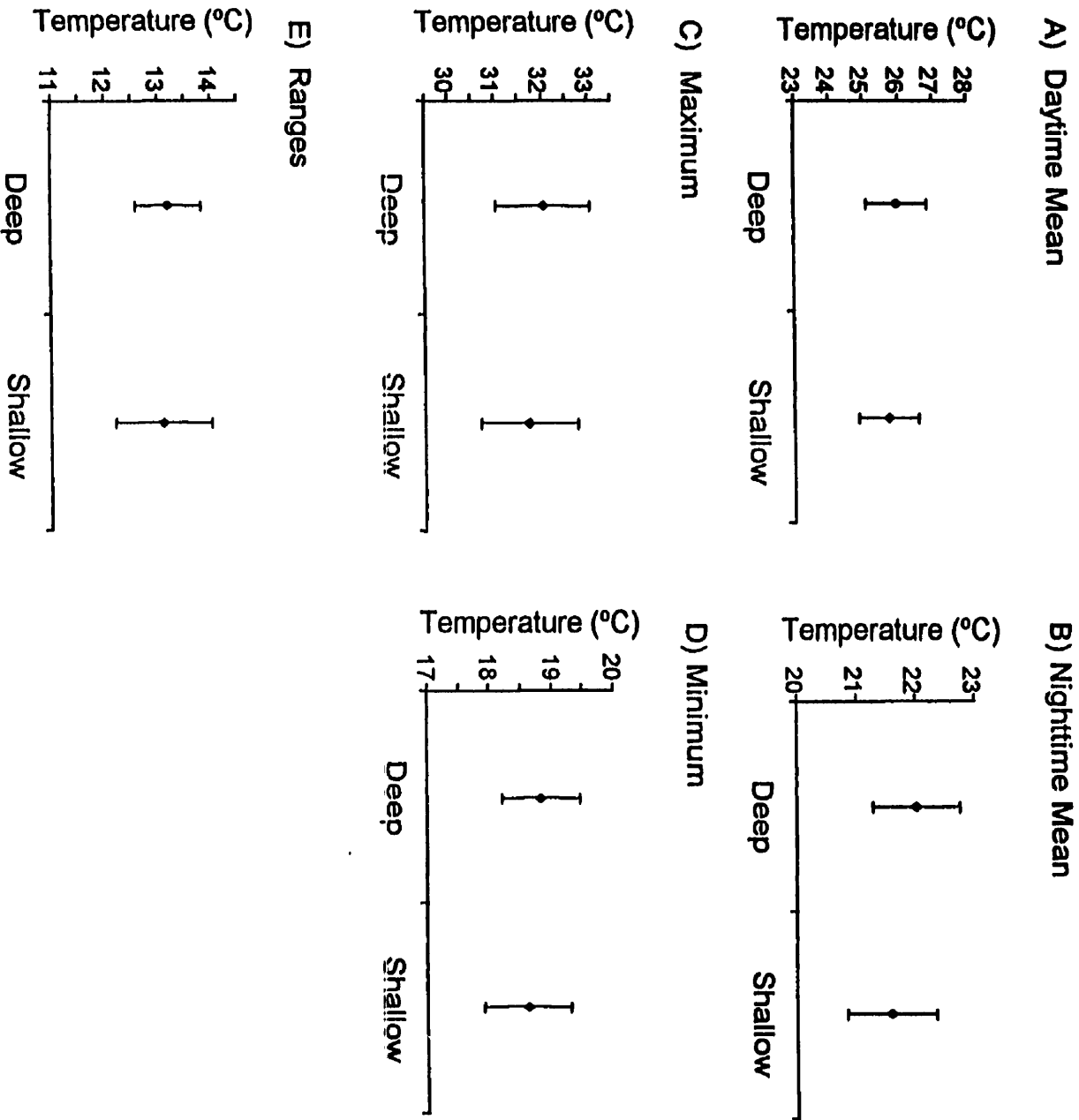


Figure 19. Thermal characteristics at two positions within roosts chosen by pregnant *Myotis evotis* (i. e. horizontal roosts) during the 1998 field season.

None of these comparisons was significant (see Figure 4 for meaning of positions). The data are from three roosts (N=28 bat bat-days).

