

THE INFLUENCE OF REPRODUCTIVE CONDITION AND ROOST TYPE ON
THERMOREGULATION AND FORAGING IN BIG BROWN BATS (*EPTESICUS*
FUSCUS)

A Thesis

Submitted to the Faculty of Graduate Studies and Research

In Partial Fulfillment of the Requirements

For the Degree of

Master of Science

in

Biology

University of Regina

by

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Regina, Saskatchewan

July, 2013

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Jody Lynn Patricia Rintoul, candidate for the degree of Master of Science in Biology, has presented a thesis titled, ***The Influence of Reproductive Condition and Roost Type on Thermoregulation and Foraging in Big Brown Bats (Eptesicus Fuscus)***, in an oral examination held on June 21, 2013. The following committee members have found the thesis acceptable in form and content, and that the candidate demonstrated satisfactory knowledge of the subject material.

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ABSTRACT

Reproduction is energetically expensive for mammalian females and seasonality limits the amount of time available to successfully reproduce. Temperate mammals often have methods to cope with time constraints, such as thermoregulatory and foraging flexibility, but typically at a cost. However, foraging and thermoregulation are often studied separately, which leads to limited knowledge about what, if any, relationship exists between these two factors. The purpose of my research was to determine how thermoregulation and foraging patterns vary among reproductive stages in big brown bats (*Eptesicus fuscus*) that switched between building and tree roosts. I equipped pregnant and lactating bats with temperature sensitive radio-transmitters in southwest Saskatchewan, Canada. While transmitters were active, skin temperature data were collected using a datalogger and foraging patterns determined by triangulation. Thermoregulatory patterns remained similar between reproductive conditions, but with slightly more heterothermy employed during lactation, especially when roosting in trees. Lactating bats had a tendency to forage for longer duration than pregnant bats, and often took more foraging trips as well. When coupled together, I found that foraging duration and torpor duration were not directly related during pregnancy, but exhibited a slightly inverse relationship during lactation. These data provide support for the hypothesis that the relationship between thermoregulation and foraging is not constant throughout reproduction, which may be due to the trade-off between slowed development of young through torpor use and risky foraging for the female during suboptimal conditions.

ACKNOWLEDGEMENTS

First and foremost I would like to thank Mark Brigham for his encouragement, patience, and advice (and coffee!). The time he spent in providing guidance and support during this journey is greatly appreciated. I would also like to thank my committee, Ray Poulin and Richard Manzon for their thoughtful comments and suggestions to make my project better. I could not have done this work without the hands and backs of my field assistants, Emily Boutilier, Thomas Allen, Paul Preston, and Sam Jaques; thank you for your willingness to work all night and occasionally all day as well. Special thanks also to Leanne Heisler, Carolyn Gaudet, and Brandon Klüg for advice and perspective on previous versions of this thesis. And finally, thank you to the rest of the Bird and Bat lab and the Somers lab for great discussions and statistical help.

Thanks to the landowners, Mel and Darlene Hoffer, Ray and Noelene MacDougald for letting us traipse around their land at all hours of the night. Without funding through the Faculty of Graduate Studies and Research, the Natural Sciences and Engineering Research Council (to RMB), and Fish and Wildlife Development Fund, this project would not have been possible.

POST DEFENSE ACKNOWLEDGEMENTS

I would like to thank the external examiner of my defense, Patrick Neary, as well as my committee members for a challenging and thoughtful discussion. Thank you also to Larena Hoeber for being the chair of my defense.

DEDICATION

I would like to dedicate my thesis to my family and friends. Although you did not understand why I was interested in catching and chasing bats through the night, you stood by and listened. Thank you for providing me with a place to escape to, and hours of hiking, snowshoeing, and skating.

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LIST OF ABBREVIATIONS AND DEFINITIONS

Active Period – Time from first emergence to final return to roost (night time)

Bat – Individual bat, identified by the last three digits of the radio-transmitter frequency

Bat day – one bat carrying an active transmitter for one day

Bouts – number of nightly foraging trips made. Considered a trip when the individual returned to the roost area and remained stationary for >20 mins

Date – date of measurement in numeric form (e.g., Jan 1, 2012 = 40909 in excel as number format)

Degree-minutes (degmin) - area under the curve, incorporates the total duration and depth of torpor bouts, summed for the inactive period

DEM – digital elevation model in GIS

GIS – geographic information systems

Hiday – Heterothermy Index for the day of first foraging emergence being tracked

Inactive Period – Time between final return from foraging in the morning until evening emergence (day time)

Julian date – date of measurement from January 1

Min daily T_a (mdt) – minimum temperature ($^{\circ}\text{C}$) recorded outside occupied roost area during daily inactive period

Min nightly T_a (Temp foraging) – Minimum temperature ($^{\circ}\text{C}$) recorded at Environment Canada station (Maple Creek) between sunset and sunrise. For insect models – it was the temperature recorded at time of insect sweep sample recorded by Kestrel – averaged over 3 minutes

Min T_{sk} (Tskmin) – Minimum skin temperature recorded during daily inactive period by temperature sensitive radio-transmitters

Previous night foraging (pnf) – sum of the time spent flying on the night prior to thermoregulatory response.

Repro cond (fRC) – reproductive condition at time of capture. Binary 1= Pregnant, 2 = Lactating

Roost type (fRT) – in 2011, only used building (Hoffer garage), but 2012 either tree (Balsam Poplar – 4 trees used) or building (MacDougald House). Binary 1= building, 2 = tree

T_{99ci} – Torpor threshold that is the temperature 3°C below the lower limit of 99% confidence interval of the mode skin temperature (McKechnie et al. 2007)

T_a – ambient temperature

T_{active} – Torpor threshold determined as the lowest temperature (°C) recorded from a bat that is known to be active (prior to emergence (Barclay et al. 2001)

TNZ – Thermal neutral zone; the T_a range of minimal metabolic rate

T_{onset} – Torpor threshold incorporating roost or ambient temperature (°C) and mass of bat (g) (Willis 2007)

T_{sk} - skin temperature

Time (fT) – Time of insect sweep (within an hour, i.e. 0100 and 0130 are both 1)

Total Torpor – sum of time spent in torpor during daily inactive period – excluding torpor bouts that occur during active period

Wind – Average wind speed recorded at Environment Canada weather station (Maple Creek) between sunset and sunrise. For insect models – it is the wind speed recorded at time of insect sweep samples using Kestrel – averaged over 3 minutes

1. INTRODUCTION

1.1 Mammalian Reproduction

It is generally understood that mammalian reproduction is unevenly costly between sexes. Males typically have a lower reproductive cost than females, as males usually provide little to no parental care, cannot carry the foetus, or provide milk to the offspring. The costs incurred by males generally start and end with spermatogenesis, copulation, and mating displays (Bronson 1985; Gittleman and Thompson 1988). For female mammals, copulation itself is not energetically costly but the subsequent supply of nutrients to the foetus prior to birth and feeding young after parturition incurs the greatest costs. During gestation, female body mass increases substantially due to growth of foetal, uterine, placental, and mammary tissues (Kurta and Kunz 1987; Racey and Speakman 1987), which in flying mammals increases the cost of flight due to increased wingloading and consequently reduced maneuverability (Norberg and Rayner 1987). During lactation, the energy required by the mother increases dramatically from gestation, and typically rises from early lactation to a peak expenditure in mid-lactation and declines once again when young are capable of flight (Kurta and Kunz 1988). Throughout lactation, between 20-40% of daily energy intake is allocated to milk production (Racey and Speakman 1987; Speakman 2008). In addition to increased energy demands due to milk production, female bats also incur energetic costs in transporting non-volant young to new roost sites, and post weaning care. Therefore, female bats incur higher energetic costs for longer periods of time than males and thus might be expected to employ specific strategies to gain sufficient energy for the process.

There are three main strategies that female mammals employ in response to the increased energetic demands imposed by reproduction (i.e., gestation and lactation; Racey and Speakman 1987). The strategy most commonly employed by small mammals (<25 g) is to increase energy intake (e.g. cotton rats (*Sigmodon hispidus*); Randolph et al. 1977) or increase energy assimilation efficiency. The second strategy is to exploit either internal or external energy stores, specifically fat reserves or food caches, respectively. For small mammals, only 2-3 days' worth of energy can be stored, therefore, fat reserves are typically only used in emergency situations (Bronson 1985). The final strategy is to reduce energy expenditure by remaining inactive, or in some cases, reducing metabolism. In captivity, small terrestrial mammals tend to increase energy consumption and/or remain relatively inactive during gestation and lactation, in a location where there is a constant food supply (Racey and Speakman 1987; Speakman 2008). In free-ranging species, especially insectivorous species where food is not cached, it is rare that obtaining food requires no energy, which makes the use of alternative energy compensation strategies more likely to be necessary to mitigate the expenses of reproduction.

Bats (Chiroptera), especially Microchiroptera found in temperate regions, make good models for studying energy compensation during reproduction because they often employ a variety of strategies to cope with energy shortages. Like other small mammals, bats have been observed to consume more food (e.g., Anthony and Kunz 1977; Kunz et al. 1995) and use energy reserves as reproduction progresses (Reynolds and Kunz 2000). However, the increased energy intake in most cases does not appear to provide enough energy to balance the increased requirements for reproduction (McLean and Speakman

1999) as well as the additional constraints placed on flight by carrying extra mass (Barclay 1994; Norberg and Rayner 1987). Female temperate bats have the tendency to alter patterns of thermoregulation, and thus the associated energy expenditures, through the use of torpor. In temperate regions, bats have strict time constraints for reproduction due to seasonality and corresponding prey availability. In only a few months, females must complete gestation, raise young, and then store enough energy to survive the period of subsequent hibernation or migration. Pups are under perhaps even more stringent time constraints as they must learn to fly and echolocate to become proficient foragers and acquire enough fat reserves for winter hibernation or migration as well. Therefore, it may be essential for adult females to use a combination of strategies during reproduction to enhance the likelihood of success for both herself and her pup.

1.2 Torpor

Bats, like all mammals and birds, usually maintain a stable high body temperature through metabolic heat production (endothermy; IUPS Thermal Commission 2003), the energetic costs of which increase as the difference between body temperature (T_b) and ambient temperature (T_a) increase. Every individual has a T_a range in which metabolic rate is minimal (the thermoneutral zone; TNZ), but outside of this temperature range, metabolic rate must increase to warm or cool the body. To counteract high energy expenditure at low T_a , torpor is sometimes employed. Torpor is the controlled lowering of metabolic rate which in turn leads to a lowering of an individual's temperature set-point (i.e., the temperature at which the body is maintained) and body functions are slowed if not virtually halted (Geiser and Ruf 1995; Speakman and Thomas 2003; Wang 1989).

Many orders of mammals (Chiroptera, Didelphimorphia, Dasyuromorphia, Notoryctemorphia, Diprotodontia, Eulipotypla, Monotremata, Primates, Rodentia) and some birds use torpor (Dausmann 2005; Geiser et al. 2005b; Wang and Wolowyk 1988), especially during periods of prolonged resource shortage and adverse weather conditions. By using torpor, individuals are able to reduce the amount of energy expended until better conditions occur, after which time they actively initiate arousal. Arousal can be either energetically expensive and occur rapidly through endogenous heating (shivering and non-shivering thermogenesis) or inexpensive when passive and slow through exogenous heating (Lovegrove et al. 1999). The amount of energy saved during torpor is not a linear relationship with temperature declines due to Q_{10} effects. Each species has as a specific temperature coefficient (Q_{10}) by which metabolic rate is depressed for every 10°C decline.

Although torpor in mammals is energetically beneficial, there are also associated costs, especially during reproduction and growth of offspring. When torpid, the immune response is suppressed and heart and metabolic rates decrease (Wang 1989), which, during gestation, is thought to cause temporary delays in foetal development and possibly foetal death (Racey 1973). While torpor has been reported to occur during pregnancy in some mammals (e.g., stripe-faced dunnart (*Sminthopsis macroura*); Geiser et al. 2005b), it is rarely employed by lactating mammals (although occasionally in sugar gliders (*Petaurus breviceps*); Christian and Geiser 2007), aside from bats (e.g., McLean and Speakman 1999; Solick and Barclay 2006; Dzal and Brigham 2013). It is likely then that the costs of torpor use during reproduction outweigh the benefits for most mammalian groups.

In bats, it has traditionally been thought that torpor and reproduction are mutually exclusive. This paradigm can be traced to a laboratory study of pipistrelle bats (*Pipistrellus pipistrellus*) showing that parturition was delayed by the same number of days that females were forced into torpor, which gave support to the idea that torpor halts development during gestation (Racey 1973). If this is the case, then there should be a trade-off between a pregnant female's survival and the maximum chance of pup survival. By minimizing torpor use in the spring, females put themselves at risk of starvation because insect abundance is often low or unpredictable. However, by not using torpor, their young will be born earlier and are more likely to be weaned when prey abundance is high and with more time to prepare for hibernation or migration (Racey and Swift 1981; Willis et al. 2006). While energy expenditure during lactation is much greater than in pregnancy (e.g., Speakman 2008), it is theoretically less advantageous to use torpor during lactation because, aside from milk, pups have no source of energy or water. By using torpor extensively in lactation, the quality and quantity of milk produced declines (Wilde et al. 1995; Wilde et al. 1999), which decreases the chance of pup survival. Therefore, to increase the chance of successful reproduction, female bats must employ strategies that will not be overly detrimental to either her pup or herself.

There are often varying patterns of thermoregulation used by bats during pregnancy and lactation. Torpor depth is often greater during pregnancy than lactation, but torpor bouts are more frequent in lactation than pregnancy (e.g., western long-eared bat (*Myotis evotis*), big brown bat (*Eptesicus fuscus*), Daubenton's bat (*Myotis daubentonii*), and brown long-eared bat (*Plecotus auritus*); Dietz and Kalko 2006; Lausen and Barclay 2003; McLean and Speakman 1999; Solick and Barclay 2006). Even

though torpor is used during lactation, it is often expressed as only a slight depression of T_b (lowering $T_b < 10^\circ\text{C}$ from torpor threshold), which may leave it possible for females to continue with milk production. There is a great deal of variation in torpor use depending on reproductive condition alone, but additional factors such as roost type (Lausen and Barclay 2006) and geographic location (Solick and Barclay 2007) also appear to influence use of torpor.

1.2.1 Assessing thermoregulation

Measurement of metabolic rates through indirect calorimetry (i.e. respirometry) is the traditional way that the energetics of torpor has been assessed and is perhaps seen as the “gold standard”. It is often not logistically possible to measure metabolism in free ranging animals in this manner because they have to be in a metabolic chamber which measures oxygen consumption as a proxy for metabolic rate. Respirometry is good for measuring baseline metabolic rates but not for assessing thermoregulation in natural settings. A direct method of metabolic measurement that has been used in some studies is doubly labeled water (e.g., Schmid et al. 2003), which measures the differential elimination of hydrogen and oxygen isotopes from blood, which can then be used to calculate field metabolic rate. This is a good method for species that have a high probability of being recaptured in a short period of time (days), but individuals often learn to avoid traps and nets and are difficult to recapture, thus making this method impractical and costly. Another method of measuring metabolic rate is heart rate telemetry, with the assumption that heart rate increases when activity increases, thus making higher heart rates a proxy for higher metabolic rate (Butler et al. 2004). However, implantable dataloggers are currently too large for small mammals, and for

external transmitters, the relationship between heart rate and O_2 consumption varies between individuals and the technology is not reliable enough for external electrode attachment (Speakman 2000). For small mammals, current technology is small and reliable enough to measure skin temperature (T_{sk}) as a realistic proxy for studying thermoregulation and energetics of free-ranging animals through the use of temperature sensitive radio-transmitters (first reported use for bats in Audet and Fenton (1988)). Ideally, measurements of core T_b would be taken; however, surgically implanted transmitters have a short range of detection that makes them logistically impractical for use with most flying animals.

A variety of studies have assessed the legitimacy of using external measures (i.e. T_{sk}) to assess internal temperature changes in small mammals (e.g., Audet and Fenton 1988; Audet and Thomas 1996; Barclay et al. 1996; Dausmann 2005). Using concurrently implanted and externally attached temperature-sensitive transmitters, Willis and Brigham (2003) reported that there can occasionally be as much as a 6°C difference between T_{sk} and T_b when bats are active, and up to 9.5°C when bats were in deep torpor. While noting the difference, Willis and Brigham (2003) concluded that there was still a direct relationship between the two measures. One additional concern is that clustering in colonial bats or T_a in solitary bats will influence records of T_{sk} . However, it has been found that ambient temperature does not greatly influence measures of T_{sk} for cavity roosting bats and likewise clustering does not substantially affect transmitter readings (Willis and Brigham 2003, Audet and Fenton 1988). Although not of concern for measuring T_{sk} of stationary bats, it has been identified that there is an effect of T_a on T_{sk} in flying bats (Klüg 2011).

1.2.2 Torpor Thresholds

There has been a great deal of debate about how to define the threshold for entry into torpor, especially for free-ranging animals. Definitions of torpor thresholds typically vary depending on the investigator. For example, torpor has been defined as T_b or T_{sk} below a specified temperature (usually 30°C; e.g., Geiser and Brigham 2000), or T_b close to T_a (e.g., Audet and Fenton 1988). Both methods are largely arbitrary and typically do not cite or employ a mathematical or physiological justification. However, with the increased volume of thermoregulatory research and a greater understanding of thermoregulation, three additional thresholds have been suggested. Barclay et al. (2001) suggested a threshold that is both individual animal and transmitter specific where torpor is defined as any temperature that falls below an individual's active temperature (T_{active}). T_{active} is defined as the T_b at a point in which the animal is known to be active such as at emergence. While this has a physiological justification, it has been found that bats can clumsily fly when they are not fully re-warmed from a bout of torpor and thus still truly below T_{active} , which could lead to underestimating torpor use (Willis and Brigham 2003); however, when averaged over several days for each individual (Barclay et al. 2001), it often leads to a similar value to T_{onset} (below). McKechnie et al. (2007) suggested that torpor be defined as the T_{sk} 3°C below the 99% confidence interval of the modal T_{sk} (T_{99ci}), the justification being that the most common temperature is the normothermic temperature. Finally, Willis (2007) developed an equation to calculate torpor onset temperature (T_{onset}) based on data collected from simultaneously measuring metabolic rate (through respirometry) and T_b (implanted transmitters) of non-reproductive bats in

captivity and identified the body temperature that was associated with the initial metabolic depression:

$$T_{b\text{-onset}} - 1SE = (0.041)*\text{Body Mass} + (0.040)*T_a + 31.083 \quad \text{EQUATION 1}$$

The above torpor thresholds represent the temperature at which bats are considered to have entered torpor. Sometimes torpor is further divided into shallow (i.e., $\leq 10^\circ\text{C}$ below cut-off), or deep (i.e., $> 10^\circ\text{C}$ below cut-off) torpor (Grinevitch et al. 1995; Hamilton and Barclay 1994). The justification for the further division is that energetic savings are greater the farther T_b is allowed to fall, depending on bout duration due to expensive arousal, because metabolic rate is decreased further by a species specific temperature coefficient (Q_{10} ; although see Heldmaier and Ruf (1992)). These divisions are arbitrary, similar to many torpor thresholds, but often convenient for categorizing distinctly different thermoregulatory patterns in terms of potential energetic savings and physiological costs.

A recent metric, the heterothermy index (HI), has been suggested to facilitate inter- and intraspecific comparisons (Boyles et al. 2011b):

$$HI = \sqrt{\frac{\sum(T_{b\text{-mod}} - T_{b-i})^2}{n-1}} \quad \text{EQUATION 2}$$

$T_{b\text{-mod}}$ = modal body temperature (used to represent optimal body temperature)

T_{b-i} = body temperature at time i

n = number of times body temperature was sampled

HI does not measure torpor use directly, but rather the degree to which the T_{sk} of individuals fluctuates from the optimal (modal) temperature for that individual, essentially a modified standard deviation. Although easy to calculate and implement, there are some limitations to this metric. Firstly, HI does not reflect the physiological consequences of heterothermy (i.e., energy savings and physiological costs during torpor). Secondly, without a T_{sk} tracing, it is impossible to tell whether an individual with $HI = 0$ is employing steady state torpor or normothermy because very little temperature fluctuation exists in either situation. In addition, when torpor is obviously being used (e.g., $HI = 7$), telling the difference between an individual that uses a long shallow torpor bout vs. a short deep torpor bout is difficult. And lastly, HI is dependent on the sampling method which requires repeated T_{sk} measurements without disturbing the subject, which is sometimes not realistic.

Assessing torpor through thresholds has inherent problems (Boyles et al. 2011a); however, these traditional methods still provide important information regarding biological consequences of different thermoregulatory patterns (Brigham et al. 2011). Using a combination of HI and T_{onset} , I suggest we can better identify individuals that are more apt to being heterothermic, but also assess whether they are spending a great amount of time in torpor (saving energy) or if they are fluctuating their normothermic temperature but not using torpor for any substantial length of time.

1.3 Roost selection

For most of the day, animals occupy sites for resting while they are not foraging or performing other activities. The sites they select should provide some protection from environmental conditions and predators, as well as a suitable set of microclimatic

characteristics (Kalcounis and Brigham 1998; Law and Chidel 2007; Lewis 1995). Female bats are likely to select roosts that will promote rapid juvenile development, which typically occurs in warm roosts (Postawa and Gas 2009; Racey 1973; Zahn 1999). Regardless of roost type and bat species, lactating bats often use roosts that have either a higher temperature that stays warmer at night than roosts used by pregnant bats (Kerth et al. 2001; Kurta et al. 1989; Lausen and Barclay 2003), or the females form large clusters (Solick and Barclay 2006; Syme et al. 2001). By forming clusters, the surface area to volume ratio of individuals effectively decreases which reduce the energy required for thermoregulation (Trune and Slobodchikoff 1976) by up to 40% (Willis and Brigham 2007). By occupying warmer roosts or forming clusters in small cavities (Kurta 1985), remaining normothermic requires less energy because the gradient between T_b and T_a is decreased (Webb et al. 1993; Willis et al. 2005). In addition, roosts that are warm at night allow the young who cannot thermoregulate proficiently to remain warm longer without the presence of their mother (Sano 2000; Zahn 1999), enabling mothers to forage for longer periods of time.

Different types of roost structures are likely to have varying microclimatic conditions and certain structures have been found to be more beneficial from an energetic and growth point of view than others. For the eastern cave bat (*Vespadelus troughtoni*), roosting under a tin roof saves approximately 27-69% of the daily energy requirements compared to those roosting in shelter caves (Law and Chidel 2007); the roof bats experienced extreme temperature fluctuations throughout the day allowing for passive rewarming in the afternoon, which is an important energy saving characteristic (Turbill et al. 2003; Vaughan and O'Shea 1976). For *E. fuscus*, pups roosting in attics

became volant one to two weeks earlier than those roosting in nearby rock crevices where temperatures were cooler and mothers used more torpor (Lausen and Barclay 2006). However, mouse-eared bat (*Myotis myotis*) pups in Poland were the same size regardless of whether they were roosting in an attic or cave, which had differing microclimates, but on years where it was unseasonably cold, young were small compared to normal years regardless of the roost (Postawa and Gas 2009). These findings suggest that roost temperature is likely important for energetic savings and development of young, possibly due in part to the requirement for torpor use.

1.4 Foraging Behaviour

Animals must acquire energy in the form of food to fuel both metabolic and maintenance processes. The amount of energy required at any particular time varies depending on several factors, such as life stage, time of year, and reproductive status. Because energy demands change throughout the annual cycle and availability of energy is often variable, organisms must be able to change the strategy used to acquire or conserve energy. Due to the physiological constraints imposed by the nature of the digestive system, most organisms are not able to drastically change the type of food they consume; what can be altered is the amount of food eaten by selecting foraging locations or amount of time spent foraging. Foraging behavior has been studied for reproductive females of several temperate bat species. As expected based on differing energy requirements between pregnancy and lactation, food intake increases by 35-48% in lactating individuals in cave myotis (*Myotis velifer*), little brown myotis (*Myotis lucifugus*), and *P. pipistrellus* (Anthony and Kunz 1977; Kunz 1974a). In these and other studies, foraging duration (i.e., amount of time flying) typically remained the same for

bats in all reproductive conditions, but lactating bats made more foraging trips than pregnant bats and pregnant bats flew further from their roost to foraging locations (hoary bat (*Lasiurus cinereus*), *M. lucifugus* and *E. fuscus*; Barclay 1989; Duchamp et al. 2004; Henry et al. 2002). In some species (northern long-eared (*Myotis septentrionalis*) and *E. fuscus*), bats have been observed to change foraging locations during different stages of reproduction, possibly exploiting patches of higher insect abundance (Henderson and Broders 2008; Menzel et al. 2001). This variation indicates that lactating bats may be able to consume more prey and use less energy, even if foraging times remain similar between gestation and lactation.