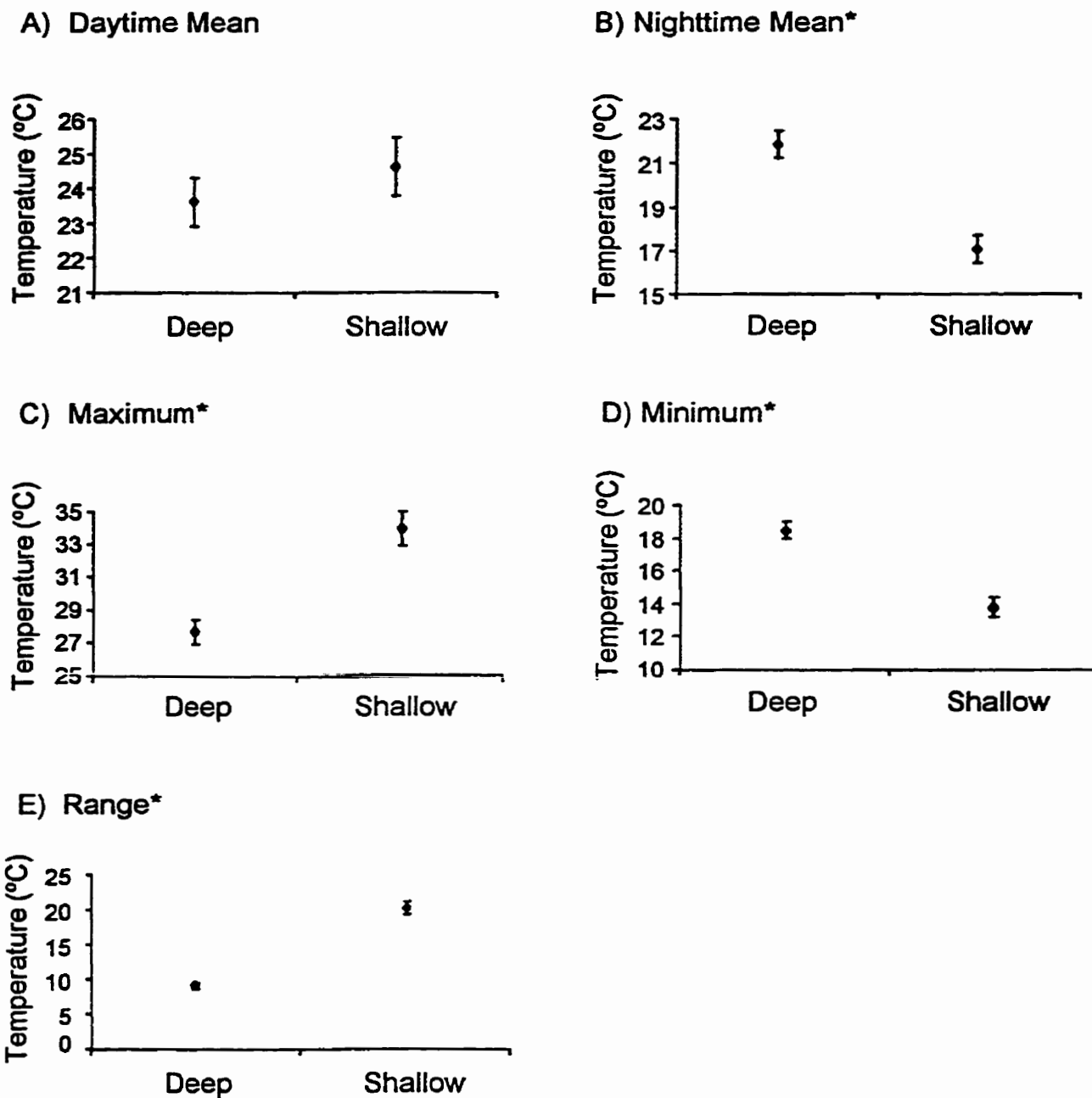


Figure 20. Thermal characteristics at two positions within roosts chosen by lactating *Myotis evotis* (i. e. vertical roosts) during the 1998 field season. * indicates a significant result. In this case all significant results have $P \leq 0.0001$ (see Figure 4 for meaning of positions). The data are from six roosts (N=62 bat-days).

DISCUSSION

Myotis evotis behaves unusually compared to other species of temperate insectivorous bats that have been studied. They forage every night and use torpor every day regardless of reproductive condition or ambient temperature. Furthermore, the amount of time that they spend foraging and in torpor is mostly determined by the amount of time available for them to do so. Pregnant and lactating females choose roosts that differ in structure and thermal characteristics. These patterns of foraging, thermoregulatory, and roosting behaviour probably help females to achieve reproductive success while balancing a unique set of energy demands.

Effect of Radio Transmitters

Radio transmitters affect flying animals by decreasing their maneuverability and possibly their foraging efficiency (Aldridge and Brigham 1988), and by increasing the energy demands of flight (Caccamise and Hedin 1985). In response to these affects, individuals may alter their behaviour. Consequently, my results may be biased and may not reflect natural behaviours. Furthermore, individuals may experience reduced long-term fitness if the application of a transmitter results in decreased survival or the abortion of young.

On average, transmitter mass was $7.3 \pm 0.1\%$ of bat mass. According to Aldridge and Brigham (1988) this equates to a decrease in maneuverability of 7.3%, 2.3% higher than the standard acceptable level. Does this mean that females carrying transmitters changed their behaviour to deal with reduced foraging efficiency?

If transmitters affect the foraging efficiency of females, I would expect them to compensate by altering their foraging behaviour. Hickey (1992), found that hoary bats, *Lasiurus cinereus*, that carried transmitters were just as successful at capturing insects as bats that did not carry transmitters. However, the transmitters used in that study were on average 3.1% of body mass, well below the accepted standard. In the current study, bats that carried transmitters tended to forage for long periods of time, on average about six hours per night. This strategy is unusual among insectivorous bats and might indicate a side effect of carrying transmitters that weigh more than 5% of body mass. However, my data suggest otherwise. On two occasions light tagged bats were observed foraging for long periods of time. I observed one for nearly four hours and the other for almost six hours. Furthermore, I captured non-radio tagged females during every hour of the night and observed captures corresponded to expected captures based on the amount of time spent netting. These results suggest that the six hour foraging bouts observed in bats carrying transmitters also occur in females not encumbered by the extra mass.

The natural range in mass experienced by individual adult bats can be substantial (Aldridge and Brigham 1988, Davis and Cockrum 1964, Hughes and Rayner 1991). Within a night, insectivorous bats may have a food intake of more than 70% of their body mass (Kunz *et al.* 1995), although this added mass may not all be carried at one time. Hibernating bats can lose 30% of their body mass during a season when they are mostly inactive (Hughes and Rayner 1991). Also, females in late pregnancy are often substantially heavier than lactating and nonreproductive females. Fetal mass often raises maternal mass by greater than

30% (Aldridge and Brigham 1988, Davis and Cockrum 1964, Hughes and Rayner 1991). In this study changes in mass were greatest between early and late pregnancy. On average, females weighed 1.4g (20.3%) more during the second half of pregnancy than during the first half. This extra mass is approximately two and a half times the mass of the transmitters attached to the bats in this study. In spite of this, there was no difference in the time spent foraging or the amount of time spent in torpor between the first and second half of pregnancy. Females always entered torpor and always spent most of the night hours foraging. The use of habitat was also consistent between the first and second half of pregnancy. The heaviest bat-transmitter combination in this study weighed 9.2 g. This falls within the natural range of masses experienced by the bats in my study area. The heaviest pregnant female in this study weighed 9.9 g.

If transmitters affect the foraging efficiency of reproductive females, I would expect them to gain mass at low rates or not at all. My data indicate that this is not the case. Individual pregnant and lactating females gained weight between successive captures even though they had carried transmitters during the time between the captures.

Adding radio transmitters to study animals should increase the energy requirements for locomotion (Berteaux *et al.* 1996). This is particularly true for animals that fly (Caccamise and Hedin 1985). Gessaman and Nagy (1988), found that homing pigeons (*Columba livia*) that were encumbered by a radio transmitter were significantly slower and produced significantly more CO₂ than when they were not encumbered with a radio transmitter. However, these birds were trained to fly at speeds well above the minimum power speed and

maximum range speed for the species (i.e. the speeds requiring minimum energy expenditure per unit time and per unit distance, respectively). Therefore, the results of Gessaman and Nagy (1988) may not be applicable to a natural setting, where animals probably fly at more efficient speeds. Working with nesting common terns (*Sterna hirundo*), Klassen *et al.* (1992), found no significant difference in energy expenditure or mass change between radio-tagged and control birds. Similarly, CO₂ production in tinker pigeons (*Columba livia*) did not differ between radio-tagged and control birds, although radio-tagged individuals flew for significantly shorter periods than the controls (Gessaman *et al.* 1991).