Optimal foraging theory predicts that animals will be selected to maximize net benefits in the context of the ratio between energy invested (foraging effort) and energy gained, typically in either a time minimizing or energy maximizing approach (Pyke et al. 1977). The most important factor in either case is to gain the maximum amount of energy but how this is achieved varies between the two strategies. For time minimizers, the energy is acquired in the shortest amount of time and the duration is sufficient when energy for basal metabolic and maintenance processes has been attained (e.g., non-reproductive adult males). On the other hand, energy maximizers often have time and energy constraints placed on them (e.g., lactating females with suckling young) which results with several foraging trips being concentrated closer to the roost location than time minimizers. Previous studies have found that pregnant bats tend to forage using the time minimizing strategy (one foraging trip) whereas lactating bats tend to act as energy maximizers (several foraging trips close to the roost; e.g., Barclay 1989; Duchamp et al. 2004; Henry et al. 2002; Menzel et al. 2001; Rydell 1993; Wilkinson and Barclay 1997).

There are aspects of flight and weather conditions that could influence foraging efficiency between pregnant and lactating bats. Overall foraging efficiency should be greater for lactating bats than pregnant bats because insect densities tend to be higher due to higher temperature later in the season (Anthony and Kunz 1977), although, if foraging over water, temperature may not influence prey abundance as much as over land (Bryant 1975). Lactating bats also have a lower wingloading than pregnant bats, making them more adept flyers (Norberg and Rayner 1987), although decalcification of the skeleton for calcium supply has been predicted to lead to weaker wing bones in lactating bats, increasing the possibility of wing fractures (Barclay 1994). In addition, some evidence suggests that increased forearm curvature in pregnancy could decrease the energy required for flight (Sevick and Studier 1992). With these considerations, it can be assumed that when lactating bats are flying longer, they are consuming more prey; therefore, foraging duration should be an accurate representation of foraging effort.

1.5 Study species

The big brown bat (*Eptesicus fuscus*) is a medium sized bat (11-23 g) belonging to the family Vespertilionidae. It is common across its geographic range, occurring from southern Canada down through Central America. Mating often occurs prior to or during hibernation, after which females store and feed sperm in their uterus until they ovulate and the egg is fertilized in the spring (Wimsatt 1944). Gestation lasts approximately 60 days, although it can be longer depending on environmental factors (Kurta and Baker 1990). Females give birth to one or two young, each with a body mass approximately 30% of adult size. Young are born naked, blind, and completely dependent on their

mother. Pups are capable of flight at approximately 20 days after birth and are weaned by 36-40 days (Kunz 1974b).

Eptesicus fuscus are both roost and foraging generalists; they will roost anywhere that is feasible (tree cavities, buildings, bridges, caves, rock crevices) (Kurta and Baker 1990) and feed on virtually any flying insect that is a particular size (>10 mm). *Eptesicus fuscus* are insectivorous, feeding on prey such as Coleoptera (beetles), Lepidoptera (moths), and Trichoptera (caddisflies), although the precise diet varies depending on season, geographic location and likely environmental conditions (Brigham and Saunders 1990; Fullard et al. 1983). *Eptesicus fuscus* do not forage in one specific habitat type over another, although site fidelity is common within one geographic location. In the Cypress Hills (SK), they forage over pasture land (Arbuthnott and Brigham 2007), whereas in Georgia they use forested areas (Menzel et al. 2001). At the rural-urban interface in areas of Quebec and Indiana, bats forage over water, in forests and gardens, over roads, in low density residential areas, and around street lights (Duchamp et al. 2004; Geggie and Fenton 1985). Insect abundance has been suggested to influence foraging site selection (Arbuthnott and Brigham 2007; Hamilton and Barclay 1998).

In the summer while reproductive, female *E. fuscus* form maternity colonies ranging in size from 4-700 individuals, in attics or tree cavities. When buildings are present, *E. fuscus* appear to use them in preference to trees and other natural roost structures (e.g., Hamilton and Barclay 1994; Lausen and Barclay 2006); although this pattern of roost selection may only exist in areas where there have not been suitable tree roosts available historically, or where forest structure has been altered extensively, therefore eliminating natural roosts (Brigham 1991). The apparent preference for building roosts suggests that

perhaps human structures may provide better conditions (e.g., microclimate) than natural locations, which help females conserve energy. Maternity colonies have also been reported to occur in rock crevices (Lausen and Barclay 2002) and tree cavities (e.g. Western red-cedar (*Thuja plicata*), beech (*Fagus grandifolia*), trembling aspen (*Populus tremuloides*) and ponderosa pine (*Pinus ponderosa*); Brigham 1991; Kalcounis and Brigham 1998; Rancourt et al. 2007; Vonhof and Barclay 1996).

1.6 Objectives

Foraging behaviour is potentially linked to torpor use during reproduction. If females cannot obtain enough energy through foraging, then they are more likely to use torpor (i.e., as foraging decreases, torpor use increases). There is considerable evidence that torpor is used throughout gestation and lactation in bats (e.g., Audet and Fenton 1988; Grinevitch et al. 1995; Solick and Barclay 2007; Willis et al. 2006) and there have also been studies that identify how foraging behaviour is affected by reproduction (e.g., Anthony and Kunz 1977; Henry et al. 2002; Menzel et al. 2001). However, there has been little research focused on the interaction between torpor use and foraging patterns. When they have been studied concurrently, the amount of time outside the day roost has been the foraging variable measured (Dzal 2010; Grinevitch et al. 1995). Although the amount of time flying is an important consideration, foraging location and the number of foraging trips are also important elements of foraging ecology. These variables can provide information pertaining to the strategy (i.e., time minimizer or energy maximizer) and biological constraints on reproductive females. I propose to fill the knowledge gap between energy conservation and consumption by investigating thermoregulation and

foraging together, and determining factors that are likely to push animals into torpor when it is not necessarily beneficial to do so. Therefore, the goal of my thesis was to evaluate foraging and thermoregulatory patterns in reproductive big brown bats. Given that there are different physiological costs associated with using torpor during pregnancy and lactation I hypothesize that the strategies used by big brown bats in either condition will differ to meet the requirements of reproduction. My specific objectives were to:

- 1) Compare general patterns of thermoregulation, specifically torpor use (torpor depth, duration, time of day torpor is used) between pregnant and lactating *E. fuscus*. I predicted that pregnant bats would use torpor more often, for longer periods of time and at greater depths than lactating bats, and torpor would be used early in the morning in both conditions when T_a is lowest.
- 2) Assess which factors influence torpor duration, depth, degree-minutes, HI, and whether or not *E. fuscus* use torpor. I expected that a combination of physiological and environmental factors would influence thermoregulation.
- 3) Compare general foraging patterns (foraging duration, number of foraging trips) by pregnant and lactating *E. fuscus*. I predicted that lactating bats would forage for longer and make more foraging trips closer to the roost than pregnant bats because energetic requirements are greater during lactation and suckling mothers must feed their pups.
- 4) Assess which factors influence foraging duration. I expected that a suite of environmental (e.g., temperature, wind, precipitation) and physiological (e.g., previous day thermoregulation, reproductive condition) factors would affect foraging duration.

- 5) Assess the relationship between torpor use and foraging duration. Overall, if there truly is a cost associated with torpor use during reproduction, then torpor should occur infrequently when conditions permit successful foraging (i.e., not windy, cold or rainy). When bats cannot consume enough prey (based on measures of foraging time), I predicted that they would employ torpor to a greater extent the following day. Therefore, there will be an inverse relationship between torpor use and foraging duration regardless of reproductive condition.

2. METHODS

2.1 Study area

My study took place 10 km south of Maple Creek, Saskatchewan, Canada at two sites located approximately 4 km apart (2011 site: 49°48'31" N 109°29'08" W; 2012 site: 49°48'42" N 109°26'06" W; Figure 1). Both sites had a reservoir within 1 km of the primary day roost with a small creek nearby. At the 2011 site the creek was surrounded by short shrubs with occasional *P. tremuloides* whereas at the 2012 site the creek was surrounded by balsam poplar (*Populus balsamifera*) and *P. tremuloides*, as well as hawthorn (*Crataegus* spp.). The general area is characterized by rolling hills supporting native prairie that is grazed by cattle and horses with small cultivated sections and hayed areas. In both sites, the primary roost, a building in each case, was located in a valley between two ridges. In 2011, the bats occupied a garage with an open attic, occupying several areas of the attic and the roofline. In 2012, the bats were roosting in the rafters and behind fascia of a house without an open attic space.

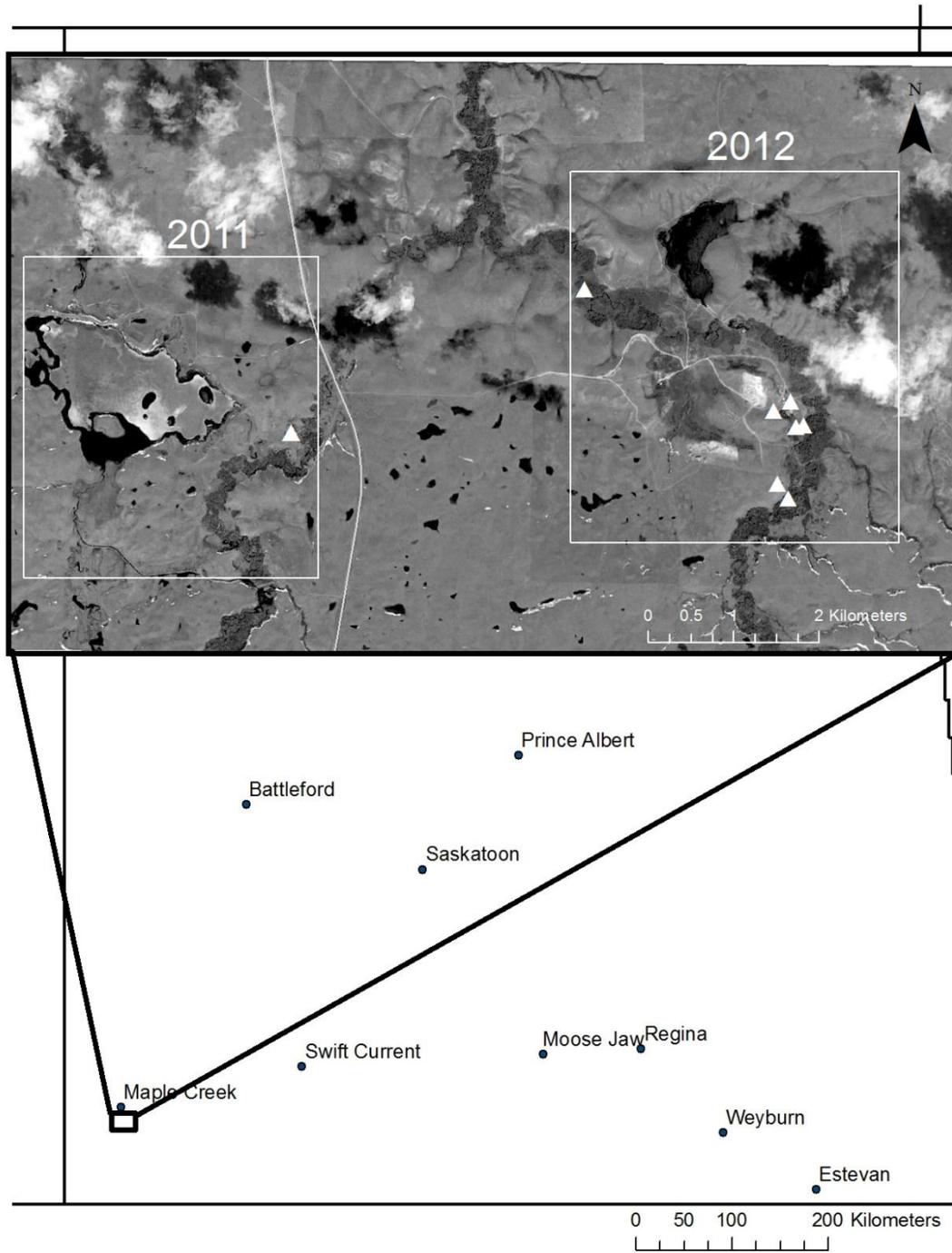


Figure 1. Location of roost structures near Maple Creek, SK. Inset is an aerial photograph with the 2011 and 2012 sites outlined in white boxes. The triangles represent location of roosts occupied by bats in each year.

2.2 Capture and Handling of Animals

From mid-May to August in both years I caught bats in mist nets placed outside the building roosts. Upon capture, I assessed reproductive condition and measured forearm length and body mass for each individual. Females were classified as pregnant by abdominal shape or the detection of a foetus when the abdomen was gently palpated (Racey 1988), or lactating if they expressed milk and had bare patches around the nipples (Racey and Swift 1981). Some females were equipped with a temperature sensitive radio-transmitter (BD-2T, Holohil Systems Limited, Carp, ON, Canada) affixed to the intrascalpular region using surgical adhesive (Ostobond, Montreal Ostomy Inc., Vaudreuil-Dorion, QC, Canada). Before transmitters were attached I used a water bath at 10°C intervals from 0-40°C and compared pulse rate and temperatures to manufacture calibration curves to ensure temperature detection accuracy. Prior to release, bats were also injected with a 0.2 g PIT tag (passive integrated transponder; Trovan ID-100 transponders, Eidap, Inc., Sherwood Park, Alberta, Canada) in 2011 for future identification. Before PIT tags were implanted, the injection site was cleaned with 95% ethanol and the skin pinched to raise a loose flap to facilitate an easy and low risk injection with the specially designed application needle. During the injection process, bats were immobilized by holding them on their stomach and applying gentle pressure to the shoulders and pelvis. Most bats were released within one hour of being captured (Appendix A). All methods were performed in accordance to the guidelines of the Canadian Council on Animal Care and approved by the University of Regina President's Committee on Animal Care (AUP#12-03).

2.3 Data collection

2.3.1 T_{sk} Measurements

Bats were tracked to their day roost in the morning following transmitter attachment and on all subsequent days. I deployed a data logger (SRX-400, Lotek Wireless Inc., Newmarket, ON, Canada) near the day roost to record transmitter signals beginning the morning following attachment. The manufacturer's calibration curves for transmitters were entered into the datalogger and, based on the interpulse intervals from the transmitter, the logger calculated and stored data on T_{sk} every 10 minutes.

Temperature dataloggers (iButton, DS1921, San Jose, CA, USA) were placed in the shade within 5 m of the roost in each of the four cardinal directions to measure T_a as a proxy for roost temperature (T_{roost} ; they have been found to be highly correlated; see Results and Dzal and Brigham (2013), Kalcounis and Brigham (1998)). For my analysis, outside T_a was used as a standardized temperature for all bats because, within each roost structure there are many locations available to bats as roosts and thus many different temperatures that they could be exposed to at a particular time. In addition to T_a recorded by iButtons, hourly and daily temperature and precipitation data were obtained from the Maple Creek weather station (Environment Canada), located approximately 10 km north of the study sites. Sunrise and sunset data were obtained for the area using the NRC Canada sunrise sunset calculator.

2.3.2 Foraging Measurements

Bats were actively tracked on all nights following transmitter attachment, but not on the night of attachment, until the transmitter was dropped. Bat locations were triangulated every 15 minutes from dusk until dawn using telemetry receivers (R-1000,

Communication Specialists, Inc., Orange, CA, USA) and 5-element yagi antennas. Two or three people, each with a receiver and antenna, were situated at predetermined and geo-referenced points. These observers simultaneously took compass bearings of a bat's location. Bats were classified as moving or stationary by all observers independently based on signal modulation. If the signal strength was variable (i.e., alternating between loud and quiet signals) then the bat was assumed to be flying, if the signal was of constant strength then the bat was assumed to be stationary (Brigham et al. 2000; Henderson and Broders 2008). Bearings were entered into Locate III (Nams 2006), a program that determines location error based on a maximum likelihood estimation. I set bearing standard deviation (*SD*) equal to 5 *SD* to allow me to assign all bearings with the same amount of variation, because due to the nature of locating flying bats, it was assumed there was considerable error associated with each bearing. Calculated locations with a standard error in either x or y axis >150 m were excluded from analysis, along with locations outside the conservative range of the receiver based on received signals from known distances. Signal strength is dependent on many factors (e.g., observer's body, topography, forest vegetation, wind, humidity; Fuller et al. 2005) and often changed throughout the night, therefore, 1 km was considered to be a conservative range.

2.3.3 Measurement of Relative Insect Abundance

I used an adapted spotlighting method to assess a relative estimate of insect abundance (Woods 2002). I chose a location that was close to the telemetry location where bats were observed foraging and was open in all directions. At the location, the observer would stand in silence while taking a wind and temperature measurement for 3 minutes. Following the 3 minutes, a spotlight (1,000,000 candlepower) held at a height

of 1.5 m and used to illuminate the area. The observer rotated in a circle, completed in approximately 30 s. While rotating, the number of insects that were either small (<10 mm) or large (>10 mm) as they appeared in the spotlight were counted. The relative size of insects was calibrated by placing known sized objects at distances up to 100 m from the observer for reference. Large insects could be seen approximately 50 m away and small insects approximately 30 m away. After each observation was completed, temperature, wind speed, cloud cover, collection time, rotation time, and insect numbers were recorded. If there was an emergence of small insects, it was indicated by a value >50. Insect abundance was recorded every 30 minutes from 1 hour after sunset until 1 hour before sunrise. Most samples were taken at the same location for logistic reasons because I was only concerned with relative abundance to determine what factors influence insect numbers.

2.4 Data Preparation

2.4.1 Torpor Characteristics

I used the recorded T_{sk} data to calculate a number of descriptive variables about torpor use. The torpor threshold I used was Willis' (2007) T_{onset} (Equation 1) for each bat day (i.e. one bat day = one transmitter active for one day) as opposed to T_{active} or T_{99ci} , although all three were calculated for comparison. I chose T_{onset} because it was developed using data for *E. fuscus* and has the greatest physiological justification of the three thresholds. Bats were considered to be in torpor if T_{sk} dropped $\geq 0.1^{\circ}\text{C}$ below T_{onset} for ≥ 2 consecutive readings (i.e. >20 minutes). Torpor depth, duration, degree-minutes, number of torpor bouts, and T_a at minimum T_{sk} , were all calculated in relation to T_{onset} , along with the heterothermy index (HI; Equation 2). Torpor depth was defined as the

number of degrees below T_{onset} that minimum T_{sk} fell, as opposed to actual minimum T_{sk} , since each bat day had a different T_{onset} . Torpor duration was calculated by summing the amount of time a bat spent in torpor per day. An integrative term, degree-minutes, was calculated as the area under the curve which takes into account the combination of torpor depth and duration, which, used alone is unclear about the amount of energy savings accrued (Studier 1981; e.g. 20 minute bout at depth of 10°C has the same value of a 10 minute bout at depth of 20°C). The minutes from sunrise to when the first entry into torpor occurred was used to determine if there was a relationship between time of day and torpor use.

2.4.2 Foraging patterns

Once locations were calculated in Locate III, they were imported and projected in a geographic information system (GIS) in ArcGIS 10 (Esri 2012). In the GIS, I imported shapefiles from GeoBase Canada, which included habitat type, a digital elevation model (DEM), satellite image, and hydrology. The DEM was converted from raster to polygon then clipped using a polygon of the study area (1 km buffer merged from each telemetry station). I also clipped the habitat type and hydrology layers to the study area. For the habitat type polygons, I calculated the area (ha) for each class to determine the proportion of the study area that was in each class. I used these data to determine the expected frequency of locations based on the number of locations for individuals in each reproductive condition. Using the foraging locations, I performed a kernel density rendering to determine concentrated activity spots. In addition, I calculated the geometric mean center (center of point concentration) and standard distance (degree of point concentration around the geometric mean center within 1 *SD*) for locations in each

reproductive condition. I calculated the point distance from the primary roost to the geometric mean center to determine if the majority of locations occurred the same distance away in each reproductive condition. I also calculated the distance to the nearest water feature (reservoir or creek). I conducted a spatial join of bat point locations, habitat type, and elevation and determined the occurrence frequency in each class. The observed frequency was then graphically and statistically compared with expected frequencies to determine if bats were using the landscape in proportion to availability. Only data from 2012 was used for this analysis.

2.4.3 Roost temperature

Once transmitters were shed from the bats, they were deemed to be located within the roost structure when transmitters emitted a pulse of similar height and signal strength as transmitters attached to bats roosting in that structure at the time. When determined to be within the roost structure, internal temperature was recorded and compiled for each structure in 2011 and 2012. When multiple transmitters were being logged at the same time, I used the mean value at each recording time as the current temperature within the roost.

2.5 Model generation

A literature review identified factors that have either been found or suggested to be important for 1) thermoregulatory response, 2) insect abundance, and 3) foraging activity in temperate animals. I built several *a priori* physiologically and ecologically relevant models based on the factors identified to be important for each response group (Dochtermann and Jenkins 2011). I used this approach rather than an all subsets

approach because an all subsets approach is largely exploratory and I did not have a biological explanation for each of the subsets and this approach would have resulted in the number of models being greater than my effective sample size (Anderson and Burnham 2002; Burnham and Anderson 2002).

2.5.1 Thermoregulation Models

I generated a candidate set of models based on my predictions and incorporating factors that have been reported to influence torpor use. Many factors have been identified as being important for prompting torpor use based on extensive field studies of both mammalian and avian species including: sex and reproductive condition (Cryan and Wolf 2003; Grinevitch et al. 1995; Turbill and Geiser 2006), lunar cycle (Riek et al. 2010; Smit et al. 2011), food availability (Doucette et al. 2012; Munn et al. 2010), ambient temperature and other environmental conditions (Willis et al. 2006; Wojciechowski et al. 2007), roost type (Jacobs et al. 2007; Lausen and Barclay 2006), geographic location (Solick and Barclay 2007), season (Brigham et al. 2000; Dietz and Kalko 2006; Geiser and Baudinette 1987), photoperiod (Geiser et al. 2005a; Geiser et al. 2007; Holloway and Geiser 1996), and time of day (Körtner and Geiser 2000; Oelkrug et al. 2011). Of these factors, lunar cycle, food availability, wind speed and precipitation would likely directly affect foraging patterns more than thermoregulatory patterns and were therefore excluded from this model set. Sex, geographic location and season were also excluded because the bats I tracked were all females located in the same area and studied in the same season. Of the remaining factors I included reproductive condition (pregnant or lactating), minimum daily ambient temperature, and roost type (tree or building) as explanatory parameters. In addition, I hypothesized that energy intake of the

night preceding daily inactive period would likely influence behaviour on the current day; therefore, information about the previous night foraging was included. The response variables were daily torpor duration, torpor depth, torpor degree-minutes, HI, and whether or not torpor was used.

Ten models were included in the candidate set for each thermoregulatory response variable (Table 1). The global model (model ID: T10) included minimum daily T_a , roost type, reproductive condition, and previous night foraging duration. Each covariate or factor was modeled separately and in various combinations and each model had a biological explanation. Minimum daytime T_a (T5) was included to account for the approximate minimum temperature an individual would experience. The duration of foraging on the previous night (T8) was included because bats cannot store food and their ability to store fat is limited, so their only energy supply would be obtained through flying. Thus, from a feeding perspective, if the previous night was successful or not would likely influence the amount of energy that may need to be conserved by entering torpor. Reproductive condition (T1) was included due to the physiological costs that likely occur with torpor use (delayed parturition or reduced milk quality and quantity) as well as energetic requirements in each. And finally, roost type (T4) was included because microclimatic conditions typically vary between different roost types (e.g., Lausen and Barclay 2006; Law and Chidel 2007). The model for roost type and minimum T_a (T6) was included because different roost types likely buffer ambient conditions in different ways. Roost type and foraging (T9) were modeled together because it is conceivable that there is an influence of where a bat day roosted and the amount of time spent foraging. Roost type and reproductive condition (T3) were

Table 1. Thermoregulatory (T), insect (I) and foraging (F) *a priori* candidate model sets. Thermoregulatory model: fRC = reproductive condition, fRT = roost type, mdt = minimum daily temperature, pnf = previous night foraging duration. Insect model: Temp = temperature at sample, Wind = wind speed at sample, Moon = days after full moon, Time_r = time of sample, Precip = daily precipitation. Foraging models: Bouts = number of foraging trips, HI_day = heterothermy index during the day before foraging, Tamin = minimum night temperature, Awind = average wind speed of night. Random intercept effects: (1|fB) = individual bat, (1|fD) = sampling date.

Model I.D.	Parameters
T1	fRC + (1 fB) + (1 fD)
T2	(1 fB) + (1 fD)
T3	fRC + fRT +(1 fB) + (1 fD)
T4	fRT + (1 fB) + (1 fD)
T5	mdt + (1 fB) + (1 fD)
T6	mdt + fRT + (1 fB) + (1 fD)
T7	pnf + fRC + (1 fB) + (1 fD)
T8	pnf + (1 fB) + (1 fD)
T9	pnf + fRT + (1 fB) + (1 fD)
T10	mdt + pnf + fRC + fRT + (1 fB) + (1 fD)
I1	Temp * Wind + Moon + Time_r + Precip + (1 fD)
I2	Temp * Wind + (1 fD)
I3	Temp + Wind + Time_r + (1 fD)
I4	Temp + Wind + (1 fD)
I5	Wind + (1 fD)
I6	Time_r + (1 fD)
I7	Temp + (1 fD)
I8	Precip + (1 fD)
I9	1 + (1 fD)
I10	Moon + (1 fD)
F1	Bouts + fRC + (1 fB) + (1 fD)
F2	fRC+(1 fB) +(1 fD)
F3	Bouts +(1 fB) +(1 fD)
F4	1 + (1 fB) + (1 fD)
F5	Bouts + HI_day + fRC + (1 fB) + (1 fD)
F6	Tamin+(1 fB) +(1 fD)
F7	Awind + (1 fB) + (1 fD)
F8	HI_day + (1 fB) + (1 fD)
F9	Tamin * Awind + fRC + (1 fB) + (1 fD)
F10	Tamin * Awind + (1 fB) + (1 fD)
F11	Bouts + Tamin * Awind + HI_day + fRC + (1 fB) + (1 fD)

modeled together because roost type selection may vary by reproductive condition which could affect thermoregulation. Finally, foraging duration and reproductive condition (T7) were modeled together because of the energetic requirements of each reproductive condition (lactation requires more energy than pregnancy) that would need to be met through foraging.

In all models, individual bat and date were included as random effects because multiple bats were often tracked simultaneously and each bat was measured over several days; this procedure accounts for pseudoreplication and dependence in these data. In addition to these models, the null or intercept model (T2; consisting of only the intercept and individual and date random effects) was run to assess whether the explanatory variables explained the response variable better than random.

2.5.2. Foraging Models

Using the same model generation protocol as for the thermoregulatory models, I built candidate model sets (Table 1) for two response variables. First, because I wanted to assess whether local factors influence relative insect abundance, I used the number of large insects seen in a light beam as a response variable. I included factors/covariates (referred to as parameters from here on) identified in published literature as affecting flying insects, such as wind (Model ID: I5), precipitation (I8), temperature (I7), moon phase (I10) and time of night (I6; e.g., Anthony et al. 1981; Beasley and Adams 1994; Benton et al. 2002; Bryant 1975). All parameters were included in the global model (I1). I modeled the interaction between wind and temperature (I2) because insect abundance may be lower when it was cool and windy, as well as an additive model for wind and temperature (I4). I included an additive model including temperature, wind, and time of

night (I3) because insect abundance has been found to change throughout the night, along with temperature and wind. Multiple samples taken each night were not completely independent; therefore, all insect models had night as a random effect.

Ideally, I would have used insect abundance as a covariate to predict foraging duration, however, insect density was only measured on 20 nights, and thus did not provide a large enough sample size. I used the most influential parameters in insect models in the foraging duration models, given that I expected that relative prey abundance likely influences foraging duration.

Parameters that I included in the foraging duration models were number of foraging bouts (Model ID: F3; Barclay 1989; Lučan and Radil 2010), reproductive condition (F2; e.g., Brigham 1991; Dietz and Kalko 2007; Encarnação and Dietz 2006), daily HI (F8), minimum nightly temperature (F6) and average nightly wind speed (km/h, F7; Arbuthnott and Brigham 2007; Barclay 1991; Kusch et al. 2004). Individual bat and night were included as random effects because there were many nights of data for individual bats and often multiple bats tracked on the same night. The models included combinations of the above variables as follows: 1) foraging bouts and reproductive condition; I hypothesized that lactating bats would make more foraging bouts (F1), 2) foraging bouts, daily HI, and reproductive condition (F5) based on whether energetic savings and energy requirements with the number of foraging bouts would influence total foraging duration, 3) minimum nightly temperature, average wind speed and reproductive condition (F9) to see whether relative insect abundance in combination with differing energetic requirements would be important, 4) an interaction model of temperature and wind speed (F10) to determine if insect abundance affects foraging

duration. Finally, I built a 6) global model (F11) with all variables and 7) an intercept model (F4) with only a random intercept with random effects.

2.6 Exploratory analysis

I assessed the data following Zuur et al. (2009) to check for homogeneity of variances, outliers, normality, multicollinearity, and independence. One response variable (torpor duration) was $\ln(y+1)$ transformed to meet the assumption of normality. Outliers were identified as points greater than 2 *SD* from the median value. When outliers were detected, they were checked to ensure human error was not the cause. In all cases, outliers proved to be true variance within the population (i.e. one day of extended use of torpor by several bats). Results with outliers removed are not discussed unless their removal changed the overall pattern.

Initially, the global model for each response variable was run as a linear or generalized linear model. I plotted the model residuals and they indicated a violation of most assumptions. There was also dependence in the data because bats were measured on multiple days and each date had multiple individuals. I plotted standardized residuals against both bat and date; both plots indicated that individual bat and day were needed in the models, therefore they were included as random intercept effects in the foraging and thermoregulation models (only date was included in insect models). Inclusion of both parameters as random effects normalized the residuals and decreased the heterogeneity of variances in the models. I ran the global models for each response variable again, but as a linear mixed-effects model (LMM) or a generalized linear mixed effects model (GLMM, package lme4; Bates et al. 2012) depending on the response variable in question. I visually assessed residuals for normality and homogeneity of variances,

influential points (Cook's D, Df Betas; package influence.ME; Nieuwenhuis et al. 2012) and goodness of fit (Hosmer Lemshow test) for each global model (Zuur et al. 2010). I also calculated the 95% confidence interval (package models; Warnes 2012) for each parameter and intercept. Once the fit of the global model was sufficient and assumptions were mostly met, I ran all models in the candidate set, then extracted log likelihood and AIC to compare models. In confidence intervals encompassed 0 they were considered to be uninformative parameters.

In the torpor depth, duration, and degree-minute models, I used a subset of the data with only bat days that had at least one bout of torpor. This subset was used to avoid zero inflation concerns that would be present because torpor was not used on at least a third of the days, and when identifying torpor patterns it is uninformative to model days during which torpor was not employed. The full data set was used for the heterothermy index and torpor or no torpor models.

2.7 Model Selection and Statistical Tests

I used the second order Akaike Information Criteria (AIC_c) for model selection, following Burnham and Anderson 2002. I used AIC_c to correct for small sample size because my sample size (n) was small compared to the number of parameters (k ; i.e. $n/k < 40$) in global models. The raw AIC_c value is not informative, but the difference between the lowest AIC_c and subsequent models in the candidate set (*a priori* determined hypotheses), ΔAIC , is important and models with $\Delta AIC < 2$ indicates the model is feasible, but if > 10 the model does not provide additional information (Burnham and Anderson 2002). I also calculated Akaike weights (w_i) for each model within the set. The weight indicates the probability that the top model in the set is in fact

the top model. The cumulative Akaike weight was calculated to identify the confidence set of models ($\sum w_i \geq 0.95$). To ascertain a relative importance value for each variable, I summed the w_i for the models in which each variable was in. When model selection uncertainty occurred ($w_i < 0.9$), I used a model averaging approach using the confidence set of models to generate a composite model (the new model averaged model; Burnham and Anderson 2002). Both the new parameter estimates and an unconditional standard error were calculated, along with 95% confidence intervals.

I used an analysis of variance (ANOVA) to compare weather variables (minimum daily temperature, maximum daily temperature, total daily precipitation, and wind speed) from May to August in both 2011 and 2012 as well as to compare the temperatures in roost structures in 2012. To assess whether the buildings in 2011 and 2012 had similar conditions I ran an analysis of covariance (ANCOVA) with external temperature as a covariate and T_{roost} as the response variable. I also performed a Pearson correlation to evaluate the relationship between torpor and foraging duration. I used a Chi-Square test to determine if bats were located within habitat classes in equal frequency to their availability. For these tests, significance is indicated by a p-value < 0.05 . All values are presented as the mean (\bar{x}) \pm standard deviation (*SD*) or parameter estimates (β) \pm unconditional standard error (*se*). All analyses were completed in program R (version 2.15.2; R Core Team 2012).

3. RESULTS

In 2011, 2 pregnant and 4 lactating bats were outfitted with radio transmitters (colony size approximately 40 bats before the young became volant). In 2012, I radio-tagged 11

pregnant and 14 lactating bats (Appendix A.). Approximately 60-65 bats were counted at the 2012 building roost; however, bats switched roosts frequently causing this number to fluctuate. I combined data from both years because there was no significant difference in weather conditions between years (Table 2) and the colonies were located within 4 km of each other. Thus I collected data for a total of 13 pregnant and 19 lactating bats. The transmitters remained attached for between 1 and 10 days ($\bar{x} = 4$ days); however, due to equipment logistic issues, skin temperature (T_{sk}) data were not collected on all days. Complete data were collected on 45 and 52 bat days for pregnant and lactating bats, respectively (7 bats with 1 complete day, 12 with 2 complete days, 7 with 3 days, 1 with 5 days, 1 with 7 days, and 2 with 8 days).

T_{onset} was similar between bats in the two reproductive conditions ($32.7^{\circ}\text{C} \pm 0.2^{\circ}\text{C}$, Table 3). The mean difference between T_{onset} and T_{active} was -1.46°C ($SE = 0.39$), and between T_{onset} and T_{99ci} threshold was 0.24°C ($SE = 0.38$). However, on an individual level the range of difference was $0-4^{\circ}\text{C}$ and $0.05-5.3^{\circ}\text{C}$ respectively (Figure 2). Also, neither T_{active} nor T_{99ci} threshold could accurately predict T_{onset} (parameter estimate $\pm SE$, 0.01 ± 0.02 , $p = 0.64$ and 0.01 ± 0.02 , $p = 0.80$, respectively).

I found three general thermoregulatory patterns used by bats, regardless of reproductive condition (Figure 3). Bats often remained normothermic with some deviation around their “normal” temperature, but never falling below the torpor onset temperature (pregnant: 10 bat days and lactating: 14 bat days). Typically, bats would lower their T_{sk} below T_{onset} , but would remain at least 15°C above T_a (shallow torpor; pregnant: 22 bat days; lactating: 24 bat days). The rarest pattern identified was when bats allowed T_{sk} to fall to within 5°C of T_a and maintained this temperature for most of the

Table 2. Weather summary and ANOVA results for 2011-2012 comparison of temperature (°C), precipitation (mm) and maximum wind speed (km/h) between the months of May, June, July, and August. Bold underscored values indicate significance ($\alpha = 0.05$).

		2011 $\bar{x} \pm SD$ (range)	2012 $\bar{x} \pm SD$ (range)	F- statistic	p-value
May	Max Temperature	16.3 ± 3.0 (10.3-21.1)	17.0 ± 5.7 (4.6-28.2)	0.37	0.55
	Min Temperature	4.0 ± 3.6 (-3.2-11.3)	2.8 ± 3.5 (-1.6-12.3)	1.58	0.21
	Mean Temperature	10.2 ± 2.6 (6.2-16.1)	10.0 ± 4.1 (2.5-20.3)	0.06	0.81
	Total Precipitation	1.8 ± 3.0 (0-9.2)	2.9 ± 6.5 (0-30)	0.39	0.41
	Max Wind Speed	45.4 ± 14.6 (<31-95)	43.2 ± 9.4 (<31-69)	0.002	0.97
June	Max Temperature	21.6 ± 4.0 (14.8-30.5)	22.9 ± 3.5 (15.4-29.8)	2.09	0.15
	Min Temperature	8.4 ± 3.1 (2.1-16.1)	8.5 ± 2.8 (3.0-14.6)	0.01	0.94
	Mean Temperature	15.0 ± 3.2 (8.7-23.3)	15.7 ± 2.7 (10.1-21.2)	0.88	0.35
	Total Precipitation	0.8 ± 1.9 (0-8.4)	2.2 ± 4.5 (0-16.9)	2.09	0.15
	Max Wind Speed	44.3 ± 11.4 (<31-80)	47.2±14.7 (<31-93)	1.33	0.25
July	Max Temperature	27.2 ± 4.1 (18-35)	29.0 ± 4.1 (20.5-36.5)	3.14	0.08
	Min Temperature	11.0 ± 4.0 (5.3-21.2)	12.7 ± 3.4 (4.1-18.3)	3.63	0.06
	Mean Temperature	19.1 ± 3.4 (13.5-28.1)	20.9 ± 2.8 (15.5-26.3)	5.13	<u>0.03</u>
	Total Precipitation	2.5 ± 9.1 (0-49.5)	0.3 ± 0.9 (0-3.2)	1.71	0.20
	Max Wind Speed	48.3±10.3 (<31-69)	44.6 ± 10.8 (32-69)	3.11	0.08
August	Max Temperature	27.6 ± 4.2 (14.6-34.4)	28.8 ± 4.9 (17.5-36.2)	1.01	0.32
	Min Temperature	9.9 ± 2.7 (3.6-16.7)	9.8 ± 3.4 (3.2-15.3)	0.01	0.93
	Mean Temperature	18.8 ± 2.7 (11.9-25.6)	19.3 ± 3.5 (12.2-25.3)	0.47	0.49
	Total Precipitation	0.8 ± 3.8 (0-21.1)	0.5 ± 1.3 (0-5.3)	0.16	0.69
	Max Wind Speed	42.5 ± 7.2 (<31-57)	44.7 ± 10.6 (<31-70)	0.66	0.42

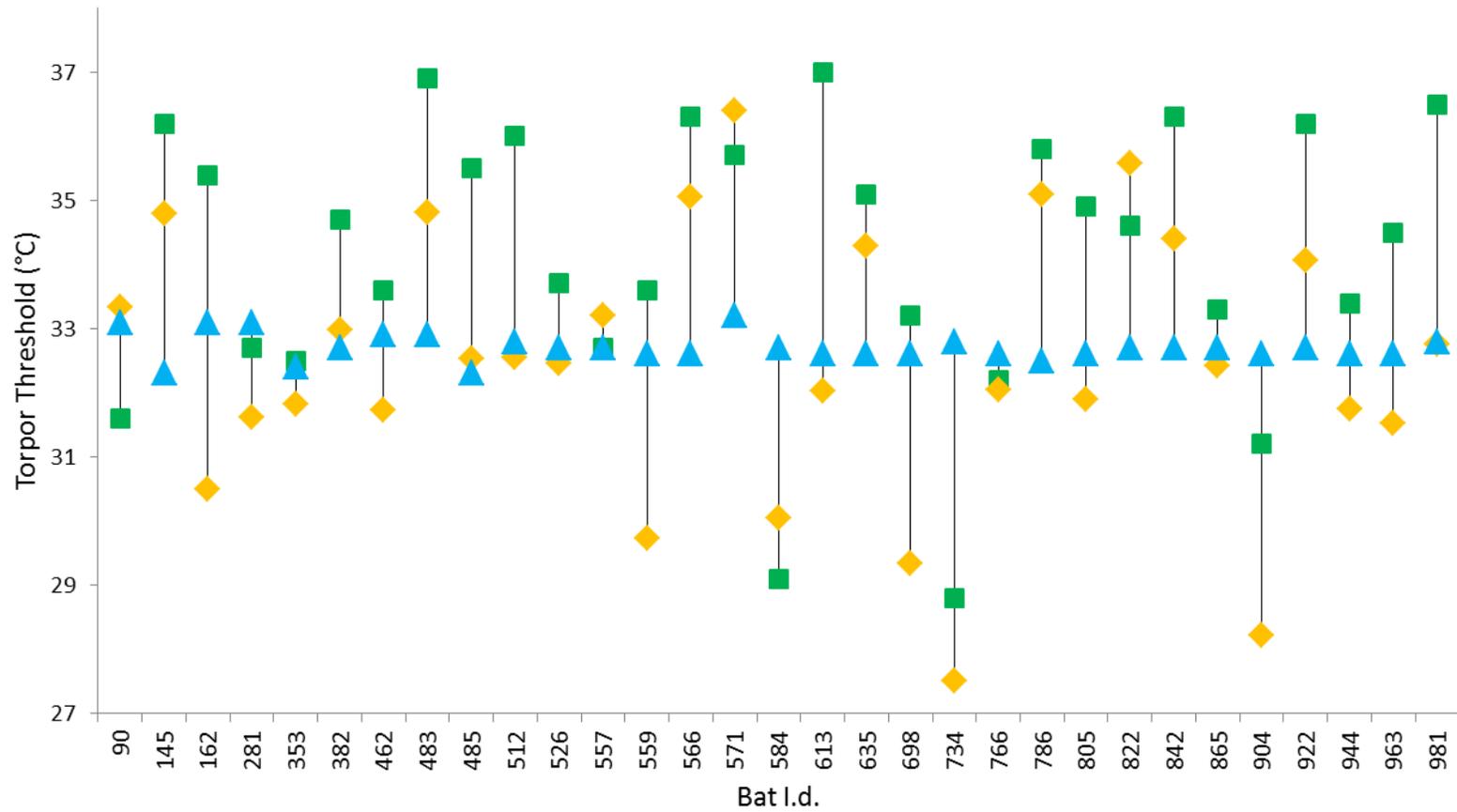


Figure 2. Torpor thresholds calculated for each individual *Eptesicus fuscus* using three definitions. Blue triangles represent T_{onset} (Willis 2007), orange diamonds represent T_{99ci} (McKechnie et al. 2007) and green squares represent T_{active} (Barclay et al. 2001). Vertical line connects each threshold value for an individual bat. [original in colour]

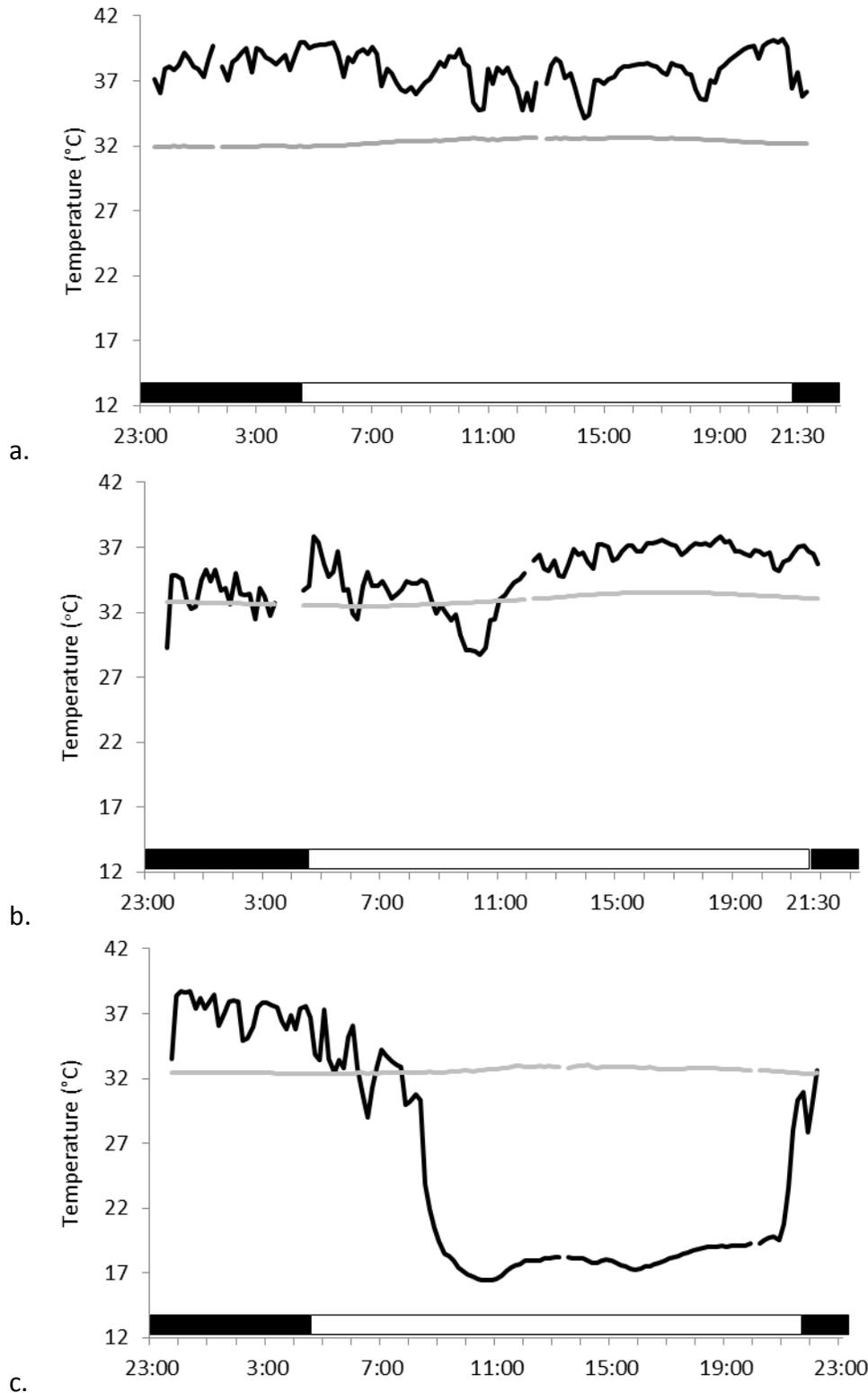


Figure 3. Examples of a) normothermy, b) “shallow” torpor, and c) “deep” torpor thermoregulatory patterns exhibited by pregnant and lactating *Eptesicus fuscus*. Grey lines represents torpor onset temperature (T_{onset}) calculated following Willis (2007) and black line represents skin temperature (T_{sk}). Black bars along the x-axis indicate night.

time spent in the roost (deep torpor; pregnant:4 bat days; lactating:5 bat days). These three patterns varied in frequency between roost types (Figure 4). During both pregnancy and lactation, there was a trend for longer torpor bout durations when torpor depth increased (Figure 5; parameter estimate $\pm SE$, pregnant: 47.3 ± 4.0 , $p < 0.001$; lactating 66.4 ± 6.2 , $p < 0.001$). For pregnant bats there was also a trend for deeper and longer torpor bouts to occur during the middle (Julian date = 155-160) range of tracking in comparison to the first and last (145-155 and 160-168) part of tracking. I could discern no pattern of torpor use during lactation. Individuals entered at least one torpor bout on 67% and 63% of bat days during pregnancy and lactation (respectively; 30/45 bat days and 33/52 bat days). During both reproductive periods, bats first entered torpor in the morning (0400 h – 1300 h) on the majority of torpor days (24/30 and 24/33 torpor days; Figure 6). There was a bimodal distribution of when lactating bats entered torpor, the majority of first torpor bouts began at sunrise and there was another small peak near sunset, whereas pregnant bats tended to enter torpor shortly after sunrise, but torpor episodes were employed throughout the day. Individuals of both reproductive conditions used an average of 2 torpor bouts per day, with the mode of each being one bout of torpor (Table 3). On average, pregnant bats spent more time in the roost per day than lactating bats (1211 ± 133 minutes and 1086 ± 88 minutes, respectively), but the proportion of time in roost that bats were torpid was higher in lactation as opposed to pregnancy ($32.1 \pm 31.8\%$ and $18.9 \pm 20.9\%$, respectively).

3.1 Roost Temperature

Overall, during the same time period (June and July) in both years the two building roosts had similar temperature conditions (parameter estimate $\pm SE$, -0.05 ± 1.0 ,

Table 3. Summary of thermoregulatory characteristics of pregnant and lactating *Eptesicus fuscus*. T_{onset} was calculated following Willis (2007).