The transmitters used in this study should decrease the maneuverability of *M. evotis* by about 7% on average (Aldridge and Brigham 1988). This reduction is not acceptable under the 5% criterion suggested by Aldridge and Brigham (1988). However, the behavioural observations for *M. evotis* discussed above suggest that the decrease in maneuverability and the increase in energy consumption during flight are not sufficient to warrant changes in behaviour. Using equations from Caccamise and Hedin (1985), I calculated the proportional reduction in the surplus power associated with the addition of a radio-transmitter to an average *M. evotis* (see Appendix for calculations). Surplus power refers to the difference between the amount of power available for sustained flight and the amount required to fly at the maximum range speed. On average, the addition of a radio-transmitter resulted in a 1.35% decrease in the surplus power available for flight. Caccamise and Hedin (1985) used a 5% reduction in surplus power as a standard of acceptability for judging appropriate transmitter masses. The

transmitters used in this study would be considered acceptable under their standard.

There is no evidence to suggest that the application of transmitters influenced long-term fitness. The initial captures of lactating females included individuals that had and had not carried transmitters during pregnancy. This suggests that gestation was not prolonged by the application of a transmitter. Pregnant females that had carried transmitters, and were recaptured during the lactation period, were always found to be lactating. In other words, the application of transmitters did not cause these females to abort. Finally, I recaptured several bats that had carried transmitters, within and between years, suggesting that the application of transmitters did not cause mortality.

To summarize: Bats with transmitters foraged in a manner similar to those without transmitters. Females in different stages of pregnancy behave in a similar fashion even though there are large mass differences between stages. Seasonal and nightly variation in mass is common in female bats. The mass of females plus their transmitters in this study fell within the range of this natural variation. Females accumulated mass while wearing transmitters. The reduction in surplus power caused by the addition of a radio-transmitter was acceptably low. Finally, the application of a transmitter did not lengthen gestation, cause abortion, or influence survival. Taken together, these observations suggest that neither foraging efficiency nor energy consumption during flight were sufficiently altered to warrant behavioural compensation. Therefore, the use of radio transmitters probably has not biased my results. Nonetheless, keeping transmitter mass to a minimum should remain a priority for

behavioural studies, especially those examining animals that fly, and each situation needs to be assessed individually.

Foraging

Habitat Use

Wing shape influences flight mode and consequently the range of habitats where bats are able to forage (Norberg 1987). A bat's agility is influenced by aspect ratio (the square of the wing span divided by wing area). When wings are long relative to their width, aspect ratio is high and bats are able to turn rapidly (i.e. they are agile). A bat's maneuverability is influenced by wing loading (mass divided by wing area). When bats are heavy relative to the area of their wings, the radius of their turns is large (i.e. they are not maneuverable). *M. evotis* has an average aspect ratio and a low wing loading relative to other vespertilionid bats (Norberg and Rayner 1987). Therefore, it should be a relatively agile and maneuverable flier. Another consequence of this wing morphology is that *M. evotis* can fly relatively slowly. Taken together, these flight characteristics are typical of bats that forage within and around vegetation (Aldridge and Rautenbach 1987, Norberg and Rayner 1987). In addition to its sensory abilities, this flight mode is what permits *M. evotis* to glean.

Wing design is correlated with echolocation call design (Aldridge and Rautenbach 1987). Bats with wings adapted for flight within and near vegetation typically have echolocation calls that are suited to cluttered habitat (Aldridge and Rautenbach 1987). Clutter is a term adapted from the literature on radar theory (Fenton 1990). In the echolocation/ecomorphology literature (Aldridge and

Rautenbach 1987, Fenton 1990, Norberg and Rayner 1987), clutter refers to habitat of high acoustic/physical complexity (eg. within the canopy of a tree). The echolocation calls of bats adapted for flight in cluttered habitat are often of high frequency, and tend to be frequency modulated (FM). Such calls attenuate rapidly and are only effective over short distances (Aldridge and Rautenbach 1987). When *M. evotis* forages as an aerial hawker, it produces high frequency FM echolocation calls (Faure and Barclay 1994). While gleaning, *M. evotis* changes its call behaviour. Individuals only produce calls in 68% of gleaning attempts, and they are usually of lower amplitude than hawking calls (Faure and Barclay 1994). Presumably, this is to prevent defensive responses of tympanate moths (Faure *et al.* 1990, Faure *et al.* 1993) and to avoid deafening itself while relatively close to clutter. Individuals often use passive hearing to detect and glean prey from vegetation (Barclay 1991, Faure and Barclay 1994). Therefore, in terms of both flight and sensory characteristics, *M. evotis* is well adapted for gleaning and hawking in and around vegetation. It is not surprising that individuals in my study spent most of their foraging time in and near trees.

In general, foraging around trees may be more profitable than foraging in open areas (Holloway 1998, Racey and Swift 1985). The presence of trees in otherwise open habitat may influence the distribution of volant insects (Holloway 1998, Racey and Swift 1985) and the energetics of flight. Trees provide shelter from the wind, which may result in an accumulation of insects in treed areas. Trees also provide a substrate on which insects can forage and breed. Holloway (1998) found that the treed areas in my study area supported a greater abundance of volant insects than either the prairies or the coulees. Flight may

also be less costly around trees if bats do not have to deal with strong headwinds.

Knowledge of a foraging site may enhance foraging efficiency (Wilkinson and Barclay 1997) by reducing search costs. The trees at my study site were located within 100-500m of the roosts where reproductive females spent their days. Therefore, the trees provided a close and probably reliable source of prey. By using this source of prey, individuals may have minimized their foraging costs.