Thermoregulatory characteristic	Pregnant		Lactating	
	$\bar{x} \pm SD$ (range)	n (bats) N (bat days)	$\bar{x} \pm SD$ (range)	n (bats) N (bat days)
Maximum Euthermic T_{sk} ($^{\circ}\text{C}$)	39 \pm 1.1 (36.9-41.5)	n = 13 N = 45	38.6 \pm 2 (32.7-42.2)	n = 18 N = 52
HI ($^{\circ}\text{C}$)	3.4 \pm 3.5 (0.7-17.0)	n = 13 N = 45	3.6 \pm 3.3 (0.8-14.3)	n = 18 N = 52
T_{onset} ($^{\circ}\text{C}$)	32.6 \pm 0.2 (32.3-32.9)	n = 13 N = 45	32.8 \pm 0.2 (32.6-33.3)	n = 18 N = 52
Time after return to first torpor bout (min)	427 \pm 306 (10-1256)	n = 11 N = 34	248 \pm 334 (0-1023)	n = 16 N = 36
First torpor bout duration (min)	96 \pm 177 (20-890)	n = 11 N = 34	221 \pm 336 (20-1160)	n = 16 N = 36
Total duration of torpor (min)	234 \pm 267 (20-890)	n = 11 N = 34	386 \pm 392 (20-1160)	n = 16 N = 36
Depth of torpor ($T_{\text{onset}} - T_{\text{sk}}$) ($^{\circ}\text{C}$)	4.2 \pm 5 (0.4-18)	n = 11 N = 34	5.5 \pm 4.9 (0.2-20.7)	n = 16 N = 36
Minimum torpid T_{sk} ($^{\circ}\text{C}$)	28.1 \pm 5.3 (14.5-32.4)	n = 11 N = 34	27.1 \pm 4.9 (12-32.2)	n = 16 N = 36
T_{a} at minimum torpid T_{sk} ($^{\circ}\text{C}$)	15.3 \pm 5.4 (2.6-24.1)	n = 11 N = 34	19 \pm 4.2 (11.3-28.1)	n = 16 N = 36
Torpor degree-minutes ($^{\circ}\text{C} \cdot \text{min}$)	1128.7 \pm 2789.7 (4.6-11103.8)	n = 11 N = 34	1742 \pm 3268.3 (11.6-13319.6)	n = 16 N = 36
Number of torpor bouts	2.4 \pm 1.5 (1.0-7.0)	n = 11 N = 34	2.3 \pm 1.5 (1.0-6.0)	n = 16 N = 36
Time spent in day roost (min)	1211 \pm 133 (934-1398)	n = 13 N = 45	1086 \pm 88 (777-1328)	n = 16 N = 36
Proportion of roosting time in torpor (%)	18.9 \pm 20.9 (1.5-65.5)	n = 11 N = 34	32.1 \pm 31.8 (1.8-98.9)	n = 18 N = 52

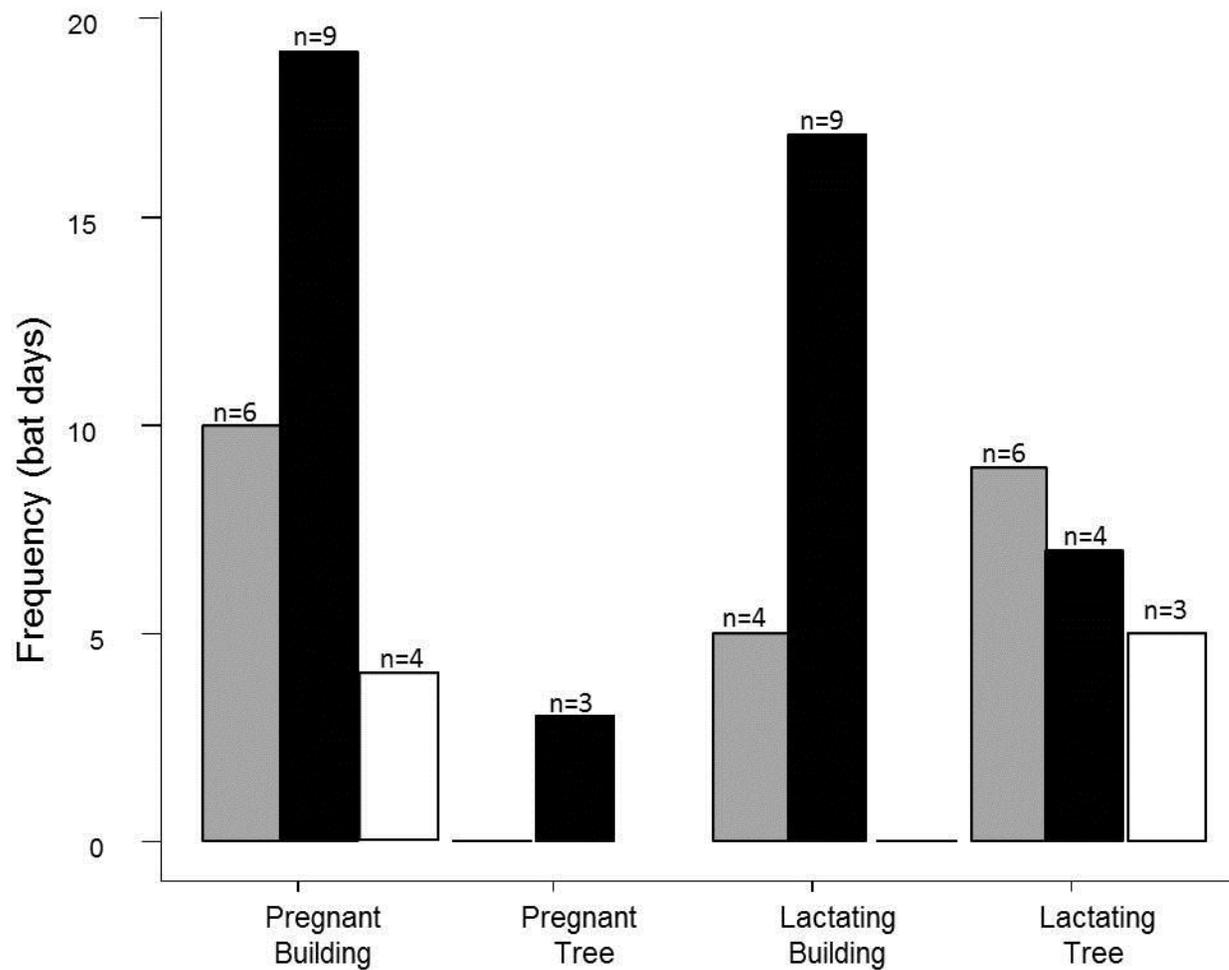


Figure 4. Frequency of each thermoregulatory pattern used by *Eptesicus fuscus* as a function of reproductive condition and roost type. Grey bars indicate normothermy, black bars indicate “shallow” torpor, and white bars indicate “deep” torpor. n = individual bats displaying the pattern in each category.

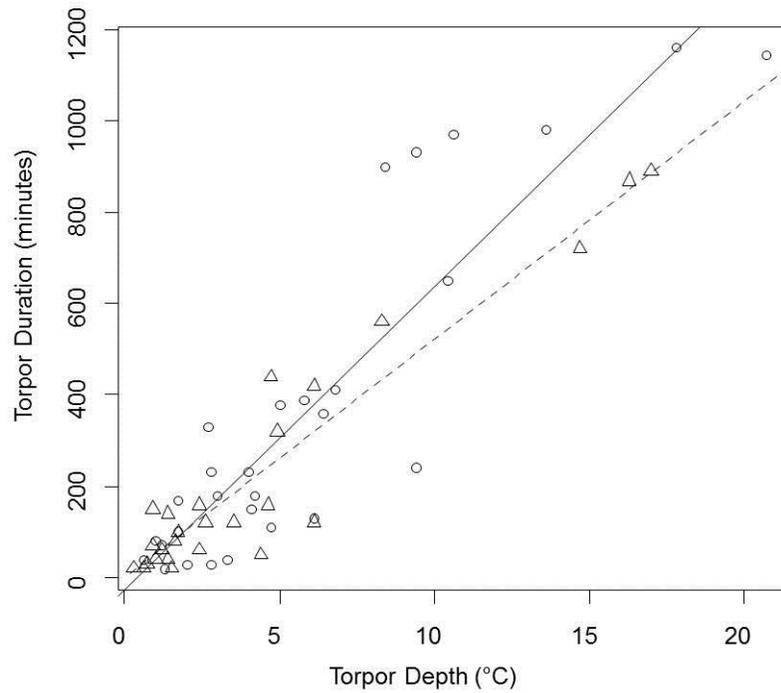


Figure 5. Relationship between torpor bout duration and torpor depth in pregnant (triangles, dotted line) and lactating (circles and solid line) *Eptesicus fuscus*. Both relationships are significant (parameter estimate \pm SE, pregnant: 47.3 ± 4.0 , $p < 0.001$; lactating 66.4 ± 6.2 , $p < 0.001$).

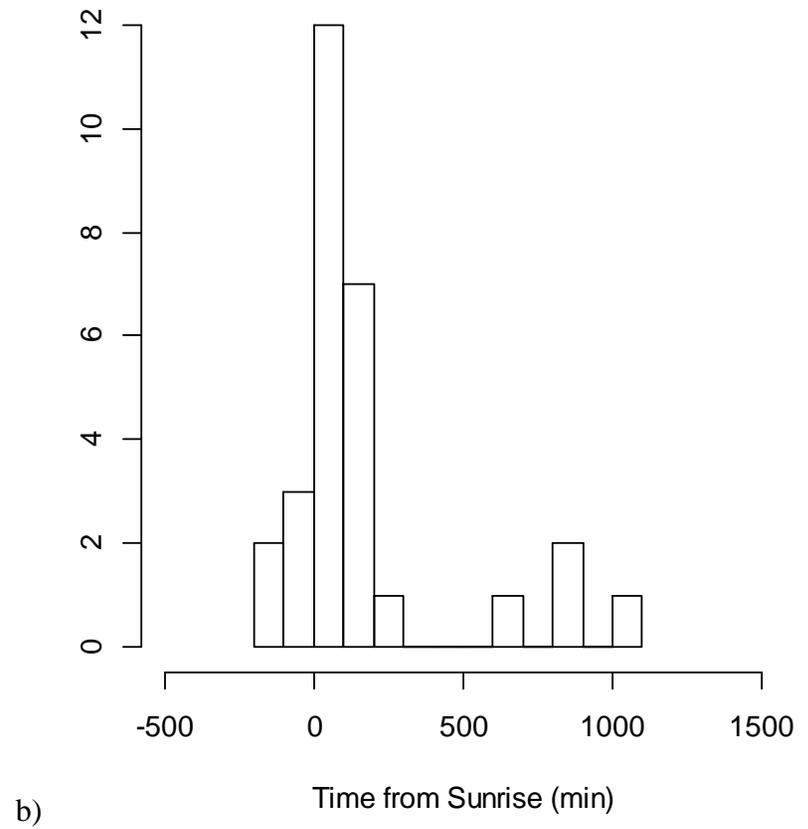
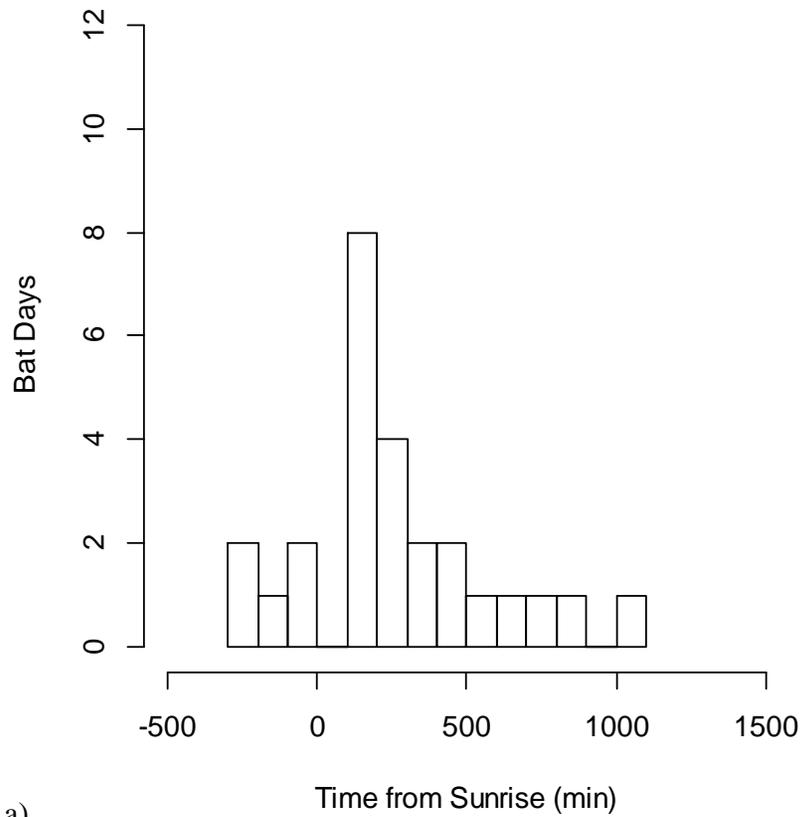


Figure 6. Time of first torpor bout entry in relation to sunrise for a) pregnant and b) lactating *Eptesicus fuscus*. Sunrise is at time 0, with values <0 being before and >0 being after sunrise.

$p = 0.96$), but in 2011 the building had less stable temperatures than 2012 and also reached temperatures $>40^{\circ}\text{C}$ more often (Table 4). During the pregnancy period (June) in 2012, the temperature of tree roosts fluctuated more than the building, but trees were more stable than the building during lactation (July; Figure 7; -2.1 ± 1.0 , $p = 0.01$). In 2012, the nightly minimum temperature was higher in the building roost than trees during the pregnancy period but similar during the lactation period (Figure 8a; -4.1 ± 0.9 , $p < 0.001$). The tree roosts also had a lower daytime maximum temperature overall than the building roost (Figure 8b; -7.2 ± 1.3 , $p < 0.001$). In all cases, the internal roost temperature was directly related to the external temperature (Figure 9; 0.4 ± 0.01 , $p < 0.001$), depended on roost structure (-5.5 ± 0.07 , $p < 0.01$) and followed similar patterns of warming throughout the day (Figure 10).

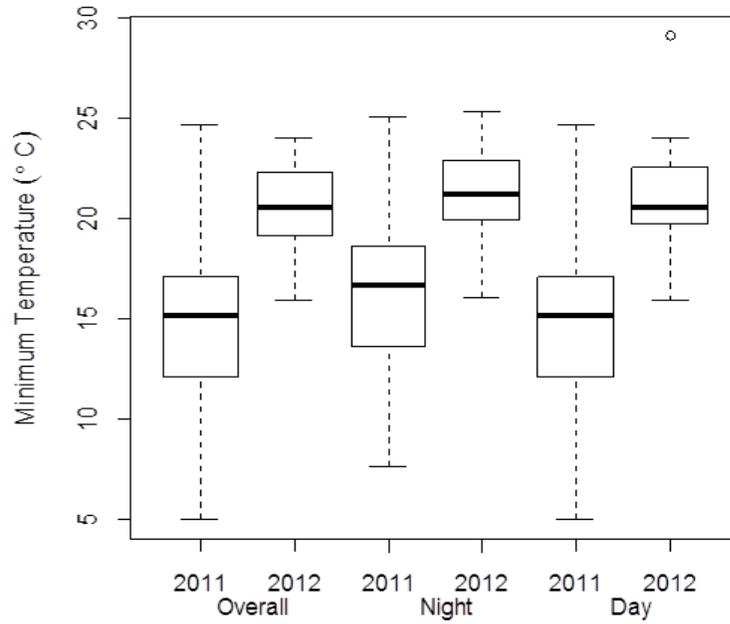
On nights that bats moved from building to tree structure, maximum daytime T_a ranged from 20.4 - 27.8°C during pregnancy and 26.3 - 35.8°C during lactation and minimum daytime T_a ranged from 2.5 - 11.1°C and 11 - 12.9°C respectively. Of the 11 confirmed roost structure switches, 10 were from the building to a tree. I did not include the switches between tree roosts because this was difficult to distinguish with certainty within an area.

3.2 Thermoregulatory models

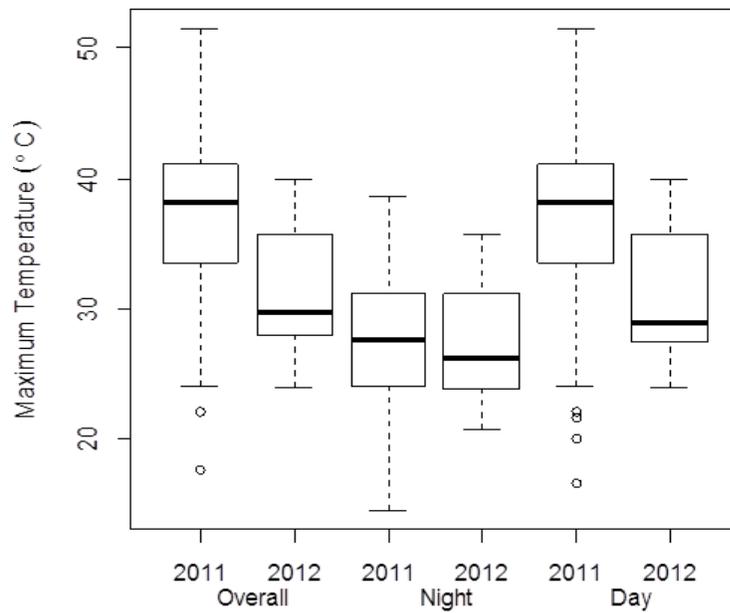
All thermoregulatory candidate model sets included the same parameters in various combinations for a total of 10 models: previous night foraging duration, roost type, minimum daily temperature, and reproductive condition as fixed effects. In all models, date of data collection and individual bat were included as random effects. Date accounted for more of the residual variance than individual bat in all models (47-66%

Table 4. Day (0500-2100) and night (2100-0500) temperature characteristics of roost structures occupied by *Eptesicus fuscus* during the pregnancy and lactation periods. In 2011, bats used a building, whereas in 2012 a building and several balsam poplar trees were used. Temperature was measured by transmitters which had been dropped by bats in the roost structure. Amplitude refers to the difference between maximum and minimum temperatures for each day and night period.

Weather parameter		Pregnant		Lactating	
		$\bar{x} \pm SD$ (range)	N (days)	$\bar{x} \pm SD$ (range)	N (days)
2011	Day Minimum (°C)	12.6 ± 3.2 (8.1-20.6)	22	16.5 ± 3.2 (12.1-24.6)	29
	Day maximum (°C)	32.1 ± 6.8 (16.6->40)		40.3 ± 4.5 (31.6->40)	
	Day amplitude (°C)	19.5 ± 6.0 (4.5-30.5)		23.9 ± 4.2 (13.5-31.0)	
	Night Minimum (°C)	13.5 ± 3.0 (9.1-20.6)	22	17.8 ± 3.3 (13.1-25.1)	
	Night maximum (°C)	23.1 ± 4.4 (14.6-32.6)		29.5 ± 3.5 (22.6-38.6)	
	Night amplitude (°C)	9.7 ± 2.6 (2.5-13.0)		11.8 ± 2.1 (8.5-16.0)	
2012 Building	Day Minimum (°C)	20.3 ± 1.8 (15.9-23.0)	15	21.8 ± 3.0 (16.9-29.1)	14
	Day maximum (°C)	27.6 ± 2.0 (24.0-31.7)		35.1 ± 4.4 (26.5-40)	
	Day amplitude (°C)	7.3 ± 2.6 (3.9-14.1)		13.3 ± 4.5 (2.8-18.8)	
	Night Minimum (°C)	20.2 ± 1.9 (16.0-23.0)	15	22.1 ± 2.4 (16.9-25.3)	
	Night maximum (°C)	24.1 ± 2.4 (20.7-28.2)		30.4 ± 3.6 (23.4-35.7)	
	Night amplitude (°C)	3.9 ± 1.3 (1.0-6.2)		8.2 ± 4.0 (2.7-18.8)	
2012 Tree	Day Minimum (°C)	13.7 ± 1.6 (10.9-16.1)	15	19.5 ± 2.0 (15.1-22.6)	14
	Day maximum (°C)	19.9 ± 2.4 (15.6-25.3)		28.4 ± 3.0 (23.1-31.3)	
	Day amplitude (°C)	6.2 ± 2.8 (2.3-12.1)		8.9 ± 2.8 (2.6-13.8)	
	Night Minimum (°C)	14.4 ± 2.2 (10.9-18.3)	15	19.9 ± 1.7 (17.4-22.4)	
	Night maximum (°C)	17.9 ± 3.0 (13.8-23.7)		24.7 ± 1.7 (20.5-26.9)	
	Night amplitude (°C)	3.4 ± 2.1 (0.9-9.0)		4.7 ± 1.4 (3.0-7.5)	

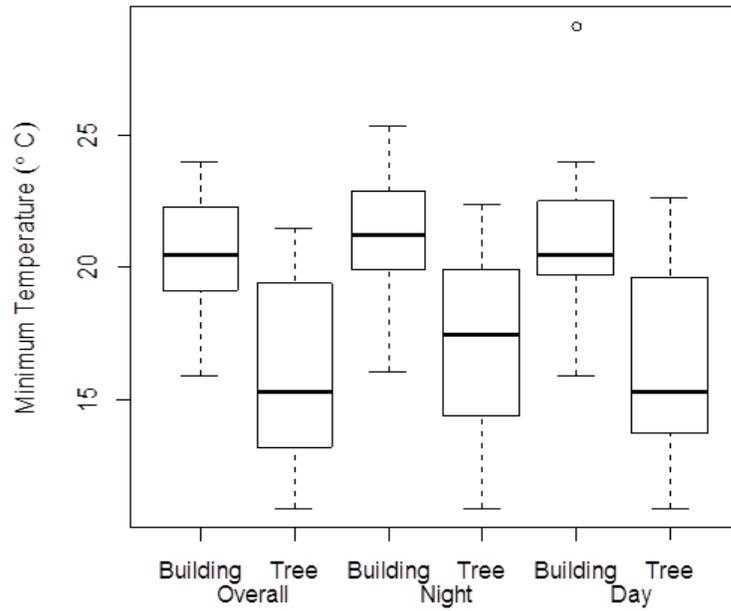


a.

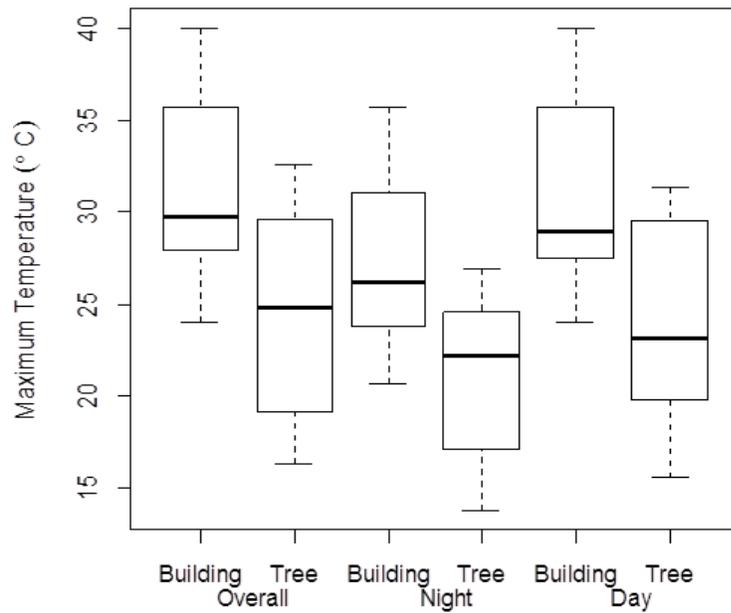


b.

Figure 7. Range of a) minimum and b) maximum temperatures in building roost structures used by *Eptesicus fuscus* in 2011 and 2012. Overall temperatures are over a 24 h period, night represents 2100-0500 h, and day from 0500-2100 h. Temperatures were recorded from transmitters dropped by bats within roost structures. Boxplots have 5 sections: thick lines indicate the median value, the upper and lower bound of the box are the 25th and 75th quartiles (the height of box is the interquartile range), the upper and lower whiskers are the minimum and maximum values or 95% confidence intervals and circles indicate outliers (1.5*IQR).



a.



b.

Figure 8. Range of a) minimum and b) maximum temperatures in tree and building roost structures used by *Eptesicus fuscus* in 2012. Overall temperatures are for a 24 h period, night was from 2100-0500 h, and day from 0500-2100 h. Temperatures were recorded over 29 days from transmitters shed by bats within roost structures. For explanation of boxplot, refer to Figure 7.

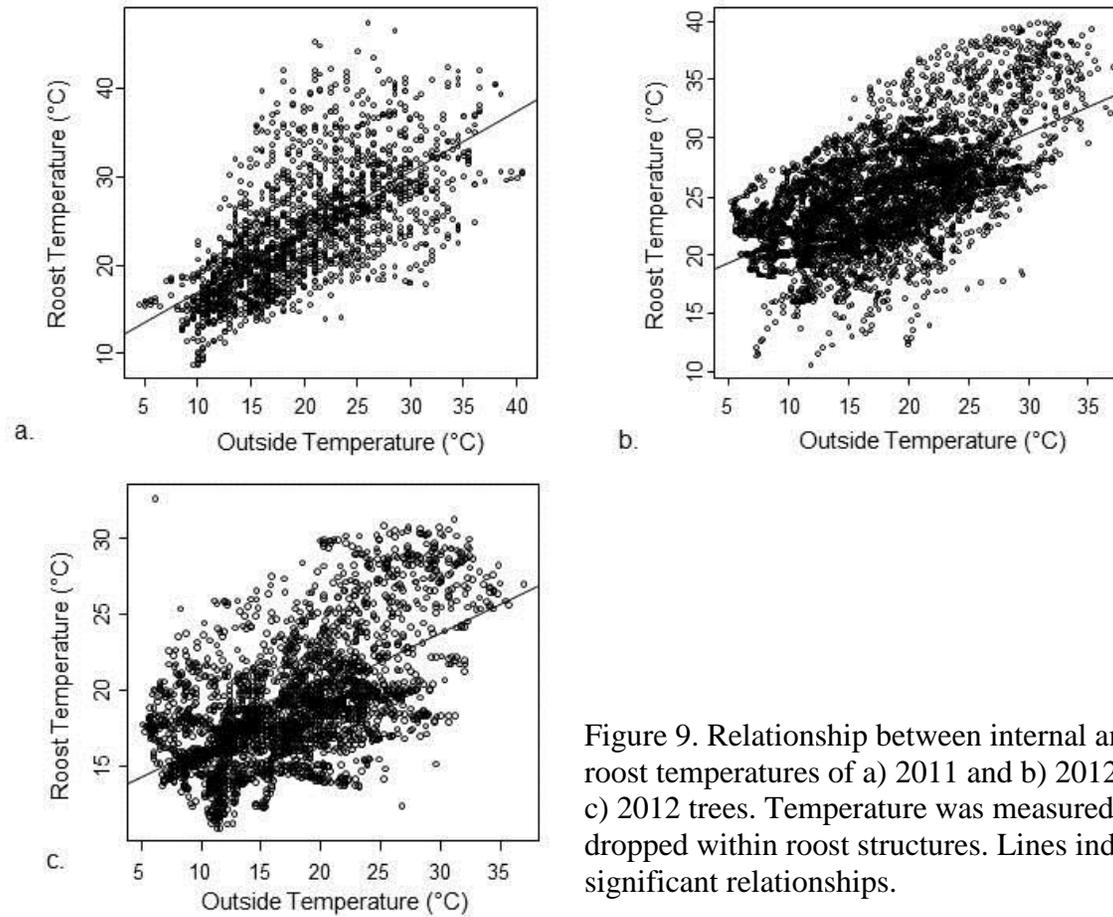


Figure 9. Relationship between internal and external roost temperatures of a) 2011 and b) 2012 buildings, and c) 2012 trees. Temperature was measured by transmitters dropped within roost structures. Lines indicate significant relationships.