Time Spent Foraging

Relative to the amount of time spent foraging, individuals spent little time roosting at night, whether pregnant or lactating. Occasionally females did stop flying, but this was only for short periods (usually less than 5 min) that may have been used to consume large prey. Therefore, I calculated foraging time as the amount of time between emergence from the roost at dusk and return to the roost at dawn. On average, pregnant females foraged for 341.2 ± 4.9 minutes per night and lactating females foraged for 397.7 ± 8.4 minutes per night. Although similar foraging times have been reported for hoary bats (*Lasiurus cinereus*, Barclay 1989), it is a large (mass 30-35g), unmaneuverable, fast-flying, hawk that tends to prey upon relatively large insects (Barclay 1985, 1986). *L. cinereus* is one of the largest bat species in North America, and its foraging strategy is not typical of most temperate insectivorous bats. Considering species that occupy ecological niches closer to that of *M. evotis* (mass 6-10g), the long foraging times that I recorded are unusual. Pregnant and lactating *Eptesicus fuscus* (mass 15-20g) forage for less than 210 minutes per night (Audet and Fenton 1988, Grinevitch et

al. 1995, Wilkinson and Barclay 1997). Similarly, pregnant and lactating *M. lucifugus* (mass 6-11g) forage for about 240 minutes per night (Kurta *et al.* 1989a). The shortest foraging bout for any *M. evotis* in my study was 280 minutes, well above the averages for *E. fuscus* and *M. lucifugus*.

In many insectivorous bats, foraging activity is reduced at low ambient temperatures (Anthony *et al.* 1981, Audet and Fenton 1988, Aldridge and Brigham 1991, Grinevitch *et al.* 1995, Hamilton 1996, Racey and Swift 1985, Rydell 1989, Wilkinson and Barclay 1997). Individual *M. evotis* never failed to emerge and ambient temperature did not affect foraging time. Individual *M. evotis* forage during periods of the night that appear to be unprofitable for other species. Holloway (1998) found that there was a peak in foraging activity in my study area at dusk in early summer and a peak at dawn in late summer. I suggest that foraging remained profitable for *M. evotis* outside the peak periods because nonvolant prey were available as a food source. Hamilton (1996) suggested that species that are limited to aerial prey return to their night roosts when low ambient temperature reduces prey density below a threshold level. At these times, *M. evotis* may focus its foraging efforts on nonvolant prey through its ability to glean.

Other gleaning animals have a similar continuous nocturnal activity pattern to the one I found for *M. evotis*. Owlet-nightjars (*Aegotheles cristatus*), nocturnal insectivorous birds, are able to forage all night, presumably because of a flexible foraging strategy that allows them to capture prey while walking, flying, and perch hunting (Brigham *et al.*, in press). Other caprimulgiforme birds do not forage all night. Tawny frogmouths (*Podargus strigoides*) pounce on their prey from

perches, and common poorwills (*Phalaenoptilus nuttalli*) restrict their foraging activity to sallying flights after flying insects (Brigham *et al.*, in press). Neither of these species are active all night. *Myotis myotis*, a gleaning bat from Europe, spends long periods of time foraging when pregnant (about 390 minutes), and when lactating (about 360 minutes) (Audet 1990). These studies, together with my results for *M. evotis*, suggest that flying insectivores that can use volant and nonvolant prey, may be able to devote a greater proportion of each night to foraging.

Although, *M. evotis* may be able to forage profitably for the entire night, the above discussion does not explain why it would choose to do so. There is no reason to suspect that daily energy and nutrient demands differ between *M. evotis* and other small insectivorous bats in my study area. If energy or nutrient demands differ between species I would expect to find differences in life history characteristics such as the date of parturition or the number of young produced per season. Although life history characteristics are often hard to determine precisely (i.e. date of parturition), data collected in this study and by Holloway (1998) suggest that the timing of reproductive events is similar amongst the four dominant species in my study area (*M. ciliolabrum*, *M. evotis*, *M. lucifugus*, and *E. fuscus*). In all four species pregnant females were caught between May 18 and July 17, lactating females between June 24 and July 29, and juveniles between July 22 and August 18 (this study, Holloway 1998). Furthermore, litter size in each of these species is typically one young per year (*M. ciliolabrum*, van Zyll de Jong 1984; *M. evotis*, pers. obs.; *M. lucifugus*, Fenton and Barclay 1980; *E. fuscus*, Holroyd 1993).

If daily energy requirements are similar amongst the dominant species in my study area, one might expect *M. evotis*' long foraging bouts to result in the accumulation of excessive fat stores. Although recaptured bats were consistently heavier than they were when they were originally captured, gains in mass did not seem excessive. For example, there was no significant change in mass between early and late lactation.

To summarize, although *M. evotis* spends more time foraging than the other dominant species in my study area, and these species appear to have similar daily energy requirements, *M. evotis* does not appear to accumulate excessive mass. Moreover, this lack of accumulation in mass occurs in spite of the consistent use of daily torpor (see below). I suggest that the other species in my study area are more efficient foragers than *M. evotis* is, and they are able to fulfil their daily nutrient and energy requirements during the peaks of insect abundance at dusk and dawn.

Myotis lucifugus and *M. evotis* are similar sized species with similar diets (Holloway 1998). Their foraging strategies, however, are quite different. *M. lucifugus* frequently hunts for flying prey over water (Barclay 1991, van Zyll de Jong 1985). On the other hand, *M. evotis* forages primarily in cluttered habitat attacking aerial as well as nonvolant prey (Faure and Barclay 1992, 1994).

Vaughan (1966) calculated a minimum flight speed of 14.1 kph for *M. lucifugus* and 12.6 kph for *M. evotis*. This ranking seems reasonable based on field observations of foraging bats and the echolocation call characteristics of the two species. *M. evotis* produces calls of higher frequency and lower amplitude than *M. lucifugus* (*M. evotis*, Faure and Barclay 1992, 1994; *M. lucifugus*, Fenton

and Barclay 1980). Quiet calls of high frequency attenuate more rapidly than louder calls of lower frequency. As a result, *M. lucifugus* may be able to detect prey at a greater range than *M. evotis*, and consequently, may be able to forage at greater speeds. By flying more rapidly, *M. lucifugus* likely encounters prey at a greater rate than *M. evotis*. *M. lucifugus* has been called an efficient forager that can fill its stomach in less than 15 minutes (van Zyll de Jong 1985). This may not be the case for *M. evotis*. Furthermore, *M. evotis* hovers as part of its gleaning sequence (Faure and Barclay 1992, 1994), a behaviour that is energetically expensive (Norberg and Rayner 1987). *M. evotis* is the only species in my study area that exhibits this behaviour. Because of its slow flight and the high energy demand of its foraging style, *M. evotis* likely has a lower net energy intake per unit foraging time than other species in the area. This may explain why *M. evotis* forages for such long periods of time, each night, while other species do not.

Daily energy demand for mammals is typically highest during lactation (Gittleman and Thompson 1988) and foraging strategies of female bats often differ between pregnancy and lactation (e.g. Anthony and Kunz 1981, Audet and Fenton 1988, Barclay 1989, Kunz 1974). This was not the case in my study. Females consistently foraged for the entire night whether they were pregnant or lactating. Their use of habitat was also similar. If *M. evotis* requires the entire night to fill its nutrient and energy demands during pregnancy, how can it fulfil these requirements during lactation when these demands are higher? I suggest three nonexclusive possibilities. First, insect abundance may increase in July and August compared to May and June due to increased ambient temperatures, although Holloway (1998) found no evidence to support this. Therefore, lactating

M. evotis would have encountered more prey per unit foraging time and net energy intake would have increased compared to pregnant females. Second, night length starts getting longer around the end of pregnancy and continues to do so throughout lactation. Therefore, lactating *M. evotis* have more time to accumulate the prey they require to balance their nutrient and energy budgets, compared to pregnant females. Finally, in postpartum *M. evotis*, foraging efficiency may increase due to low costs and increased maneuverability resulting from decreased mass. Any combination of these factors could help *M. evotis* to deal with the increased energy demands of lactation.

My explanation for the foraging behaviour of *M. evotis* assumes three things. First, I assume that the energy demands of *M. evotis* are similar to those of the other species in my study area. More data are required to determine if this is actually the case. Life history characteristics such as the length of gestation, the mass of juveniles at birth, the length of lactation, and the mass of juveniles at weaning would help to clarify this point. Second, I assume that *M. evotis* and other species accumulate mass at a similar rate on a daily basis. This also needs to be tested empirically. Finally, I assume that *M. evotis* is a less efficient forager than other species in my study area. Actual flight speeds and insect capture rates need to be determined to ascertain if this is true.

My study site is close to the northern limit of *M. evotis*' range (van Zyll de Jong 1985). The unusual foraging strategy noted in this study may result from climatic conditions that are extreme compared to those further south.

Furthermore, the aridity of the badlands region may affect insect abundance and consequently foraging strategy. *M. evotis* inhabits a wide range of habitats

throughout western North America (Manning and Jones 1989, van Zyll de Jong, 1985). Studies examining *M. evotis*' foraging times at different latitudes and in different habitats would shed light on these issues.

Torpor

Torpor is often viewed as a response to energy emergencies such as reduced prey densities resulting from inclement weather (Kurta *et al.* 1987, Kurta and Kunz 1988, Pagels and Blem 1973). In contrast to the literature linking torpor to energy emergencies (Anthony *et al.* 1981, Kissner and Brigham 1993, Körtner *et al.* in press, Kurta 1990, Racey and Swift 1981), I found that reproductive female *M. evotis* used torpor every day. Furthermore, the amount of time spent in torpor was primarily determined by the amount of time available to use it. As suggested above, the use of daily torpor may help *M. evotis* compensate for inefficient night-long foraging bouts. *M. evotis* may arrive at their roosts at dawn with a surplus of energy sufficient to cover daily reproductive needs only if thermoregulatory costs are reduced. In other words, there may be an energetic trade off between maintenance and production.

Pregnant *M. evotis* used two distinct thermoregulatory strategies. Females either maintained T_b at around 25°C (regulators) or allowed it to fall to ambient levels (conformers). Similar behaviour occurs in captive female *M. lucifugus* and *M. thysanodes* (Studier and O'Farrell 1972). Although pregnant *M. evotis* conform more frequently than they regulate, females may occasionally choose to regulate to reduce the costs associated with reduced fetal growth rates. Sporadic insect emergences during the spring could provide pregnant

females with opportunities for increased foraging efficiency. In turn, females could use the excess energy gained from these foraging opportunities to regulate their body temperatures at higher levels.

At T_b 's near 25°C , females could still save considerable energy compared to maintaining T_b near their active temperature (Webb *et al.* 1993). In *M. lucifugus*, small reductions in T_b from high T_b 's resulted in greater energy savings than subsequent T_b reductions of equal increment (Studier 1981). In other words, there are diminishing returns in energy savings as T_b is reduced. Therefore, by maintaining T_b near 25°C , pregnant *M. evotis* may be able to maintain fetal growth rates while still saving some energy.

There was no clear dichotomy in the thermoregulatory behaviour of lactating *M. evotis*, although there was still a significant positive relationship between minimum body temperature and ambient temperature. Judging from the r^2 's, this relationship was not as strong as it was for pregnant conformers. Insect availability is probably higher during lactation resulting from warmer ambient temperatures. Night length is also longer. Furthermore, lactating females may have been more maneuverable due to the lack of fetal weight. For these reasons, foraging may be more profitable during lactation. This may explain the lack of a tight fit to the regression line in lactating females. Lactating females may have greater energy reserves at the end of a foraging bout compared to pregnant females and may be able to avoid dropping to ambient temperature upon return to their roosts. In pregnant females, brief insect emergences may provide just enough additional energy to allow females to regulate at around 25°C and 25°C may be an optimal level for fetal growth. In lactating females,

consistently higher insect availability may allow females to fine tune Tb to their daily maintenance and production requirements.

Previous studies of free ranging bats have shown that torpor is used infrequently during lactation (Audet and Fenton 1988, Grinevitch *et al.* 1995, Hamilton and Barclay 1994, Vaughan and O'Shea 1976). Although this was not the case in my study, I did find that deep torpor was used less frequently by lactating compared to pregnant females. This result agrees with findings for *E. fuscus* (Grinevitch *et al.* 1995, Hamilton and Barclay 1994). Increased ambient temperatures during lactation compared to pregnancy limited the number of days that deep torpor was possible. Furthermore, higher ambient temperatures made deeper bouts of torpor less profitable than they were for pregnant females. This, together with the fact that foraging may be more profitable during lactation, may explain why lactating females do not use deep torpor as frequently as pregnant females.

The consistent use of torpor in the *M. evotis* in my study may also be a strategy to conserve water. The badlands of the South Saskatchewan River Valley are semi-arid, receiving an average of 16-17cm of precipitation from May through August (Environment Canada). Low relative humidity, particularly during lactation, may result in high levels of evaporative water loss (EWL) in *M. evotis*. In general, small bats have high surface area to volume ratios which are enhanced by large, naked flight membranes (Webb *et al.* 1995). Although bats lack sweat glands, are able to restrict blood flow to their wings, and tend to fold their wings when at rest, the rate of evaporative water loss in resting bats is high

relative to similarly-sized terrestrial mammals and birds (Herreid and Schmidt-Nielsen 1966, Studier 1970, Webb *et al.* 1995).