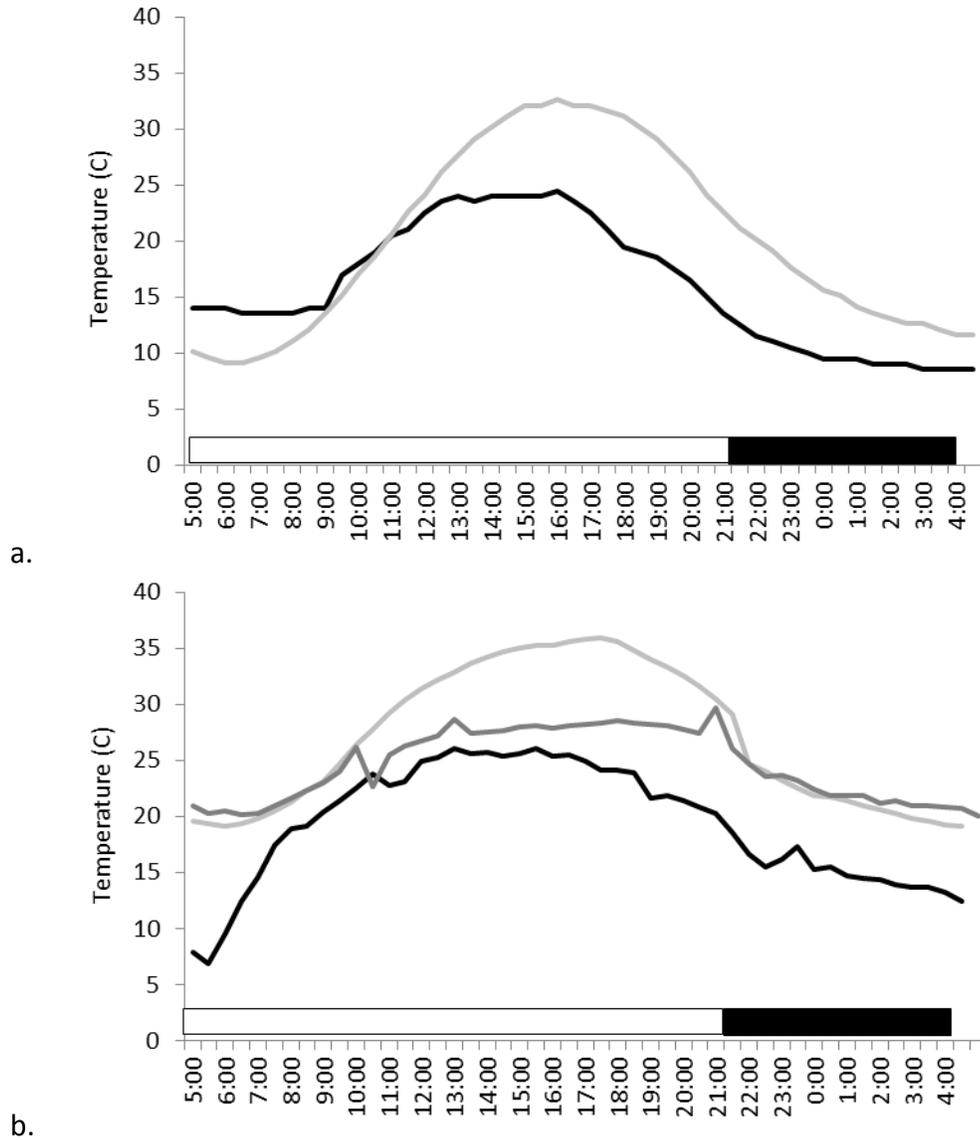


Figure 10. Temperature profile of roost structures used in a) 2011 and b) 2012 by *Eptesicus fuscus* on similarly warm days (same day in 2012). Light grey lines represent temperature in building structure, dark grey represents tree structure and black line represents external roost temperature. Black bars indicate night. Temperatures within roost structures were measured by transmitters shed by bats.

and 0-16%, respectively). Refer to Table 1 for candidate model structure and Appendix B for AIC_c results.

3.2.1 Torpor or no torpor

Regardless of either reproductive condition or roost type, the number of days females used torpor was similar to that with no torpor when the minimum daily temperature was either high (>20°C), or low (<5°C) but torpor was used more often than not when T_a was intermediate (Figure 11). This is especially true for temperatures between 10°C and 17°C.

I modeled variables that potentially contributed to whether or not torpor was employed using data for 79 bat days from 30 bats on 42 different days. Of the 79 bat days, torpor was used on 55 bat days, 26 by pregnant and 29 by lactating. The top model in the candidate set was the intercept model (Model ID =T2) with an Akaike weight (w_i) of 0.27. There were an additional 4 models $\Delta AIC_c \leq 2$ of the top model, indicating large model uncertainty. I used parameters in the confidence set of models (8 models) to compile the composite model which included previous night foraging (parameter estimate (β) = -0.008, unconditional standard error (\widehat{se}) = 0.009), roost type (β = -0.565, \widehat{se} = 0.635), minimum daily temperature (β = -0.031, \widehat{se} = 0.064) and reproductive condition (β = -0.182, \widehat{se} = 0.635). The confidence intervals were wide in all cases except in the intercept (β = 1.221, \widehat{se} = 0.578). Even though the four parameters were included, none of them had a high relative importance (<0.3).

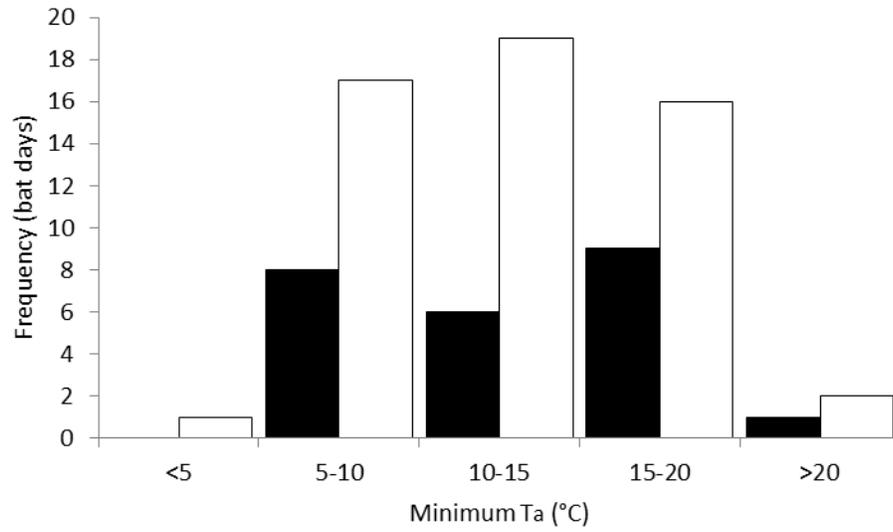


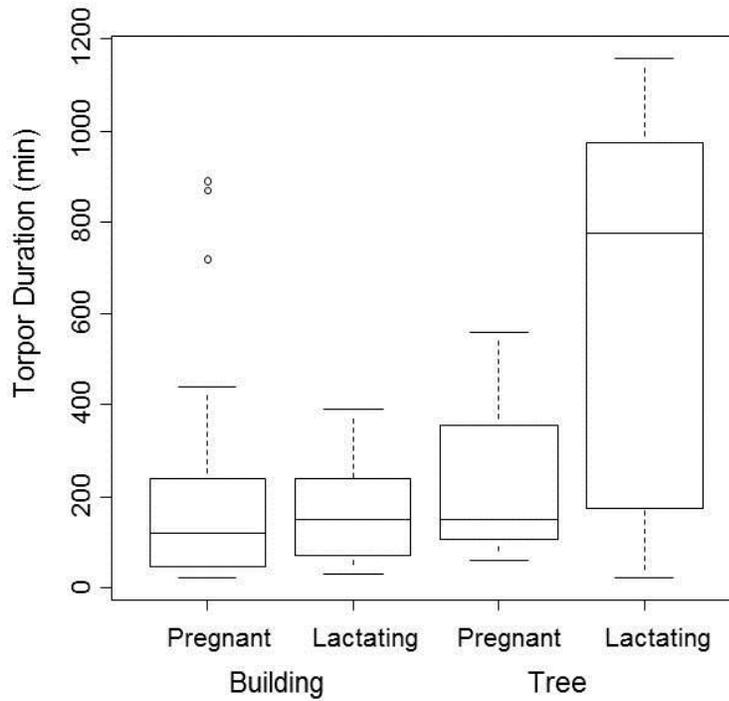
Figure 11. Frequency of bat days when torpor was (white bars) or was not (black bars) employed by female *Eptesicus fuscus* over a range of minimum daily temperatures.

3.2.2 Total Torpor Duration

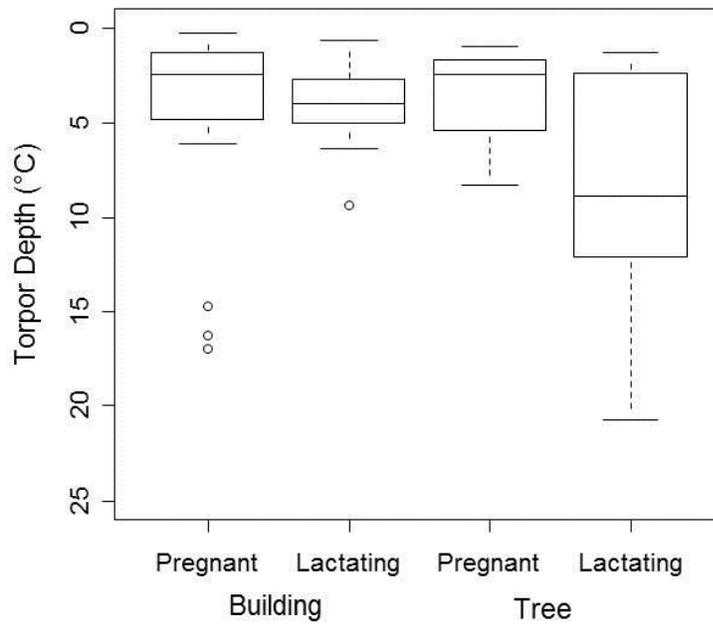
Pregnant and lactating bats had a large overlap in total minutes of torpor used per day in the inactive period (Figure 12a). Pregnant bats used slightly less torpor per day than lactating bats (234 ± 267 minutes and 386 ± 392 minutes, respectively). The first torpor bout, which occurred closer to sunrise during lactation than pregnancy (248 ± 334 minutes and 427 ± 306 minutes, respectively), was longer for lactating bats than pregnant bats (221 ± 336 minutes and 96 ± 117 minutes, respectively).

Total torpor duration was modeled using data from 55 bat days (25 individuals on 35 days) when at least one bout of torpor was used. The top model in the candidate set was roost type (T4) with $w_i = 0.55$. The second model, with $\Delta AIC_c = 1.83$ included reproductive condition and roost type (T3). Roost type was of greatest importance in explaining torpor duration with a parameter weight of 0.8 while reproductive condition was less important at 0.31.

The confidence set included 4 models, and when averaged, yielded only the inclusion of roost type and reproductive condition. Both parameters had a positive relationship (roost type $\beta = 0.923$, $\widehat{se} = 0.339$; reproductive condition $\beta = 0.397$, $\widehat{se} = 0.406$, intercept $\beta = 4.781$, $\widehat{se} = 0.242$) with the amount of torpor used. Confidence intervals for reproductive condition overlapped 0, roost type and intercept confidence intervals did not.



a.



b.

Figure 12. Parameters of torpor in pregnant and *lactating Eptesicus fuscus* during the inactive period (from return to roost until emergence). a) Torpor duration is the sum of time spent in torpor per day and b) torpor depth ($T_{\text{onset}} - \text{minimum } T_{\text{sk}}$), 0 on y- axis represents the torpor threshold. Circles represent outliers. Refer to Figure 7 for explanation of boxplot.

3.2.3 Torpor Depth

Minimum torpid T_{sk} was similar between reproductive conditions but with a large amount of variation. Lactating bats had a larger range of minimum T_{sk} than did pregnant (12-32.2°C and 14.5-32.4°C, respectively). The depth of torpor (minimum T_{sk} - T_{onset}) was greater in lactating ($5.5 \pm 4.9^\circ\text{C}$) than pregnant bats ($4.6 \pm 5.0^\circ\text{C}$) (Figure 12b). The ambient temperature at minimum T_{sk} was lower in pregnant than lactating bats but did not have an overall relationship for either condition (Figure 13).

Torpor depth was modeled using data from 55 bat days (25 bats on 35 days). The top model with $w_i = 0.27$ included reproductive condition and roost type (T3). Two other models, previous night foraging with roost type (T9), and roost type alone (T4), were $\Delta\text{AIC}_c \leq 1$ and thus close competitors. Roost type had the highest importance at 0.77 but reproductive condition was also high at 0.70. Previous night foraging was less important for explaining torpor depth with a relative importance of 0.36 and minimum ambient temperature had little influence at 0.09. Three outlying values were removed from the initial analysis, which resulted in the second and third models reversed ranking order, but the general patterns were the same albeit with more uncertainty.

The confidence set of models included 7 models, and when averaged, included the intercept ($\beta = 4.309$, $\widehat{se} = 1.109$), reproductive condition ($\beta = 1.312$, $\widehat{se} = 1.792$), roost type ($\beta = 2.716$, $\widehat{se} = 1.465$), previous night foraging ($\beta = -0.836$, $\widehat{se} = 0.632$), and minimum daily temperature ($\beta = 0.015$, $\widehat{se} = 0.221$). Except for the intercept, all the parameters had confidence intervals that encompassed 0.

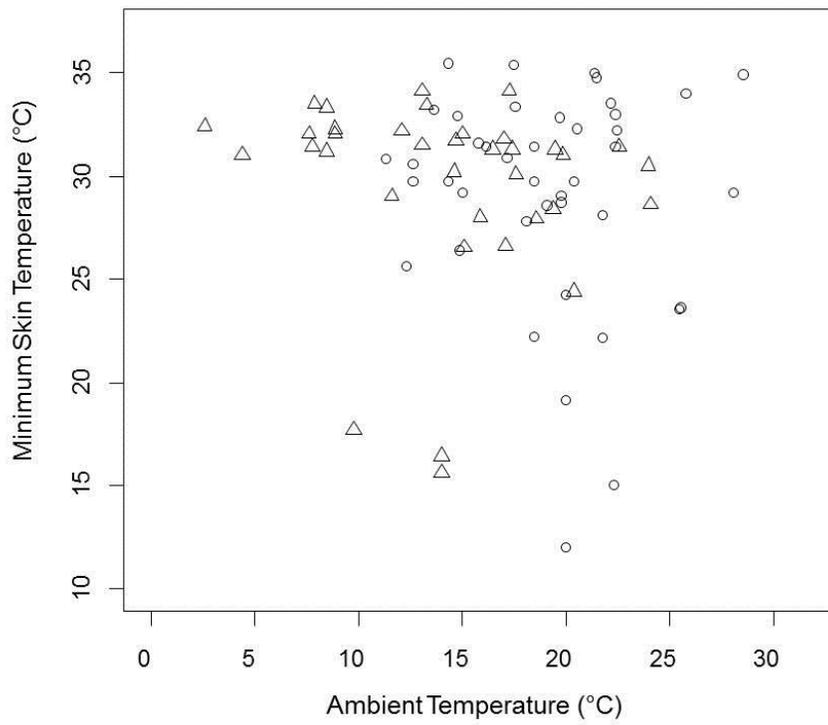


Figure 13. Lack of a relationship between ambient temperature at time of minimum T_{sk} of pregnant (triangles) and lactating (circles) *Eptesicus fuscus*.

3.2.4 Degree Minutes

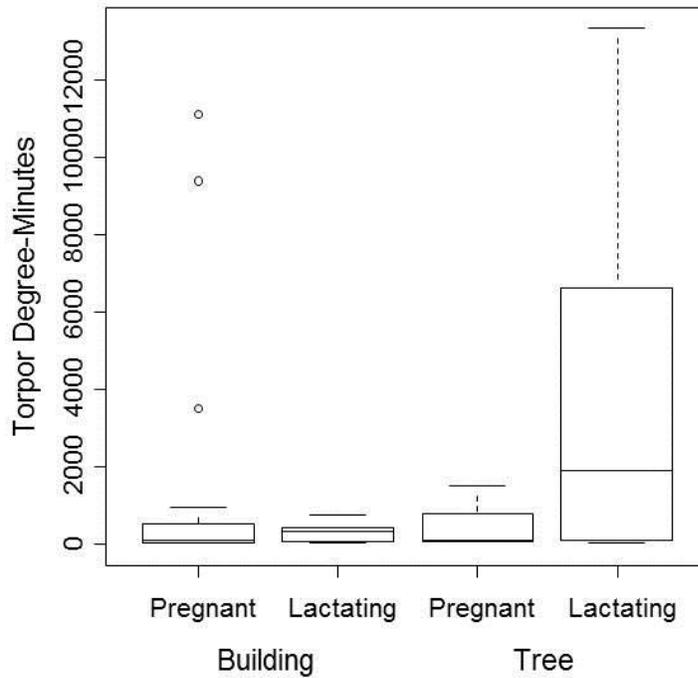
The integrative torpor variable, torpor degree-minutes, was higher in lactating than pregnant bats, especially in lactating bats roosting in trees. There was a larger range of values for degree-minutes for lactating bats over pregnant bats ($1742 \pm 3268.3^\circ\text{C}\cdot\text{min}$ and $1128.7 \pm 2789.7^\circ\text{C}\cdot\text{min}$, respectively; Figure 14a).

Torpor degree-minutes was modeled using data from 55 bat days for 25 bats on 35 different days. The top model with $w_i = 0.69$ was the null (intercept only) model (T2). The second top model with $\Delta\text{AIC}_c = 2.32$ was reproductive condition (T1). Reproductive condition had the highest importance at 0.23 and roost type at 0.20.

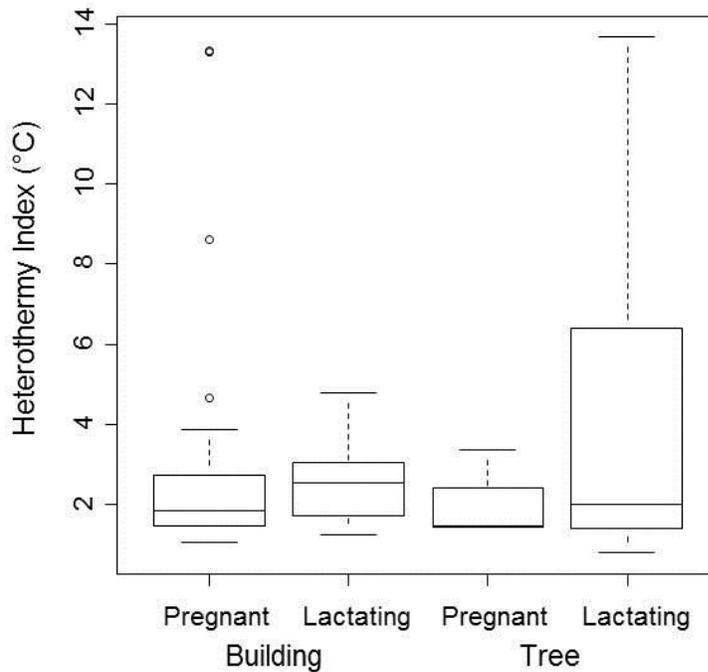
Four models were included in the confidence set, and when averaged, included the intercept ($\beta = -0.088$, $\widehat{\text{se}} = 0.178$), reproductive condition ($\beta = 0.231$, $\widehat{\text{se}} = 0.331$), and roost type ($\beta = 0.297$, $\widehat{\text{se}} = 0.228$). All parameters had confidence intervals that encompassed 0.

3.2.5 Heterothermy Index

The degree of heterothermy, heterothermy index (HI), did not differ between reproductive conditions ($3.4 \pm 3.5^\circ\text{C}$ and $3.6^\circ\text{C} \pm 3.3^\circ\text{C}$, respectively), although lactating bats were slightly more heterothermic (Figure 14b). Both pregnant and lactating bats expressed only a few instances of higher temperature fluctuations with an HI in the 10-14°C range ($n = 2$ and 4, respectively).



a.



b.

Figure 14. Measures of thermoregulation that incorporate torpor depth and duration in pregnant and lactating *Eptesicus fuscus* as a function of roost structures. a) The comprehensive torpor measure, torpor degree-minutes (to make patterns clear, outliers for lactating bats in trees were removed (3 points)). b) Heterothermy Index (HI; Boyles et al. 2011), an HI of approximately 0 indicates a normothermic individual. Refer to Figure 7 for explanation of boxplot.

Ten models were generated with data including 79 bat days from 30 bats on 42 days. Of the candidate models, reproductive condition (T1) was the top model, with $w_i = 0.40$. There were two additional models with $\Delta AIC_c \leq 2$, the intercept model (T2) and the reproductive condition plus roost type (T3). Reproductive condition and roost type were important for predicting HI, with parameter weights of 0.60 and 0.34 respectively.

The confidence set of models was made up of 4 models, including the intercept ($\beta = 2.807$, $\widehat{se} = 0.576$), reproductive condition ($\beta = 1.15$, $\widehat{se} = 0.865$) and roost type ($\beta = 0.277$, $\widehat{se} = 0.613$). Reproductive condition was more influential than roost type in explaining HI. Both roost type and reproductive condition had confidence intervals which encompassed 0.

3.3 Foraging

3.3.1 Insect abundance

Relative insect abundance was modeled using data from 180 samples collected over 20 nights. Most samples were taken at one location ($n = 170$) with the rest within 500 m in a similar habitat. The main location was chosen because bats were observed foraging there on the majority of tracking nights. Wind, temperature, time of sample, days to full moon and precipitation over the day were used as explanatory variables. I included night as a random effect because samples were taken every 30 minutes throughout the night. The top model with $w_i = 0.64$ included an interaction between temperature and wind, days from full moon, sample time and precipitation (I1). The second model, with $\Delta AIC_c = 2.4$, included a temperature by wind interaction (I2), with $w_i = 0.19$. Wind and temperature were the two most important parameters in determining insect density with relative importance measures of 1, followed by their interaction at

0.83, and in all cases, the confidence intervals did not include 0, therefore are equally as strong.

The top model had $w_i < 0.90$, so a composite model using the candidate set of the top 3 models was generated. This included the intercept ($\beta = 0.80$, $\widehat{se} = 0.72$), temperature-wind interaction ($\beta = 0.005$, $\widehat{se} = 0.002$), temperature ($\beta = 0.046$, $\widehat{se} = 0.039$), wind ($\beta = -0.103$, $\widehat{se} = 0.037$), moon ($\beta = -0.018$, $\widehat{se} = 0.016$), time ($\beta = 0.014$, $\widehat{se} = 0.005$), and precipitation ($\beta = -0.196$, $\widehat{se} = 0.144$). The temperature-wind interaction, wind and time had confidence intervals that did not encompass 0, but all other parameter confidence intervals did.

3.3.2 Foraging Duration

On average, lactating bats foraged for 100 minutes longer per night than pregnant bats (Table 5), although the range was similar between conditions (Figure 15). The mean number of foraging trips was 1.6 and 2.4 for pregnant and lactating bats, respectively. Pregnant and lactating bats emerged at similar times in relation to sunset; however, timing of emergence was more concentrated in lactating than pregnant bats (Figure 16). Final return to the roost was similar in both reproductive condition, but lactating bats returned just before or after sunrise more frequently than pregnant bats (Figure 17). Pregnant bats tended to exhibit a major peak of foraging activity around emergence, and then another minor peak before sunrise, whereas lactating bats were active throughout the night.