Evaporative water losses above 20% of body mass can cause death in vespertilionid bats and may occur at ambient temperatures around 40°C (Hosken 1997, Hosken and Withers 1997, Studier 1970). Ambient temperatures in my study area often reach 40°C. Furthermore, individuals spent more than 17 hours per day in their roosts without access to water. This period included the hottest part of the day. Also, the solitary roosting habits of *M. evotis* mean that they can not take advantage of clustering to conserve water (Kurta *et al.* 1989b), and solitary individuals are less likely to affect the relative humidity of their roosts than are groups. High relative humidities can significantly reduce EWL (Webb *et al.* 1995). Torpor significantly reduces EWL (Herreid and Schmidt-Nielsen 1966, Hosken 1997, Hosken and Withers 1997, Studier and O'Farrell 1976, Webb *et al.* 1995). During lactation, temperatures are higher and females lose water in the form of milk (Kurta *et al.* 1989b). Therefore, one explanation for the unusual finding that lactating females used torpor every day is that they were trying to balance their daily water budgets. Studies measuring daily water economy in different climatic zones would help to ascertain the importance of water flux on the use of torpor in *M. evotis*.

Roosts

Buildings, cracks in the ground, caves, mines, rock crevices, loose bark, tree cavities, and tree stumps in clear cuts are all used as roosting sites by *M. evotis* (Manning and Jones 1989, Vonhof and Barclay 1996, 1997). In my study,

M. evotis roosted in crevices in cemented sandstone boulders that lay above the more permeable surrounding sandstone. Pregnant females roosted in crevices that were horizontal relative to the ground, beneath flakes of rock that were weathering off the upper surface of the boulders. Lactating females roosted in crevices that were vertical relative to the ground, in cracks where the boulder was split in two.

The shift between roost types may occur as a result of changes in precipitation between reproductive periods. In my study area rain is more common during the pregnancy period than the lactation period (Holloway 1998). Horizontal roosts did not open upwards where as vertical roosts did. Females may start using lactation roosts as the probability of getting wet through exposure to rain declines later in the season. Although some authors have observed wet bats in roosts exposed to rain (Lewis 1996), choosing such roosts may be detrimental energetically, because fur loses its insulative properties when wet (Hovorka *et al.* 1996).

Microclimate is an important determinant of roost site selection in bats (Audet and Fenton 1988, Churchill *et al.* 1997, Hamilton and Barclay 1994, Kunz 1982, McNab 1982, Tidemann and Flavel 1987, Vaughan and O'Shea 1976, Vonhof and Barclay 1997). Temperature may be particularly important because (1) bats are able to use heterothermy as an energy-saving strategy and (2) fetal and juvenile growth rates may decline with decreased temperatures. The fact that pregnant and lactating *M. evotis* use torpor every day and that minimum T_b is significantly influenced by minimum T_a suggests that roost temperature may be an important factor in roost choice.

I found that the thermal characteristics of roosts (daytime and nighttime means, and daily maxima, minima, and ranges) were primarily determined by ambient temperature. Nonetheless, roosts were buffered against ambient conditions. Roosts were warmer than ambient at night, and daily highs and lows were less extreme than ambient highs and lows. Extreme ambient temperatures above 40°C and below 0°C occurred while females were in the study area. The buffering capacity of the roosts chosen by females in my study protects them against these extremes.

Passive rewarming is an important part of the energy saving strategy of heterothermic animals (Hamilton and Barclay 1994, Prothero and Jurgens 1986, Vaughan and O'Shea 1976). The most energetically costly phase of torpor is rewarming (Prothero and Jurgens 1986). *M. evotis* may choose roosts that are influenced by ambient temperature to take advantage of passive rewarming. Individuals often allowed their Tb's to rise passively with Ta, thereby avoiding the need for costly metabolic heat production.

Pallid bats, *Antrozous pallidus*, choose roosts that are responsive to ambient temperature in the spring, but roosts with stable temperature regimes are preferred during the summer (Vaughan and O'Shea 1976). By choosing roosts responsive to ambient temperature, pallid bats are able to take advantage of the energy savings of torpor at a time of year when insect abundance is low (Vaughan and O'Shea 1976). I found that minimum temperatures were lower in horizontal roosts than vertical roosts. Furthermore, pregnant females often allowed body temperature to drop to ambient levels (see above). Therefore, pregnant female *M. evotis* may choose roosts that allow them to take advantage

of deeper torpor than lactation roosts would allow, at least for the coldest part of day. However, the use of torpor is costly in terms of slowed fetal growth (Racey 1973). Although horizontal roosts drop lower in temperature compared to vertical roosts, horizontal roosts have higher mean daytime temperatures than vertical roosts during pregnancy. Therefore, females may gain the energetic benefits of low daytime minimum temperatures while maintaining fetal growth at an adequate level.

Mean daytime temperatures of horizontal and vertical roosts were similar during lactation. Females may choose horizontal roosts during pregnancy to avoid rain and/or because of costs/benefits associated with the use of torpor and fetal growth, but why are vertical roosts chosen during lactation? Vertical roosts maintain temperatures within narrower limits than horizontal roosts during pregnancy and lactation. This is not surprising because the boulders containing vertical roosts are larger than those that contain horizontal roosts (Holloway 1998) and the roost crevices are bounded by thicker rock. Therefore, vertical roosts probably have more thermal inertia, limiting fluctuations in temperature compared with horizontal roosts. Thermal stability may be important for the growth of juveniles. Bats that roost in maternity colonies may achieve thermal stability through clustering behaviour and the accumulation of metabolic heat within the roost (Kunz 1982). *M. evotis* in my study area can not take advantage of these strategies because of their solitary roosting habit. They may compensate by choosing roosts with more stable temperatures.

Although horizontal and vertical roosts had similar mean daytime temperatures during lactation, vertical roosts had higher daily minimum

temperatures than horizontal roosts did. Females could benefit in two ways by choosing such roosts. First, increased minimum roost temperatures probably result in a higher rate of milk production, because females can maintain their body temperatures at higher levels or spend less on thermoregulation (Wilde *et al.* 1995). More milk may mean faster growth of young. Second, juvenile bats may not be able to maintain body temperature when roosting alone (Lewis 1993) and growth rates of young bats are sensitive to temperature (Tuttle and Stevenson 1982). Clustering behaviour helps to prevent heat loss in juveniles of colonial species (Tuttle and Stevenson 1982), but this behaviour was not available to the bats in this study. Therefore, roost temperature may be an important factor determining roost choice in lactating females.

Juveniles are left alone in their roosts while females forage at night. I never captured females flying with their young. Therefore, roost temperature at night must also be important for maintaining juvenile growth rates. Mean nighttime roost temperature was significantly higher in lactation roosts compared to pregnancy roosts. Considering the amount of time adult *M. evotis* spend foraging at night and that their offspring are thus left alone, higher nighttime roost temperatures may be a critical determinant of suitable roosts for lactating females.

Small differences in temperature may produce significant differences in the metabolic rate (Webb *et al.* 1993), production of milk (Wilde *et al.* 1995), and the growth rates of juvenile bats (Tuttle 1976). Therefore, although the differences in minimum and average temperature discussed in this section are

only about two degrees, the consequences for growth rates and energy savings may still be significant.

Why might *M. evotis* in the badlands of the South Saskatchewan River valley choose a solitary roosting habit? Elsewhere females form maternity colonies (Manning and Jones 1989). Solitary roosting may be necessary to deal with tight thermoregulatory requirements imposed by foraging that may be inefficient, or by limited resources. I have suggested that females are unable to make use of metabolic heat build up and clustering. Perhaps females actually choose roosts to avoid these factors. Females use torpor every day. Clustering and metabolic heat build up could impede the use of torpor. Thermal regimes may also be more predictable in solitary roosts because they would not be influenced by the thermoregulatory decisions of other bats. If females "walk a fine line" in terms of their daily energy requirements, disturbance by other bats may be detrimental.

Differences in the temperature of different parts of roosts may be used for behavioural thermoregulation in bats (Hamilton and Barclay 1994, Vaughan and O'Shea 1976). I found that the thermal regime of horizontal roosts does not differ between deep and shallow positions, but it does in vertical roosts. In vertical roosts the deep position is warmer at night on average and has more stable temperatures (lower maxima, higher minima, and consequently smaller ranges) than the shallow position. Therefore, there is the potential for behavioural thermoregulation in vertical roosts. As discussed above, the relationship between minimum T_b and T_a is more variable in lactating compared to pregnant females. Lactating females may choose specific T_b 's according to their daily

energy demands, and their chosen position within a roost. Optimal Tb's in pregnant females may be limited as a consequence of their inability to use behavioural thermoregulation and this may lead to the tighter relationship between minimum Tb's and Ta.

The thermal properties of horizontal roosts do differ between the top and deep positions. The upper surface of the roost cavity is cooler on average at night and thermally less stable (higher maxima, lower minima, and consequently larger ranges) than the lower surface. The thin flakes of rock that make up the upper surface of the roost cavity heat up rapidly during the day causing the roost cavity to heat up. Similarly, this thin layer probably does not provide much protection against heat loss at night. This may explain why horizontal roosts do not buffer temperature as well as vertical roosts.

Conclusions

This was the first study to examine foraging and thermoregulation in individual bats inhabiting natural crevice roosts. For this reason, the unusual behaviours described in my study are particularly interesting. Individual *M. evotis* foraged every night and were able to forage all night probably because of their ability to glean and hawk. I suggest that long foraging bouts may be a general pattern for species that can capture volant and nonvolant prey. Individual *M. evotis* also used torpor every day and the amount of time spent in torpor was primarily determined by the amount of time available to do so. These findings imply that individual *M. evotis* are on a tight energy budget and I suggest that inefficient foraging may lead to this situation. Alternatively, this situation may

reflect the fact that my study area is at the northern limit of *M. evotis*' range, that the habitat is semi-arid, or that the bats roosted under natural conditions. My results also suggest that torpor is not limited to energy emergencies. Pregnant individuals roosted in horizontal crevices and lactating individuals roosted in vertical crevices, and these roosts differed in thermal regimes. Females may select roosts to maximize embryonic and juvenile growth rates while minimizing energetic costs.

This study raises a number of questions requiring further examination: (1) Are the behaviours described here the result of inefficient foraging? (2) Are the behaviours described here typical of *M. evotis* throughout its range? (3) Do *M. evotis* roosting in manmade structures in the north of their range behave in a similar way to the *M. evotis* in this study? (4) Do other species roosting in natural habitat behave in a similar way to *M. evotis*?

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Appendix 1. Calculations to determine the reduction in surplus power caused by the addition of a radio transmitter to individual *M. evotis* (based on Caccamise and Hedin 1985).

I calculated the base mass (m_b) of female *M. evotis* as the mean mass of not-obviously-pregnant females caught before June 15 in both years of the study. I assumed that these females had not accumulated fat stores or fetal mass by this time. $m_b = 6.59 \times 10^{-3} \text{kg}$

The adjusted mass (m_a) represents the natural increase in mass expected for a species. I used an increase of 30% based on values in the literature (Aldridge and Brigham 1988, Hughes and Rayner 1991).

$$m_a = 8.57 \times 10^{-3} \text{kg},$$

$$\text{Flight muscle mass } (m_f) = 0.17m_b = 1.12 \times 10^{-3} \text{kg},$$

$$\text{Wingspan } b = 1.1m_b^{0.3333} = 0.21 \text{m},$$

$$\text{Flap frequency } f = 3.816/b^{1.029} = 19.37 \text{ s}^{-1},$$

The available power (P_a) represents the maximum sustainable rate of power output during flight.

$$P_a = m_f Q f = 1.24 \text{ watts},$$

where Q is the specific work of flight muscles (57 joules/kg).