Data collected over 83 bat days from 29 bats on 42 days were used to model foraging duration. Variables included in the candidate set were number of foraging bouts, reproductive condition, HI during the day prior to emergence, minimum night

Table 5. Summary of foraging data for pregnant (n =12 bats, N = 36 bat days) and lactating (n = 18, N = 47) *Eptesicus fuscus*. Total foraging time refers to the amount of time each individual was moving (determined through telemetry) outside of the roost. A complete foraging trip occurred when a bat emerged from the roost, flew and returned to the same roost after >20 minutes.

Foraging Characteristic	Pregnant $\bar{x} \pm SD$ (range)	Lactating $\bar{x} \pm SD$ (range)
Total foraging time (minutes)	142.5 \pm 78.4 (40-310)	236.7 \pm 71.5 (75-350)
Number of foraging trips	1.6 \pm 0.8 (1-4)	2.4 \pm 0.9 (1-4)
Duration of first foraging trip (minutes)	108.8 \pm 59.8 (40-270)	115.4 \pm 58.7 (30-330)
Emergence (minutes past sunset)	109.6 \pm 20.1 (72-190)	113.6 \pm 34.7 (90-245)
Final return to roost (minutes past sunrise)	-155.3 \pm 125.4 (-301-57)	-32.2 \pm 81.1 (-300-37)
T_a at emergence (°C)	12 \pm 2.6 (8.3-17.2)	17.5 \pm 2.4 (9.8-22.9)
Minimum night T_a (°C)	8.6 \pm 2.7 (3-14.6)	13.9 \pm 3.0 (6.1-19.1)

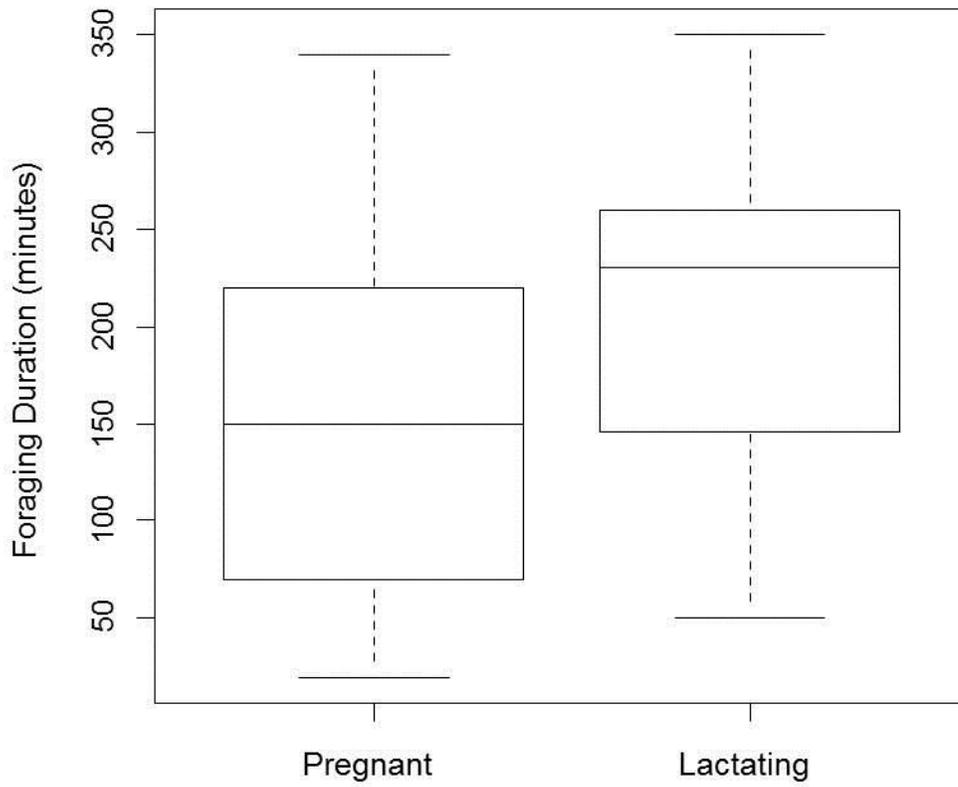


Figure 15. Total amount of time spent foraging per night by pregnant and lactating *Eptesicus fuscus*. For explanation of boxplot, refer to Figure 7.

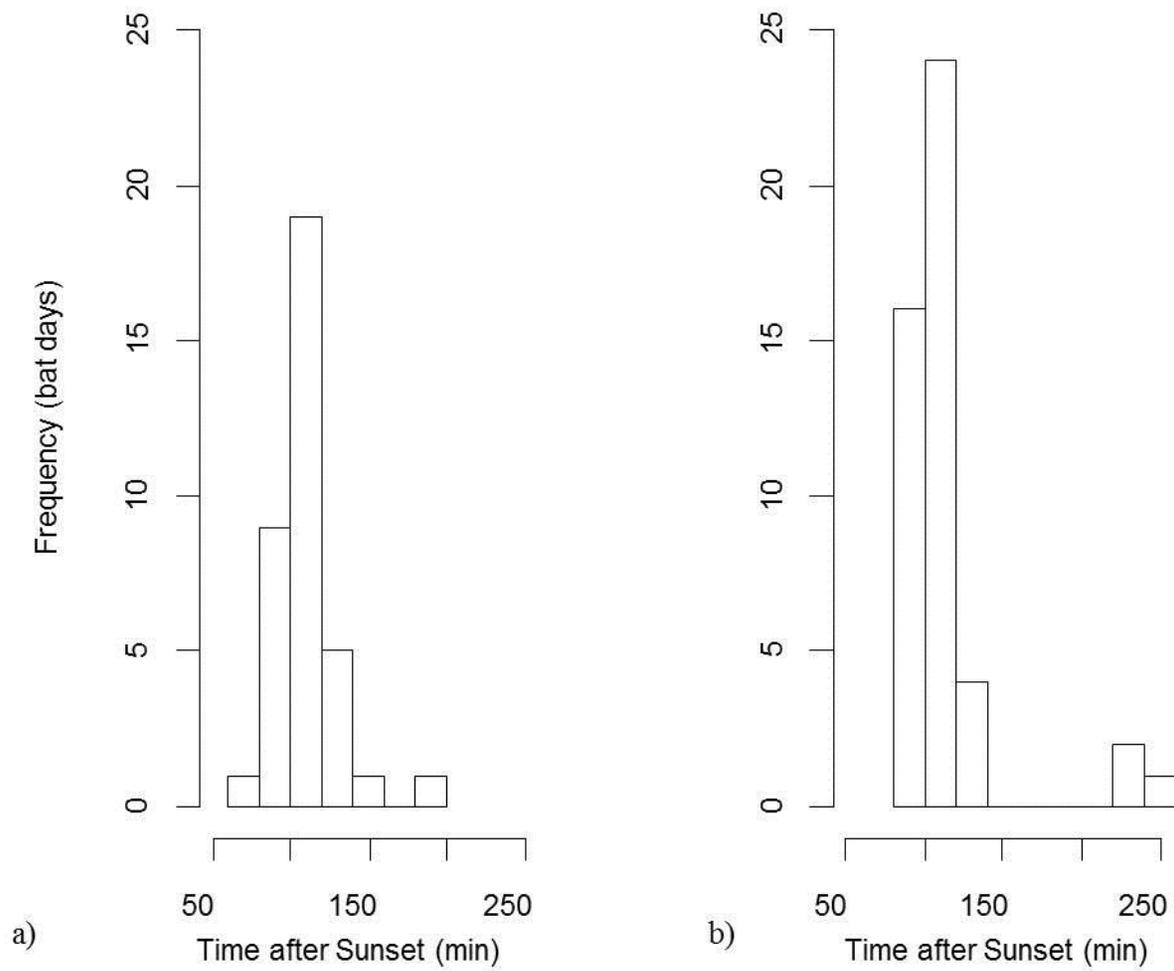


Figure 16. Frequency of evening emergence time in relation to sunset for a) pregnant and b) lactating *Eptesicus fuscus*.

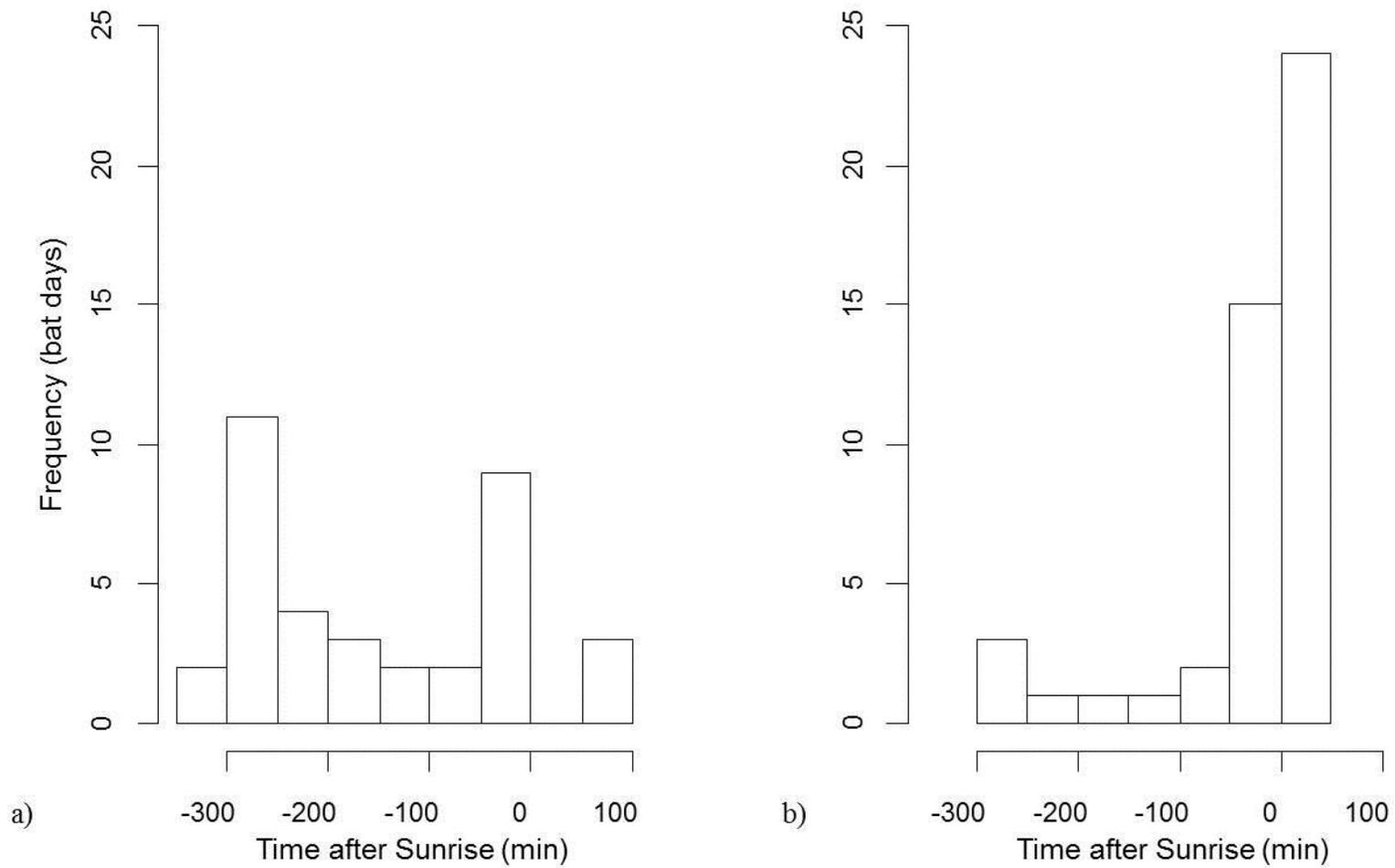


Figure 17. Frequency of final return time to roost in relation to sunrise, for a) pregnant and b) lactating *Eptesicus fuscus*.

temperature and average nightly wind speed in multiple combinations. Wind and temperature were used because they were the most influential parameters in explaining insect abundance. Individual bat and day were included as random effects and accounted for 4-15% and 48-70% of the residual variance, respectively. The top model with $w_i = 0.54$ was number of bouts and reproductive condition (F1). Second and third were reproductive condition ($\Delta AIC_c = 1.77$; F2) and number of bouts ($\Delta AIC_c = 2.27$; F3), respectively. Reproductive condition was the most important variable in predicting foraging duration with a relative parameter weight of 0.78 and number of bouts was second best with 0.73. The confidence intervals for both variables did not encompass 0.

Number of foraging bouts and reproductive condition were included in the composite model generated from model averaging the confidence set (4 models). Both parameters had a positive relationship with foraging duration ($\beta = 0.288$, $\widehat{se} = 0.102$ and $\beta = 0.661$, $\widehat{se} = 0.239$, respectively). Confidence intervals for intercept ($\beta = -0.699$, $\widehat{se} = 0.340$), bouts and reproductive condition did not encompass 0.

3.4 Foraging Locations

Once foraging locations from 2012 were reduced to a set with acceptable observational error (SE in x or $y < 150$ m), I had data on 130 locations from 11 pregnant bats and 205 locations from 12 lactating bats. Overall, bats had a tendency to forage in the same areas independent of reproductive condition. Pregnant bats had a center of activity (geometric mean center) approximately 740 m from the primary roost, located north of a water catchment. For lactating bats, the center of activity was approximately 630 m from the primary roost, south of the same water catchment (Figure 18). All foraging locations within the standard distance (1 standard deviation of the mean center)

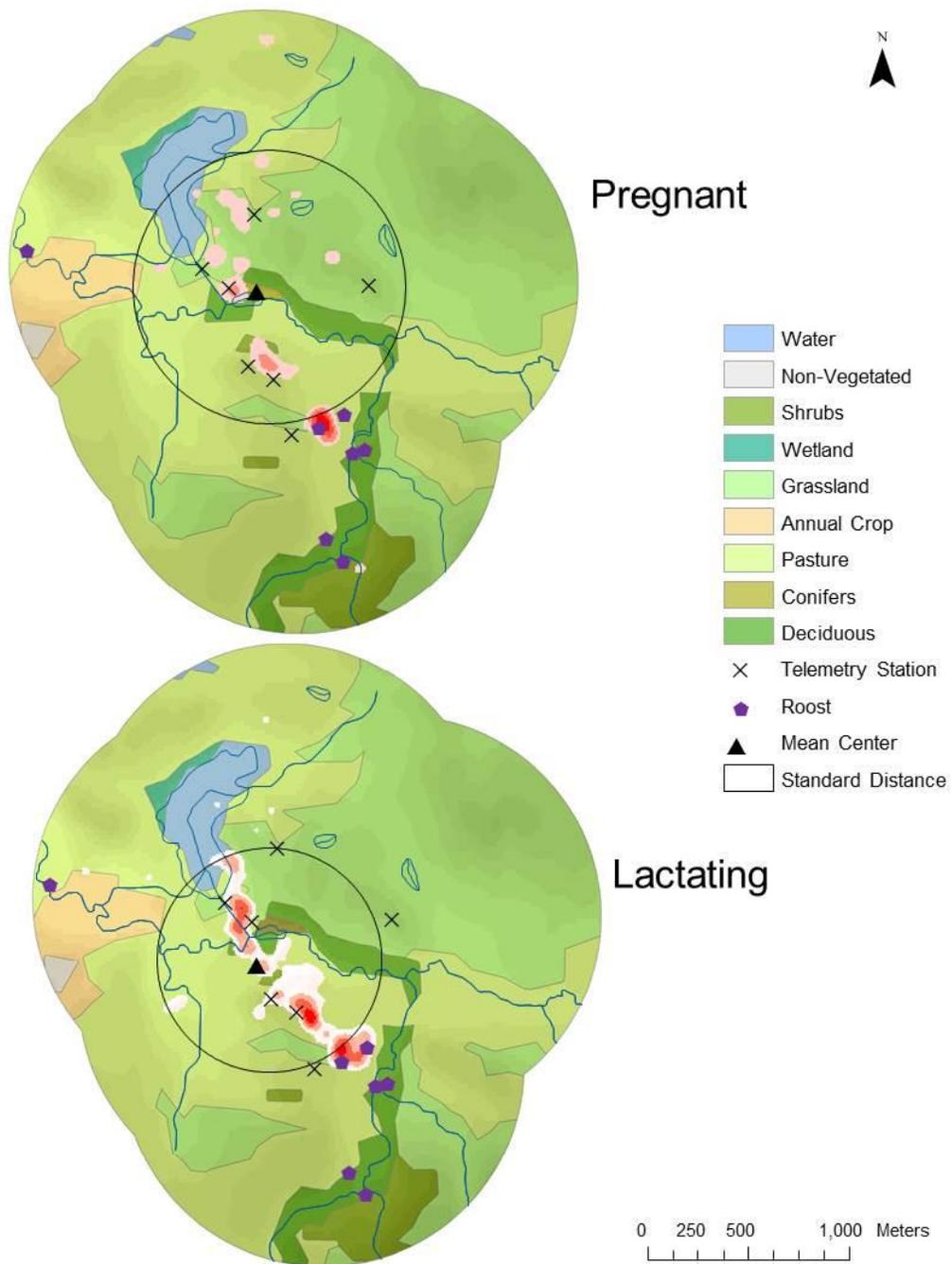


Figure 18. Concentration of foraging sites in pregnant and lactating *Eptesicus fuscus* in relation to cover type and elevation. Density of locations (calculated by kernel density estimates) is represented by the red shaded areas, the more intense the colour, the more concentrated the activity. Center of point concentration (geometric mean center) is indicated by triangles, and standard distance, the black circle, indicates how concentrated points are around the geometric mean center, so the amount of activity within 1 SD of the mean center. [original in colour]

were contained within an area of 145 ha during pregnancy and 98 ha during lactation. Kernel density analysis showed that bat activity was generally concentrated in the same areas regardless of reproductive condition.

Areas of pasture/grass were used more frequently than expected by individuals of both reproductive conditions (Figure 19; $\chi^2 = 191$, $p < 0.001$). Shrub land was used more by pregnant than lactating bats, which was more and less often than expected, respectively ($\chi^2 = 3.8$, $p = 0.05$). Bats generally foraged in locations near water features (reservoir or creek; pregnant: $\bar{x} = 121$ m, range = 0.3-300 m; lactating: $\bar{x} = 127$ m, range = 2.7- 450 m), with observed locations occurring either equal to or greater than expected based on proportion of these areas within the study area (riparian: $\chi^2 = 4.6$, $p = 0.05$, water: $\chi^2 = 0.33$, $p > 0.05$). Crop land was used less than expected during pregnancy but more than expected during lactation ($\chi^2 = 3.3$, $p > 0.05$), but not by a significant margin.

3.5 Foraging vs. Torpor

I assessed the relationship between torpor and foraging in two ways. 1) Torpor during the day after foraging at night: The relationship between the previous night's foraging time and total torpor varied between pregnant and lactating bats (Figure 20a). In pregnant bats, there was no relationship between the previous night's foraging and torpor duration. There was a slightly negative correlation for lactating bats ($r = -0.3$, $p = 0.04$), albeit different from a directly inverse relationship. A similar pattern was found when any thermoregulation parameter was used (HI, torpor depth, degree-minutes). 2) Foraging at night after torpor during the day: There was no relationship between torpor and foraging in either reproductive condition (Figure 20b).

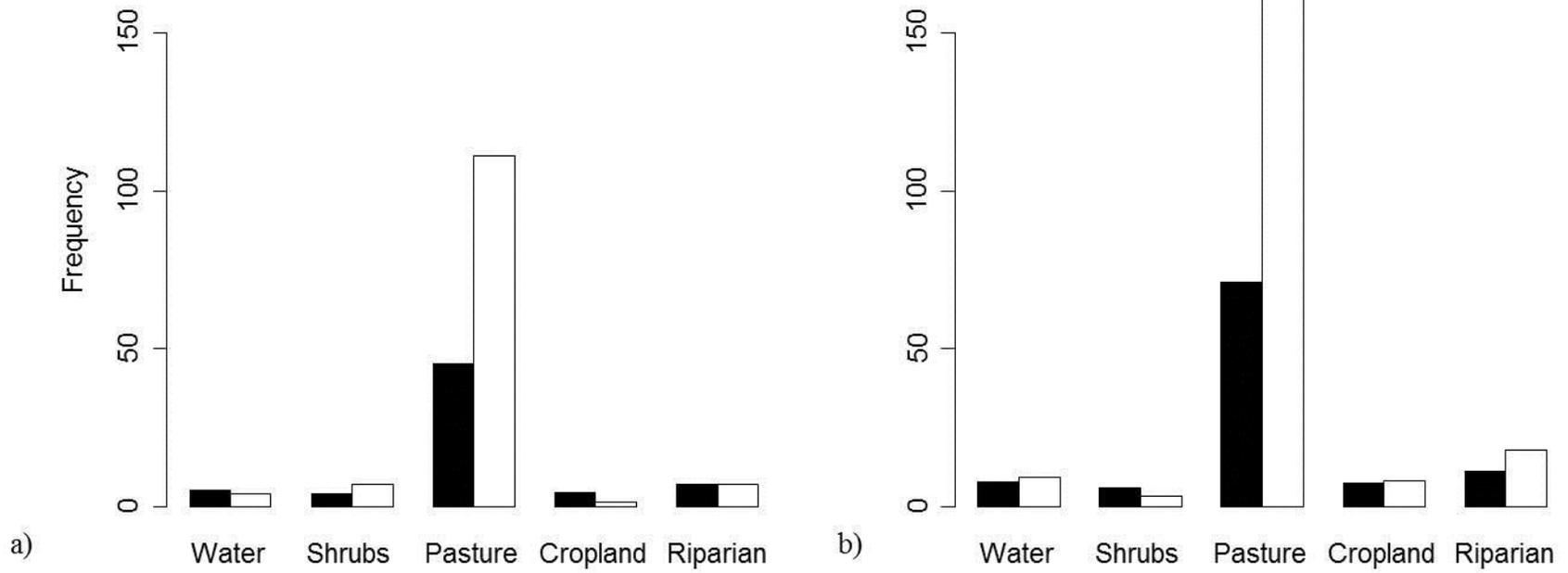
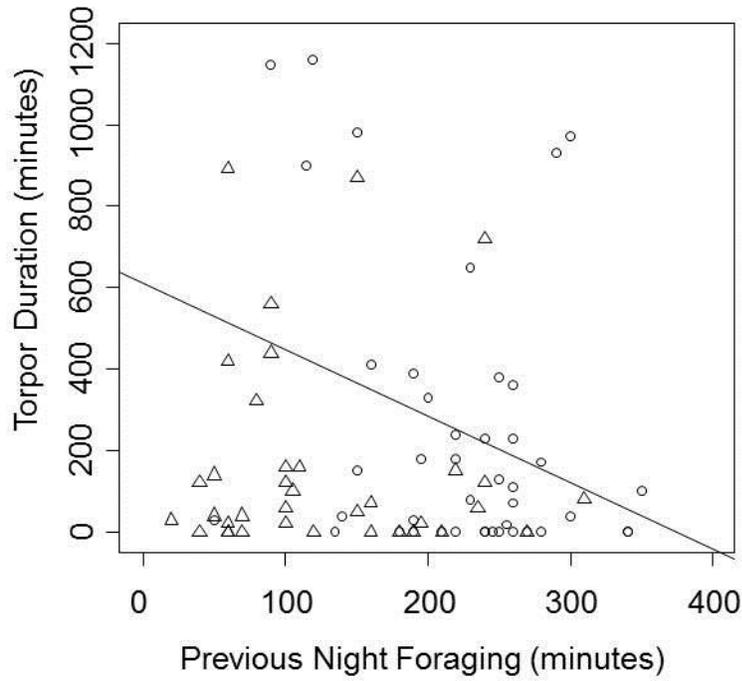
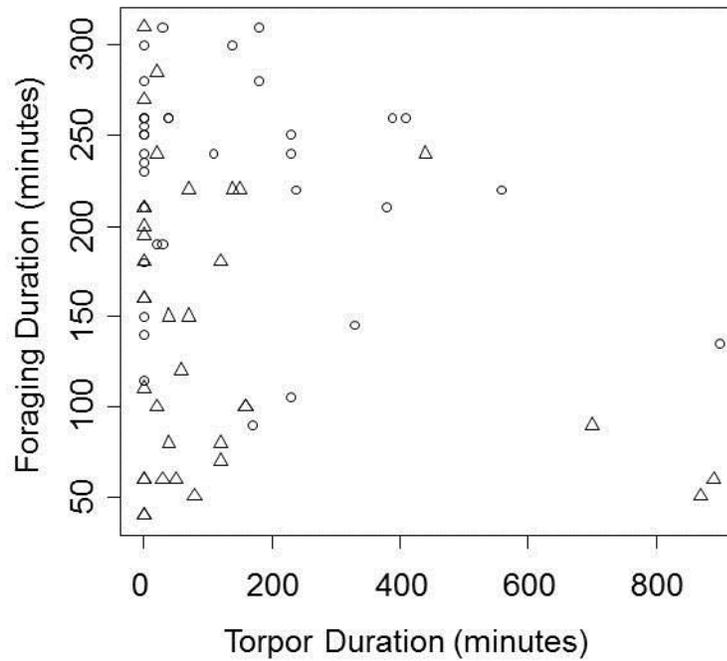


Figure 19. Expected based on availability (black bars) and observed (white bars) frequency of foraging locations in different habitat types for a) pregnant and b) lactating *Eptesicus fuscus* in 2012.



a.



b.