Flat plate area (A) represents the area of a flat plate yielding a drag equivalent to that produced by the frontal area of the bat.

$$A = 0.00334m_a^{0.660} = 1.44 \times 10^{-4} \text{ m}^2,$$

Wing disk area (S_d) represents the circular area through which the flapping wings travel.

$$S_d = 0.75b^2 = 3.34 \times 10^{-2} \text{ m}^2,$$

V_{mr} is the maximum range velocity.

$$V_{mr} = 1.13\{(9.81m_a)^{0.5}/(\rho^{0.5}A^{0.5}S_d^{0.25})\} = 6.52 \text{ m/sec},$$

The induced power (P_i) represents the power required to overcome the force of gravity.

$$P_i = 2(9.81ma)^2 / (3.14159pb^2 0.7V_{mr}) = 2.01 \times 10^{-2} \text{ watts,}$$

where ρ is the air density at the elevation of my study site = 1.15 kg/m^3 ,

The parasite power (P_p) represents the power required to overcome the resistance of the body moving through air.

$$P_p = \rho AV_{mr}^3 / 2 = 2.30 \times 10^{-2} \text{ watts,}$$

The profile power (P_o) represents the power required to overcome profile drag of the wing as it moves through air.

$$P_o = 1.8m_a^{-0.16667} V_{mr}^{-0.5} (P_i + P_p) = 6.72 \times 10^{-2} \text{ watts,}$$

Power maximum range ($P_{mr,a}$) represents the power required to fly at the most efficient velocity for birds at adjusted mass.

$$P_{mr,a} = P_i + P_p + P_o = 1.10 \times 10^{-1} \text{ watts,}$$

The surplus power (P_s) represents the difference between the amount of power required to fly at V_{mr} ($P_{mr,a}$) and total amount of power available (P_a).

$$P_s = 1.13 \text{ watts,}$$

Transmitter mass (m_t) = 0.56g ,

$$\text{The flat plate area of the transmitter } (A_t) = 0.0334m_t^{0.660} = 2.39 \times 10^{-5} \text{ m}^2,$$

¹ indicates that the transmitter effect has been included in the calculation.

$$\text{The flat plate area of the bat plus the transmitter } (A^1) = A + A_t = 1.68 \times 10^{-4} \text{ m}^2,$$

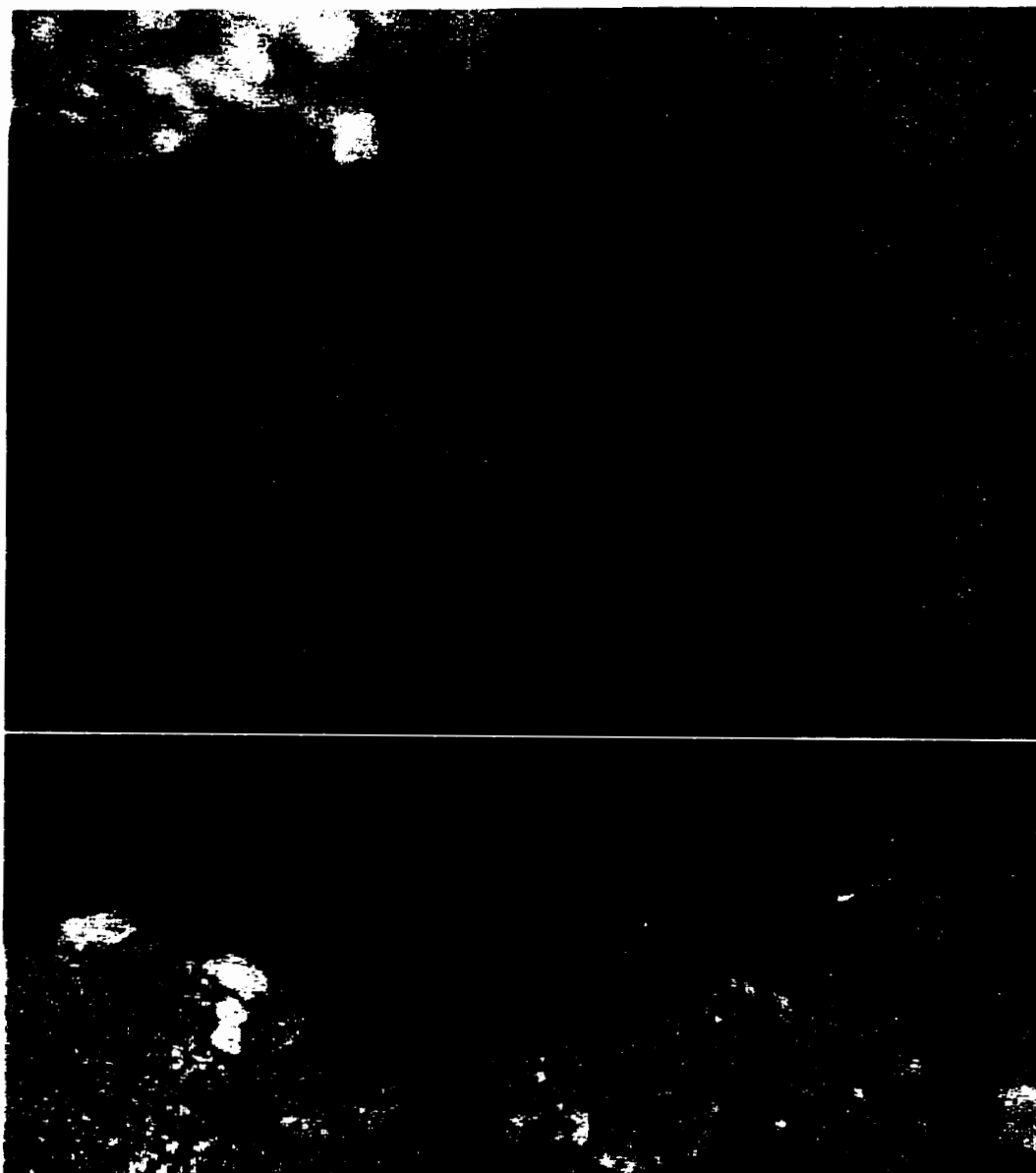
The adjusted mass or the bat plus the mass of the transmitter (m_a^1) =

$$9.13 \times 10^{-3} \text{ kg,}$$

$$V_{mr}^1 = 6.48 \text{ m/sec, } P_i^1 = 2.30 \times 10^{-2} \text{ watts, } P_p^1 = 2.63 \times 10^{-2} \text{ watts,}$$

$$P_o^1 = 0.08 \times 10^{-2} \text{ watts, } P_{mr,a}^1 = 1.26 \times 10^{-1} \text{ watts,}$$

The proportionate reduction in surplus power caused by the added costs of transporting a transmitter are = $(P_{mr,a}^1 - P_{mr,a}) / P_s = 1.35 \times 10^{-2}$ or 1.35%.



LONG-EARED BAT (*MYOTIS EVOTIS*)