Figure 20. Relationship between daily torpor duration and nightly foraging duration for pregnant (triangles) and lactating (circles and solid line) *Eptesicus fuscus*. Data are for a) foraging duration prior to torpor use and b) torpor duration prior to foraging. Line indicates a significant relationship for lactating bats.

4. DISCUSSION

The goal of my project was to assess the energetic trade-offs associated with behavioural decisions made during reproduction by female *E. fuscus*. I did this by tracking body temperature, assessed as T_{sk} , during the inactive period (day) coupled with measures of foraging during the active period (night) for pregnant and lactating bats. Reproductive condition was classified when individuals were captured, and bats were tracked for a sufficiently short time that they were unlikely to become lactating or post-lactating. Because there is evidence for apparent physiological detriments to torpor use in both pregnancy and lactation, I expected that torpor would only be used when normothermy was costly (i.e. ambient conditions did not allow for roost temperatures within their TNZ, below 27°C; Willis et al. 2005) or foraging was not sufficient to cover the increased energy demands. When torpor was employed, I expected that pregnant bats would use torpor more readily than lactating. In addition to this, due to the time and energy constraints placed on lactating bats, I expected that they would forage for longer throughout the night and also return to the roost several times throughout the night in comparison to pregnant bats. Overall, I expected that there would be a relationship between energy gains through foraging and energy conservation through torpor throughout reproduction.

4.1 Thermoregulation

Contrary to my predictions, I found that torpor use frequency was independent of reproductive condition. Overall, at least one torpor bout was used on the majority of bat days (approximately 60%) by individuals in both reproductive conditions, but the specific characteristics of torpor bouts differed. I found that lactating bats had a tendency

to use slightly deeper and longer torpor bouts than pregnant bats, however this difference was not a significant one. Bats entered a similar number of torpor bouts regardless of reproductive condition and lactating bats were more likely to enter torpor closer to sunrise than pregnant bats. Contrary to the expected inverse relationship between foraging duration and torpor duration, I found a slightly negative relationship existed between these two activities for lactating bats only. My results provide further evidence that reproduction and torpor are not mutually exclusive and that the relationship between energy consumption and conservation is not a direct one in reproductive female *E. fuscus*.

Several thresholds have been suggested to identify torpor onset in birds and mammals; I used T_{onset} (Willis 2007) as my threshold to differentiate torpor from normothermy. The amount of torpor used by bats would have been estimated differently had I used either T_{active} (Barclay et al. 2001) or the $T_{99\text{ci}}$ (McKechnie et al. 2007) cutoff. T_{active} would have overestimated the amount of torpor used in comparison to T_{onset} . Interestingly, other *E. fuscus* studies in western North America using T_{active} found values similar to those in my study using T_{onset} (approximately 33°C). Even with a similar threshold, the bats in my study used torpor differently throughout reproduction when compared to individuals using either rock crevice or building roosts in southeast Alberta (e.g., Grinevitch et al. 1995; Hamilton and Barclay 1994; Lausen and Barclay 2003). Thus, an essential consideration when comparing studies of torpor is the threshold that is used.

Based on the assumption that bats assess their physiological state as well as the ambient conditions before entering torpor, it would then be expected that a collection of

environmental factors (e.g., temperature or wind) and physiological factors (e.g., foraging effort and reproductive condition) would be important. Similar to other studies (Brigham et al. 2000; Christian and Geiser 2007), none of the potential factors I measured predicted whether or not torpor was used. This suggests that other elements affect torpor use in reproductive females. If, as some surmise (Racey 1973; Wilde et al. 1999), torpor is truly detrimental during reproduction, bats could first employ a strategy of slightly lowering metabolic rate and subsequent T_{sk} , while remaining normothermic for several days before initiating torpor (Christian and Geiser 2007) which would save energy without the physiological detriment. Unfortunately I did not have a sufficient data set to identify whether this pattern exists.

Reproductive female bats exhibited two patterns of torpor depth and duration. Generally, the depth and duration of torpor were not different between reproductive conditions, especially when only bats roosting in buildings were considered. However, lactating bats that roosted in trees used deeper and longer bouts of torpor than all other groups. Reproductive condition and roost type were the most important factors in explaining torpor depth, duration, degree-minutes. Only reproductive condition was important for explaining heterothermy index (HI). Even though HI is not a direct measure of torpor, it is interesting that it was not affected by roost type like the other measures of thermoregulatory responses. This suggests that bats were using similar degree of temperature fluctuation regardless of where they roosted.

Torpor needs to be of sufficient depth and duration to accrue energetic savings because arousal is costly (Lovegrove et al. 1999). Through Q_{10} effects, shallow torpor bouts of long duration should have great benefits both energetically (Webb et al. 1993)

and possibly physiologically (i.e., fewer negative effects on foetal development or milk production). I argue that this is the case for the bats I tracked. Torpor was used most frequently at ambient temperatures between 10-15°C, a range which coincides with the lowest metabolic rate, and therefore greatest energetic savings (Hoary bat (*Lasiurus cinereus*), dasyruoid marsupials; Geiser and Baudinette 1987, Cryan and Wolf 2003). However, because there were fewer days with $T_a < 10^\circ\text{C}$, this trend could be due to my limited sample size. Overall, I found that females were likely using torpor at times that would yield the greatest energetic savings, while minimizing the potential detriments to their young.

4.1.1 The effect of reproduction on thermoregulation

Torpor bouts were of similar depth and duration in *E. fuscus* during both reproductive conditions but lactating bats had a tendency to have slightly longer and deeper torpor bouts than pregnant bats. Dzal and Brigham (2013), also using T_{onset} to set the torpor threshold, found lactating *M. lucifugus* used more torpor than pregnant individuals, but other studies have found the opposite (*E. fuscus* $T_b < 5^\circ\text{C}$ above T_a , Audet and Fenton (1988), T_{active} Grinevitch et al. (1995) and Lausen and Barclay (2003)), little to no difference between pregnant and lactating bats (*M. evotis* T_{active} , Solick and Barclay (2006); *E. fuscus* T_{active} , Hamilton and Barclay (1994)), or in some species, bats did not use torpor at all during reproduction (*M. daubentonii* 6°C below T_{active} ; Dietz and Kalko (2006). If Dietz and Kalko (2006) had used a different threshold, the bats they studied would have been deemed to have used torpor in both pregnancy and lactation (range of recorded temperatures: pregnant 30.7-39.5°C; lactating 27.9-36.3°C) and likely the same for the data on *E. fuscus* of Audet and Fenton (1988; no temperature values provided).

Solick and Barclay (2006) used a threshold of 26.6°C in pregnancy and 30.2°C in lactation, both of which would have underestimated torpor use in comparison to my data. Using either a consistent torpor threshold or the heterothermy index (although HI does not measure actual physiological consequences of torpor) would have allowed for more accurate comparison between studies. However, the T_{active} threshold for Hamilton and Barclay (1994) and Lausen and Barclay (2003) led to thresholds similar to my study (pregnant = 33°C for both studies; lactating = 31.8°C and 33°C, respectively), but the identification of different thermoregulatory patterns. This inconsistency points to the potential for differences between populations (both studies in southeast Alberta were within 200 km of mine), roost structure, and/or year.

Torpor during pregnancy may not always be detrimental and likely enhances the survival of both mother and pup in some situations. The first empirical evidence identifying the detriments of torpor during gestation in bats suggested that pregnant *P. pipistrellus* had a torpor depth at which females did not give birth ($T_a < 5^\circ\text{C}$) and that foetal development is halted during torpor bouts (Racey 1973). One factor that was not included in Racey's (1973) experiment was daily T_a fluctuations and depth of torpor, both of which naturally deviate. In contrast to Racey (1973), free-ranging *L. cinereus* entered hibernation (average $T_{\text{sk}} = 7.6^\circ\text{C}$ for up to 5.6 consecutive days) in response to a storm during late pregnancy and gave birth soon after arousal from torpor (Willis et al. 2006). I found that pregnant females used torpor on the majority of bat days, with a maximum torpor depth of 18°C ($T_{\text{sk}} = 15^\circ\text{C}$) and duration of 890 min. Although unconfirmed, these individuals likely gave birth at both sites because later captures were

comprised mostly of lactating females. In addition, these bats did not enter multiday torpor and T_{sk} was never $<15^{\circ}\text{C}$, therefore torpor use likely did not hinder foetal growth.

The stage of foetal development may influence the depth and duration of torpor use in pregnant bats. There was a trend for deeper and longer torpor bouts to occur during the middle (Julian date = 155-160) range of tracking pregnant bats in comparison to the first and last (145-155 and 160-168) period. A similar pattern was found for pregnant Hemprich's long-eared bats (*Otonycteris hemprichii*) which used torpor frequently and deep torpor often during the first two trimesters of pregnancy but only used shallow torpor in the final trimester (Daniel et al. 2010). This pattern suggests that greater depths of torpor late in pregnancy could be more detrimental to foetal development (in contrast to Willis et al. (2006)) than early in pregnancy, even though the more highly developed foetus requires greater energy because greatest foetal growth in terms of mass occurs then (Kunz 1973; Speakman and Racey 1987).

I found lactating bats to frequently use torpor throughout the day and the deepest bouts of torpor I recorded occurred during this reproductive period. This was unexpected because torpor during lactation has been proposed to be more detrimental to pups than during gestation. Although the foetus is dependent on the mother during in utero growth, their growth slows or halts during gestation, however, if pups do not receive enough milk the probability of starvation and death are increased. Metabolic rate and offspring growth are highly correlated, possibly due to reduced milk production (Glazier 1985) and further, the milk produced may be of lesser quality and in lower quantities when mothers are at torpid (22°C) compared to normothermic (37°C) temperatures (Wilde et al. 1999). Although Wilde et al. (1999) did not assess tissue

responses at intermediate temperatures between 22°C and 37°C, it is clear that torpor reduces milk production. Using 22°C as a limit for when torpor impacts milk production, I assumed that bats would keep T_{sk} above 22°C as often as possible. Consistent with this hypothesis, T_{sk} was >22°C on all but 3 days, all of which occurred for bats roosting in trees. In a mammary tissue explant experiment, Wilde et al. (1999) kept the tissues at a constant 22°C or 37°C which does not reflect natural patterns of torpor use. I found that bats would often use several short and shallow bouts of torpor throughout their inactive period interrupted by periods of normothermy, a pattern which has been suggested may not be detrimental to the pups during either gestation or lactation (Turbill and Geiser 2006). Ultimately, both the Racey (1973) and Wilde et al. (1999) experiments indicate that when held at cold temperatures for long periods of time, there are considerable costs associated with torpor; however, in most situations, unless severe and prolonged periods of inclement weather arise, these types of torpor patterns do not commonly occur in the field.

Pups require more milk as lactation progresses, placing greater energetic pressures on the mother with peak requirements occurring during late lactation (Kurta and Kunz 1988; Racey and Speakman 1987). As such, thermoregulatory patterns should change accordingly with torpor being used less as pups get older (Klüg and Barclay 2013). I tracked lactating bats over a period of 25 days, which encompasses most of the lactation period (although parturition can occur over multiple weeks, so it is likely that not all bats were in the same stages of lactation), and found that torpor expression did not change throughout the tracking period. Although I do not have enough data to conclude with confidence why there were no differences of torpor use throughout lactation, I

hypothesize four explanations for my findings: 1) females that use extensive amounts of torpor might not have had pups that required care, but without recapturing bats throughout the season, I was unable to identify precisely when lactation ceased for individuals, 2) the bats could have been obtaining enough energy through foraging so they do not need to use more torpor when energy demands increased, 3) bats had accrued fat reserves during pregnancy and could use them when needed, reducing the need for more torpor, or 4) bats produced enough milk at night during their active period or in between torpor bouts that when employed, torpor was not detrimental to the pups. Henry et al. (2002) hypothesized that because of the high demand of water and energy for milk production, *M. lucifugus* would likely nurse their young solely during the active period at night. If this hypothesis is correct, most milk production should occur at night which could promote both offspring and mother survival. There are no data at present that provide a direct test of this hypothesis, and it represents a major limitation in our current understanding of bat biology. It would be interesting to observe bats throughout the inactive period when in the roost to identify when bats suckle their young and how that relates to thermoregulatory patterns during lactation.

4.1.2 The effect of roost type on thermoregulation

The primary roost structures used by bats in both years were buildings. Roost switching was not observed in 2011, but bats switched roosts frequently in 2012. In addition, roost switching frequency was different between the two reproductive conditions. Lactating bats used tree roosts as often as the building roost, but pregnant bats used the building roost considerably more often than trees. Ellison et al. (2007) found that *E. fuscus* switched roost locations more frequently during hot years than cool.

This suggests that *E. fuscus* avoid high temperatures, likely due to an upper limit of heat tolerance as reported for other mammalian groups (Pennycuick 1964; Shelton and Huston 1968). From this line of thought, I expected that when bats moved from the building roost in 2012, T_a (and corresponding T_{roost}) would be above the upper limit of the TNZ of *E. fuscus* (36°C; Willis et al. 2005), and that 2011 did not reach these temperatures, which would explain why roost switching did not occur. Unexpectedly, both 2011 and 2012 had similarly high temperatures during lactation, and the 2011 building roost reached temperatures >40°C more often than 2012. The buildings had different structural characteristics, with the 2011 roost having an open attic while the 2012 site did not. The open attic likely created different microclimatic conditions that individuals could select, and there was evidence of bats occupying many areas within it. It is likely that there were spaces within the roost structure that provided cooler areas when ambient temperatures were hot, which would lead to use of changing locations within the roost but not roost structure switching as seen in 2012. Previous studies have found that within the same roost structure, there is evidence that bats use the warmest areas on cool days and avoid those areas on hot days (Audet and Fenton 1988; Burnett and August 1981; Garroway and Broders 2008; Lučan and Radil 2010; Studier and O'Farrell 1972; Wojciechowski et al. 2007), indicating that bats exhibit within roost structure selection of microclimates as much as between roost structure selection. However, days in 2012 when roost switching occurred did not coincide with either extremely hot or cold days, both of which could decrease reproductive success (e.g., Kerth et al. 2001), which indicates that extreme temperatures, either hot or cold, were likely not affecting roost switching.

Thermal lability of roosts could also be an important factor in roost selection, as building roost temperatures are often more variable than caves and rock crevices (Lausen and Barclay 2006; Law and Chidel 2007; Postawa and Gas 2009; Zahn 1999), and possibly trees. In 2012 when some bats were occupying the building structure and others occupying trees, I found that the building roost exhibited greater variation in temperature during both reproductive periods and also during day and night. During pregnancy, there was a difference of 6°C in maximum T_{roost} , whereas during lactation this difference was at least a 9°C. The mean nightly minimum temperature was similar between the two roost types during both reproductive periods; therefore there may be less fluctuation in nightly temperature in tree roosts than in the building. It is unlikely the bats were moving in response to high temperature in the building, therefore, the bats were likely moving to tree roosts with a more stable temperature which did not decline as much through the night. A more stable roost temperature at night would be beneficial for unattended pups as they would not cool as rapidly without their mother present (Sano 2000)

I found that pregnant *E. fuscus* showed a preference for building roosts over trees, but the opposite was found for lactating individuals. Similar to the data for 2011, a variety of studies found that building structures are commonly preferred over natural roosts by cavity roosting species such as *E. fuscus* or *M. lucifugus*. Building roosts may be more commonly used because they are thought to be more beneficial for pup development in comparison to other structures due to earlier weaning of pups, and larger pups at weaning (Lausen and Barclay 2006; Law and Chidel 2007). However, lactating bats in 2012 often occupied trees over buildings, similar to *E. fuscus* in other studies (Brigham 1991; Rancourt et al. 2007). Lučan and Radil (2010) found a comparable

pattern in *M. daubentonii* where this species occupied artificial roosts and caves when non-reproductive but were found only in trees during the reproductive period. Since bats are probably selecting roosts based on microclimatic conditions, it is likely that not all structures within a category are the same. In addition, in cases like 2011 when bats remained in the building, this roost provided conditions that were more amenable to pup development, whereas in 2012, the trees provided these conditions over buildings at least during some days when bats were tracked.

The potential to dissipate heat during lactation (an exothermic process), has been hypothesized to limit milk production (Król and Speakman 2003). Studies on laboratory rodents have found that greater heat dissipation can result in higher milk production and heavier young at weaning (Król et al. 2007), although this is not a universal response (Paul et al. 2010; Zhao and Cao 2009). On all days during which I concurrently measured tree and building roost temperature, tree roosts were consistently cooler than the building throughout most of the day, which produced a larger gradient between T_{roost} and T_{sk} in trees than buildings. The larger temperature gradient would increase heat dissipation potential, which I argue may allow bats to produce more milk when they were normothermic during the day, making up for presumed reduced milk production when torpid. This ability would make cooler roosts better for lactating bats than hot roosts.

4.2 Foraging patterns

As expected, lactating bats spent more time foraging, measured as time spent flying, and made more foraging trips than pregnant bats, which makes lactating bats energy maximizers and pregnant bats time minimizers (Pyke et al. 1977). Based on the

differences in energetic requirements during pregnancy and lactation, lactating bats were expected to forage for longer than pregnant ones, assuming that, since bats remained close to the roost at all times, longer foraging equates to greater prey consumption. Also, because young cannot thermoregulate proficiently at a young age and require warming (Sano 2000; Zahn 1999) as well as feeding, it is not surprising that lactating bats made more foraging trips than pregnant. My findings are consistent with several studies (e.g., Aldridge and Brigham 1991; Brigham 1991; Grinevitch et al. 1995; Lučan and Radil 2010; O'Donnell 2002) but others found no difference in foraging duration between reproductive conditions (e.g., Dzal and Brigham 2013; Wilkinson and Barclay 1997) or that pregnant bats foraged longer than lactating bats (Dietz and Kalko 2007). Sample size and methods were similar in all of these studies; therefore it is likely that species, site, and year influence foraging. For example, Grinevitch et al. (1995) and Wilkinson and Barclay (1997) studied *E. fuscus* at the same site but in different years. The different response suggests an influence of year on foraging behaviour.

I found that reproductive condition and number of foraging trips were the most important factors in explaining total foraging duration. Surprisingly the amount of torpor used on any given day did not influence the amount of foraging that occurred during the night. I expected that if bats used torpor more during the day they would likely need to forage less. However, if the bats had to use torpor because they did not have sufficient energy reserves to remain active throughout the day, it is then possible that they would forage for the same amount at night regardless of how much energy they saved during the day. One factor that could have influenced this is the amount of fat reserves that individuals had accumulated and could possibly exploit. Small mammals (<25 g) can

only store enough fat to provide 2-3 days of energy, however, when ambient temperature is reduced, maintaining normothermy would burn through any reserves in far less time (Bronson 1985; Speakman and Racey 1987). Bats would be less likely than other mammals to have fat reserves during reproduction in general because of the energetic costs associated with greater wingloading in addition to reduced maneuverability during flight (Norberg and Rayner 1987), as well as the space constraints placed on pregnant bats. So bats that do not have large fat reserves in place would be more likely to forage regardless of what they did the previous day because they do not have a “safety net”, something that I could not measure.

Inclement weather did not influence the timing or duration of foraging bouts. Bats exited the roost on all nights for at least 30-40 minutes, even when $T_a < 10^\circ\text{C}$, and foraging duration was not different than when $T_a > 10^\circ\text{C}$. Several authors have also reported that weather did not influence foraging duration (e.g., Chruszcz and Barclay 2003; Ciechanowski et al. 2007; Dietz and Kalko 2007; Geggie and Fenton 1985; Lučan and Radil 2010; Rydell 1993). Equally as common, it has been found that bats do not forage during inclement weather (i.e. windy, $T_a < 12^\circ\text{C}$, rain; Audet 1990; Catto et al. 1995; De Jong 1994). The inconsistency of these results is likely a function of which species are being studied and life stage of the bats. For instance, a gleaner bat, such as *M. evotis* would likely be less affected by wind and lower temperature because insects would be found on plant surfaces rather than airborne in these conditions, whereas an aerial hawker, such as *E. fuscus* would be more affected by inclement weather because they feed on airborne insects. In the above studies, species studied range from aerial hawkers (e.g., *Eptesicus* spp., *M. lucifugus*, *Pipistrellus* spp., *Nyctalus* spp.), to water

surface foragers (e.g., *M. daubentonii*) and gleaners (e.g., *M. evotis*); a mix of species exhibiting a negative or neutral foraging response to weather. Theoretically, lactating bats should be more apt to forage during inclement weather because the consequence of obtaining insufficient energy increases the potential for pup starvation (Harbusch and Racey 2006).

4.2.1 Habitat Selection

Bats did not travel far from roosts to forage, with foraging efforts concentrated in a small area (~150 ha) within 1.5 km of the roost sites for at least 95% of the time. This pattern suggests that the local area near the roosts was rich in necessary resources, or that food resources are not a limiting factor for this species. By remaining close to the roost, bats minimize commuting time and distance from the roost which would increase foraging time in patches and, during lactation, allow bats to make several trips back to the roost to feed and warm the young. In a study conducted near to mine, *E. fuscus* often travelled up to 11 km from the roost to forage (Arbuthnott and Brigham 2007). This distance can be covered in approximately 20 minutes (Norberg 1987), which is likely not energetically expensive but may pose time constraints during lactation when females have to return to feed their young.

During both pregnancy and lactation, *E. fuscus* appeared to select foraging sites. They tended to use pastureland more often than would be predicted based on its availability. Grassland was more important for pregnant bats than lactating ones. Although these two habitat types are similar, there is a possibility that the presence of livestock in pasture influenced the diversity and abundance of beetles (Arbuthnott and Brigham 2007; Galante et al. 1995; Williams et al. 2011). By foraging in different

habitat classes that are typically composed of different insects throughout reproduction, *E. fuscus*, a generalist forager, could be consuming prey of differing nutrient contents (Studier et al. 1994), such as fat, protein, and calcium which are especially important during lactation (Hood et al. 2006; Speakman 2008). In addition, bats had a tendency to remain in low lying areas which would shelter them and the insects they eat from the effects of wind (Verboom and Spoelstra 1999). In temperate areas, insects are often found in higher abundance along tree lines than in open areas (Downs and Racey 2006; Johnson and Lacki 2013) and along the water edge than over it (Ciechanowski et al. 2007), which explains why most of foraging occurred close to either riparian areas or along the reservoir.

4.3 Torpor vs. foraging

I expected to find an inverse relationship between energy conservation and consumption if torpor use during reproduction has no physiological costs. I assessed the potential for this relationship in two ways: 1) torpor use following a night of foraging and 2) the amount of foraging time spent following time spent torpid during the day. Of the two scenarios in each reproductive condition, the expected inverse relationship was only weakly present for lactating bats when torpor was used following foraging. The difference between reproductive conditions suggests the detriments of using torpor during reproduction are not equal but likely greater for pregnant bats than lactating. The lack of relationship between foraging at night after torpor during the day reinforces the hypothesis that torpor is used to maintain a positive energy balance, but bats will forage as much as possible regardless of torpor. In temperate regions where the growing season

is short, the possibility of delaying parturition could outweigh the benefits of saving energy when conditions are not amenable to foraging.

Foetal growth, in terms of mass, is most rapid during the last trimester of pregnancy (Kunz 1973; Speakman and Racey 1987), which makes it possible that torpor is more costly later in pregnancy than earlier. However, the developing foetus early in pregnancy could be more sensitive to the cooling associated with torpor, while at the same time fewer calories are being allocated to foetal growth. This combination could make torpor more costly in terms of foetal survival but also less necessary in terms of maintaining a positive energy balance for maternal survival. This situation could explain the lack of evidence for a direct relationship between torpor and foraging in pregnant bats. Furthermore, pups require the most energy and milk in the later stages of their development. Depending on what stage of lactation bats were in, the energetic needs of mother and pup could differ. For instance, pups require less milk early in development which reduces the need for females to produce high quantities of milk, allowing them to enter torpor without cost. However, neonates cannot maintain high body temperature and often require warming from the mother, which makes maternal torpor detrimental to the young. This conflict can be counteracted by roosting in places where the females could roost with the young to warm them in the morning when T_{roost} is low, then roost away from the young in cooler areas (O'Farrell and Studier 1973) and save energy by entering torpor while the pups stay warm independently in warmer areas of the roost. Therefore, it is likely that bats were employing a combination of behavioural thermoregulation and torpor, which was conducive to both reproduction and growth of young (Studier and O'Farrell 1972; Willis and Brigham 2007).

4.4 Conclusions

My results are different from other thermoregulation studies in temperate regions. Reproductive condition did not have a large influence on thermoregulatory characteristics but did influence foraging patterns. In addition, most studies report that building roosts are better for reproductive females; however, I found lactating bats used both building and tree roosts, which implies that sometimes building roosts are not best. In contrast, even though there were trees in the area that were occupied by bats in 2011, all radio-tagged pregnant or lactating bats always occupied the building. This is an area of research that needs further attention to identify what characteristics of a tree roost may be more beneficial than a building during specific times in an individual's life.

My study provides further evidence that reproduction and torpor are not mutually exclusive. Further work needs to be done to address if there is a temperature threshold at which either gestation ceases and the foetus dies, or milk production ceases or quality declines greatly. I hypothesize that this is the case because lactating females did not enter deep torpor often but regularly used shallow bouts of torpor. It is likely that both gestation and lactation are affected in varying degrees along a gradient, but it is essential to understand when torpor is completely detrimental to either the foetus or pup. Additionally, it would be interesting to determine what about temperate bat physiology allows them to use torpor extensively throughout reproduction whereas other heterothermic mammalian species do not.

REFERENCES

- ALDRIDGE, H. D. J. N., AND R. M. BRIGHAM. 1991. Factors influencing foraging time in two aerial insectivores: the bird *Chordeiles minor* and the bat *Eptesicus fuscus*, *Canadian Journal of Zoology* 69:62-69.
- ANDERSON, D. R., AND K. P. BURNHAM. 2002. Avoiding pitfalls when using information-theoretic methods, *Journal of Wildlife Management* 66:912-918.
- ANTHONY, E. L. P., AND T. H. KUNZ. 1977. Feeding strategies of the little brown bat, *Myotis lucifugus*, in southern New Hampshire, *Ecology* 58:775-786.
- ANTHONY, E. L. P., M. H. STACK, AND T. H. KUNZ. 1981. Night roosting and the nocturnal time budget of the little brown bat, *Myotis lucifugus*: effects of reproductive status, prey density, and environmental conditions, *Oecologia* 51:151-156.
- ARBUTHNOTT, D., AND R. M. BRIGHAM. 2007. The influence of a local temperature inversion on the foraging behaviour of big brown bats, *Eptesicus fuscus*, *Acta Chiropterologica* 9:193-201.
- AUDET, D. 1990. Foraging behavior and habitat use by a gleaning bat, *Myotis myotis* (Chiroptera: Vespertilionidae), *Journal of Mammalogy* 71:420-427.
- AUDET, D., AND M. B. FENTON. 1988. Heterothermy and the use of torpor by the bat *Eptesicus fuscus* (Chiroptera: Vespertilionidae): a field study, *Physiological Zoology* 61:197-204.
- AUDET, D., AND D. W. THOMAS. 1996. Evaluation of the accuracy of body temperature measurement using external radio transmitters, *Canadian Journal of Zoology* 74:1778-1781.
- BARCLAY, M. R. 1991. Population structure of temperate zone insectivorous bats in relation to foraging behaviour and energy demand, *Journal of Animal Ecology* 60:165-178.
- BARCLAY, R. M. R. 1989. The effect of reproductive condition on the foraging behavior of female hoary bats, *Lasiurus cinereus*, *Behavioral Ecology and Sociobiology* 24:31-37.
- BARCLAY, R. M. R. 1994. Constraints on reproduction by flying vertebrates: energy and calcium, *The American Naturalist* 144:1021-1031.
- BARCLAY, R. M. R., ET AL. 1996. Can external radiotransmitters be used to assess body temperature and torpor in bats?, *Journal of Mammalogy* 77:1102-1106.

- BARCLAY, R. M. R., C. L. LAUSEN, AND L. HOLLINS. 2001. What's hot and what's not: defining torpor in free-ranging birds and mammals, *Canadian Journal of Zoology* 79:1885-1890.
- BATES, D., M. MAECHLER, AND B. BOLKER. 2012. lme4: Linear mixed-effects models using S4 classes.
- BEASLEY, C. A., AND C. J. ADAMS. 1994. Relationships between environmental factors and capture time of male pink bollworm (Lepidoptera: Gelechiidae) moths in traps baited with sex pheromone, *Journal of Economic Entomology* 87:986-992.
- BENTON, T. F., D. M. BRYANT, L. COLE, AND H. Q. P. CRICK. 2002. Linking agricultural practice to insect and bird populations: a historical study over three decades, *Journal of Applied Ecology* 39:673-687.
- BOYLES, J. G., B. SMIT, AND A. E. MCKECHNIE. 2011a. Does use of the torpor cut-off method to analyze variation in body temperature cause more problems than it solves, *Journal of Thermal Biology* 36:373-375.
- BOYLES, J. G., B. SMIT, AND A. E. MCKECHNIE. 2011b. A New Comparative Metric for Estimating Heterothermy in Endotherms, *Physiological and Biochemical Zoology* 84:115-123.
- BRIGHAM, R. M. 1991. Flexibility in foraging and roosting behaviour by the big brown bat (*Eptesicus fuscus*), *Canadian Journal of Zoology* 69:117-121.
- BRIGHAM, R. M., G. KÖRTNER, T. A. MADDOCKS, AND F. GEISER. 2000. Seasonal Use of Torpor by Free-Ranging Australian Owlet-Nightjars (*Aegotheles cristatus*), *Physiological and Biochemical Zoology* 73:613-620.
- BRIGHAM, R. M., AND M. B. SAUNDERS. 1990. The diet of big brown bats (*Eptesicus fuscus*) in relation to insect availability in southern Alberta, Canada, *Northwest Science* 64:7-10.
- BRIGHAM, R. M., C. K. R. WILLIS, F. GEISER, AND N. MZILIKAZI. 2011. Baby in the bathwater: Should we abandon the use of body temperature thresholds to quantify expression of torpor?, *Journal of Thermal Biology* 36:376-379.
- BRONSON, F. H. 1985. Mammalian reproduction: an ecological perspective, *Biology of Reproduction* 32:1-26.
- BRYANT, D. M. 1975. Breeding biology of house martins *Delichon urbica* in relation to aerial insect abundance, *Ibis* 117:180-216.
- BURNETT, C. D., AND P. V. AUGUST. 1981. Time and energy budgets for dayroosting in a maternity colony of *Myotis lucifugus*, *Journal of Mammalogy* 62:759-766.

- BURNHAM, K. P., AND D. R. ANDERSON. 2002. Model Selection and Multi-Model Inference. 2nd ed. Springer Science + Business Media, Inc. , New York 497.
- BUTLER, P. J., J. A. GREEN, I. L. BOYD, AND J. R. SPEAKMAN. 2004. Measuring metabolic rate in the field: the pros and cons of the doubly labelled water and heart rate methods, *Functional Ecology* 18:168-183.
- CATTO, C. M. C., P. A. RACEY, AND P. J. STEPHENSON. 1995. Activity patterns of the serotine bat (*Eptesicus serotinus*) at a roost in southern England, *Journal of Zoology* 235:635-644.
- CHRISTIAN, N., AND F. GEISER. 2007. To use or not to use torpor? Activity and body temperature as predictors, *Naturwissenschaften* 94:483-487.
- CHRUSZCZ, B. J., AND R. M. R. BARCLAY. 2003. Prolonged foraging bouts of a solitary gleaning/hawking bat, *Myotis evotis*, *Canadian Journal of Zoology* 81:823-826.
- CIECHANOWSKI, M., T. ZAJĄC, A. BILAS, AND R. DUNAJSKI. 2007. Spatiotemporal variation in activity of bat species differing in hunting tactics: effects of weather, moonlight, food abundance, and structural clutter, *Canadian Journal of Zoology* 85:1249-1263.
- CRYAN, P. M., AND B. O. WOLF. 2003. Sex differences in the thermoregulation and evaporative water loss of a heterothermic bat, *Lasiurus cinereus*, during its spring migration, *Journal of Experimental Biology* 206:3381-3390.
- DANIEL, S., C. KORINE, AND B. PINSHOW. 2010. The use of torpor in reproductive female Hemprich's long-eared bats (*Otonycteris hemprichii*), *Physiological and Biochemical Zoology* 83:142-148.
- DAUSMANN, K. H. 2005. Measuring body temperature in the field—evaluation of external vs. implanted transmitters in a small mammal, *Journal of Thermal Biology* 30:195-202.
- DE JONG, J. 1994. Habitat use, home-range and activity pattern of the northern bat, *Eptesicus nilssoni*, in a hemiboreal coniferous forest, *Mammalia* 58:535-548.
- DIETZ, M., AND E. K. V. KALKO. 2006. Seasonal changes in daily torpor patterns of free-ranging female and male Daubenton's bats (*Myotis daubentonii*), *Journal of Comparative Physiology B* 176:223-231.
- DIETZ, M., AND E. K. V. KALKO. 2007. Reproduction affects flight activity in female and male Daubenton's bats, *Myotis daubentonii*, *Canadian Journal of Zoology* 86:653-664.

- DOCHTERMANN, N. A., AND S. H. JENKINS. 2011. Developing multiple hypotheses in behavioral ecology, *Behavioural Ecology and Sociobiology* 65:37-45.
- DOUCETTE, L. I., R. M. BRIGHAM, C. R. PAVEY, AND F. GEISER. 2012. Prey availability affects daily torpor by free-ranging Australian owlet-nightjars (*Aegotheles cristatus*), *Oecologia* 169:361-372.
- DOWNES, N. C., AND P. A. RACEY. 2006. The use by bats of habitat features in mixed farmland in Scotland, *Acta Chiropterologica* 8:169-185.
- DUCHAMP, J. E., D. W. SPARKS, AND J. O. WHITAKER, JR. 2004. Foraging-habitat selection by bats at an urban– rural interface: comparison between a successful and a less successful species, *Canadian Journal of Zoology* 82:1157-1164.
- DZAL, Y., AND R. M. BRIGHAM. 2013. The tradeoff between torpor use and reproduction in little brown bats (*Myotis lucifugus*), *Journal of Comparative Physiology B* 183:279-288.
- DZAL, Y. A. 2010. Thermoregulatory and foraging strategies of the little brown bat (*Myotis lucifugus*) during the reproductive season, University of Regina, Regina.
- ELLISON, L. E., T. J. O'SHEA, D. J. NEUBAUM, AND R. A. BOWEN. 2007. Factors influencing movement probabilities of big brown bats (*Eptesicus fuscus*) in buildings, *Ecological Applications* 17:620-627.
- ENCARNAÇÃO, J. A., AND M. DIETZ. 2006. Estimation of food intake and ingested energy in Daubenton's bats (*Myotis daubentonii*) during pregnancy and spermatogenesis, *European Journal of Wildlife Research* 52:221-227.
- ESRI. 2012. ArcGIS Desktop 10. Environmental Systems Research Institute, Redlands, CA.
- FULLARD, J. H., M. B. FENTON, AND C. L. FURLONGER. 1983. Sensory relationships of moths and bats sampled from two Nearctic sites, *Canadian Journal of Zoology* 61:1752-1757.
- FULLER, M. R., J. J. MILLSPAUGH, K. E. CHURCH, AND R. E. KENWARD. 2005. Wildlife Radiotelemetry, Pp. 377-417 in *Techniques for wildlife investigations and management* (C. E. Braun, ed.). The Wildlife Society, Bethesda, Maryland, USA.
- GALANTE, E., J. MENA, AND C. LUMBRERAS. 1995. Dung beetles (Coleoptera: Scarabaeidae, Geotrupidae) attracted to fresh cattle dung in wooded and open pasture, *Environmental Entomology* 24:1063-1068.

- GARROWAY, C. J., AND H. G. BRODERS. 2008. Day roost characteristics of northern long-eared bats (*Myotis septentrionalis*) in relation to female reproductive status, *Ecoscience* 15:89-93.
- GEGGIE, J. F., AND M. B. FENTON. 1985. A comparison of foraging by *Eptesicus fuscus* (Chiroptera: Vespertilionidae) in urban and rural environments, *Canadian Journal of Zoology* 63:263-267.
- GEISER, F., AND R. V. BAUDINETTE. 1987. Seasonality of torpor and thermoregulation in three dasyurid marsupials, *Journal of Comparative Physiology* 157:333-344.
- GEISER, F., AND R. M. BRIGHAM. 2000. Torpor, thermal biology, and energetics in Australian long-eared bats (*Nyctophilus*), *Journal of Comparative Physiology B* 170 153-162.
- GEISER, F., B. S. LAW, AND G. KÖRTNER. 2005a. Daily torpor in relation to photoperiod in a subtropical blossom-bat, *Syconycteris australis* (Megachiroptera), *Journal of Thermal Biology* 30:574-579.
- GEISER, F., B. M. MCALLAN, AND R. M. BRIGHAM. 2005b. Daily torpor in a pregnant dunnart (*Sminthopsis macroura* Dasyuridae: Marsupialia), *Mammalian Biology* 70:117-121.
- GEISER, F., B. M. MCALLAN, G. J. KENAGY, AND S. M. HIEBERT. 2007. Photoperiod affects daily torpor and tissue fatty acid composition in deer mice, *Naturwissenschaften* 94:319-325.
- GEISER, F., AND T. RUF. 1995. Hibernation versus daily torpor in mammals and birds: physiological variables and classification of torpor patterns, *Physiological Zoology* 68:935-966.
- GITTLEMAN, J. L., AND S. D. THOMPSON. 1988. Allocation in mammalian reproduction, *American Zoologist* 28:863-875.
- GLAZIER, D. S. 1985. Relationship between metabolic rate and energy expenditure for lactation in *Peromyscus*, *Comparative Biochemistry and Physiology* 80A:587-590.
- GRINEVITCH, L., S. L. HOLROYD, AND R. M. R. BARCLAY. 1995. Sex differences in the use of daily torpor and foraging time by big brown bats (*Eptesicus fuscus*) during the reproductive season, *Journal of Zoology* 235:301-309.
- HAMILTON, I. M., AND R. M. R. BARCLAY. 1994. Patterns of daily torpor and day-roost selection by male and female big brown bats (*Eptesicus fuscus*), *Canadian Journal of Zoology* 72:744-749.

- HAMILTON, I. M., AND R. M. R. BARCLAY. 1998. Diets of juvenile, yearling, and adult big brown bats (*Eptesicus fuscus*) in southeastern Alberta, *Journal of Mammalogy* 79:764-771.
- HARBUSCH, C., AND P. A. RACEY. 2006. The sessile serontine: the influence of roost temperature on philopatry and reproductive phenology of *Eptesicus serotinus* (Schreber, 1774) (Mammalia: Chiroptera), *Acta Chiropterologica* 8:213-229.
- HELDMAIER, G., AND T. RUF. 1992. Body temperature and metabolic rate during natural hypothermia in endotherms, *Journal of Comparative Physiology B* 162:696-706.
- HENDERSON, L. E., AND H. G. BRODERS. 2008. Movements and resource selection of the northern long-eared myotis (*Myotis septentrionalis*) in a forest-agriculture landscape, *Journal of Mammalogy* 89:952-963.
- HENRY, M., D. W. THOMAS, R. VAUDRY, AND M. CARRIER. 2002. Foraging distances and home range of pregnant and lactating little brown bats (*Myotis lucifugus*), *Journal of Mammalogy* 83:767-774.
- HOLLOWAY, J. C., AND F. GEISER. 1996. Reproductive status and torpor of the marsupial *Sminthopsis crassicaudata*: effect of photoperiod, *Journal of Thermal Biology* 21:373-380.
- HOOD, W. R., O. T. OFTEDAL, AND T. H. KUNZ. 2006. Variation in body composition of female big brown bats (*Eptesicus fuscus*) during lactation, *Journal of Comparative Physiology B* 176:807-819.
- IUPS THERMAL COMMISSION. 2003. Glossary of terms for thermal physiology, *Journal of Thermal Biology* 28:75-106.
- JACOBS, D. S., E. J. KELLY, M. MASON, AND S. STOFFBERG. 2007. Thermoregulation in two free-ranging subtropical insectivorous bat species: *Scotophilus* species (Vespertilionidae), *Canadian Journal of Zoology* 85:883-890.
- JOHNSON, J. S., AND M. J. LACKI. 2013. Habitat associations of Rafinesque's big-eared bats (*Corynorhinus rafinesquii*) and their lepidopteran prey in bottomland hardwood forests, *Canadian Journal of Zoology* 91:94-101.
- KALCOUNIS, M. C., AND R. M. BRIGHAM. 1998. Secondary use of aspen cavities by tree-roosting big brown bats, *Journal of Wildlife Management* 62:603-611.
- KERTH, G., K. WEISSMANN, AND B. KÖNIG. 2001. Day roost selection in female Bechstein's bats (*Myotis bechsteinii*): a field experiment to determine the influence of roost temperature, *Oecologia* 126:1-9.

- KLÜG, B. J. 2011. Thermoregulation and roost selection by the solitary, tree-roosting hoary bat (*Lasiurus cinereus*), University of Calgary, Calgary, Alberta.
- KLÜG, B. J., AND R. M. R. BARCLAY. 2013. Thermoregulation during reproduction in the solitary, foliage-roosting hoary bat (*Lasiurus cinereus*), *Journal of Mammalogy* 94:In Press.
- KÖRTNER, G., AND F. GEISER. 2000. The temporal organization of daily torpor and hibernation: circadian and circannual rhythms, *Chronobiology International* 17:103-128.
- KRÓL, E., M. MURPHY, AND J. R. SPEAKMAN. 2007. Limits to sustained energy intake. X. Effects of fur removal on reproductive performance in laboratory mice, *Journal of Experimental Biology* 210:4233-4243.
- KRÓL, E., AND J. R. SPEAKMAN. 2003. Limits to sustained energy intake VII. Milk energy output in laboratory mice at thermoneutrality, *Journal of Experimental Biology* 206:4267-4281.
- KUNZ, T. H. 1973. Population studies of the cave bat (*Myotis velifer*): reproduction, growth, and development, *Occasional Papers of the Museum of Natural History, The University of Kansas* 15:1-43.
- KUNZ, T. H. 1974a. Feeding ecology of a temperate insectivorous bat (*Myotis velifer*), *Ecology* 55:693-711.
- KUNZ, T. H. 1974b. Reproduction, growth, and mortality of the Vespertilionid bat, *Eptesicus fuscus*, in Kansas, *Journal of Mammalogy* 55:1-13.
- KUNZ, T. H., J. O. WITAKER, JR., AND W. D. WADANOLI. 1995. Dietary energetics of the insectivorous Mexican free-tailed bat (*Tadarida brasiliensis*) during pregnancy and lactation, *Oecologia* 101:407-415.
- KURTA, A. 1985. External insulation available to a non-nesting mammal, the little brown bat (*Myotis lucifugus*), *Comparative Biochemistry and Physiology* 82A:413-420.
- KURTA, A., AND R. H. BAKER. 1990. *Eptesicus fuscus*, *Mammalian Species* 356:1-10.
- KURTA, A., G. P. BELL, K. A. NAGY, AND T. H. KUNZ. 1989. Energetics of pregnancy and lactation in free-ranging little brown bats (*Myotis lucifugus*), *Physiological Zoology* 62:804-818.
- KURTA, A., AND T. H. KUNZ. 1987. Size of bats at birth and maternal investment during pregnancy, *Symposia of the Zoological Society of London* 57:79-106.

- KURTA, A., AND T. H. KUNZ. 1988. Roosting metabolic rate and body temperature of male little brown bats (*Myotis lucifugus*) in summer, *Journal of Mammalogy* 69:645-651.
- KUSCH, J., C. WEBER, S. IDELBERGER, AND T. KOOB. 2004. Foraging habitat preferences of bats in relation to food supply and spatial vegetation structures in a western European low mountain range forest, *Folia Zoologica* 53:113-128.
- LAUSEN, C. L., AND R. M. R. BARCLAY. 2002. Roosting behaviour and roost selection of big brown bats (*Eptesicus fuscus*) roosting in rock crevices in southeastern Alberta, *Canadian Journal of Zoology* 80:1069-1076.
- LAUSEN, C. L., AND R. M. BARCLAY. 2003. Thermoregulation and roost selection by reproductive female big brown bats (*Eptesicus fuscus*) roosting in rock crevices, *Journal of Zoology* 260:235-244.
- LAUSEN, C. L., AND R. M. R. BARCLAY. 2006. Benefits of living in a building: big brown bats (*Eptesicus fuscus*) in rocks versus buildings, *Journal of Mammalogy* 87:362-370.
- LAW, B. S., AND M. CHIDEL. 2007. Bats under a hot tin roof: comparing the microclimate of eastern cave bat (*Vespadelus troughtoni*) roosts in a shed and cave overhangs, *Australian Journal of Zoology* 55:49-55.
- LEWIS, S. E. 1995. Roost fidelity of bats: a review, *Journal of Mammalogy* 76:481-496.
- LOVEGROVE, B. G., G. KÖRTNER, AND F. GEISER. 1999. The energetic cost of arousal from torpor in the marsupial *Sminthopsis macroura* : benefits of summer ambient temperature cycles, *Journal of Comparative Physiology B* 169:11-18.
- LUČAN, R., AND J. RADIL. 2010. Variability of foraging and roosting activities in adult females of Daubenton's bat (*Myotis daubentonii*) in different seasons, *Biologia* 65:1072-1080.
- MCKECHNIE, A. E., R. A. M. ASHDOWN, M. B. CHRISTIAN, AND R. M. BRIGHAM. 2007. Torpor in an African caprimulgid, the freckled nightjar *Caprimulgus tristigma*, *Journal of Avian Biology* 38:261-266.
- MCLEAN, J. A., AND J. R. SPEAKMAN. 1999. Energy budgets of lactating and non-reproductive brown long-eared bats (*Pleotus auritus*) suggest females use compensation in lactation, *Functional Ecology* 13:360-372.
- MENZEL, M. A., T. C. CARTER, L. R. JABLONOWSKI, B. L. MITCHELL, J. M. MENZEL, AND B. R. CHAPMAN. 2001. Home range size and habitat use of big brown bats (*Eptesicus fuscus*) in a maternity colony located on a rural-urban interface in the southeast, *The Journal of the Elisha Mitchell Scientific Society* 117:36-45.

- MUNN, A. J., P. KERN, AND B. M. MCALLAN. 2010. Coping with chaos: unpredictable food supplies intensify torpor use in an arid-zone marsupial, the fat-tailed dunnart (*Sminthopsis crassicaudata*), *Naturwissenschaften* 97:601-605.
- NAMS, V. O. 2006. Locate III. Pacer Computer Software, Tatamagouche, Nova Scotia, Canada.
- NIEUWENHUIS, R., B. PELZER, AND M. TE GROENHUIS. 2012. influence.ME: Tools for detecting influential data in mixed effects models. R package version 0.9.
- NORBERG, U. M. 1987. Wing form and flight mode in bats, Pp. 43-56 in *Recent advances in the study of bats* (M. B. Fenton, P. Racey and M. V. Rayner, eds.). Cambridge University Press, Cambridge.
- NORBERG, U. M., AND J. M. V. RAYNER. 1987. Ecological morphology and flight in bats (Mammalia: Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation, *Philosophical Transactions of the Royal Society B: Biological Sciences* 316:335-427.
- O'DONNELL, C. F. J. 2002. Influence of sex and reproductive status on nocturnal activity of long-tailed bats (*Chalinolobus tuberculatus*), *Journal of Mammalogy* 83:794-803.
- O'FARRELL, M. J., AND E. H. STUDIER. 1973. Reproduction, growth, and development in *Myotis thysanodes* and *M. lucifugus* (Chiroptera: Vespertilionidae), *Ecology* 54:18-30.
- OELKRUG, R., G. HELDMAIER, AND C. W. MEYER. 2011. Torpor patterns, arousal rates, and temporal organization of torpor entry in wildtype and UCP1-ablated mice, *Journal of Comparative Physiology B* 181:137-145.
- PAUL, M. J., C. TUTHILL, A. S. KAUFFMAN, AND I. ZUCKER. 2010. Pelage insulation, litter size, and ambient temperature impact maternal energy intake and offspring development during lactation, *Physiology & Behavior* 100:128-134.
- PENNYCUICK, P. R. 1964. The effect on rats of chronic exposure to 34°C. IV. Reproduction, *Australian Journal of Biological Science* 17:245-260.
- POSTAWA, T., AND A. GAS. 2009. Do the thermal conditions in maternity colony roost determine the size of young bats? Comparison of attic and cave colonies of *Myotis myotis* in southern Poland, *Folia Zoologica* 58:396-408.
- PYKE, G. H., H. R. RULLIAM, AND E. L. CHARNOV. 1977. Optimal foraging: a selective review of theory and tests, *The Quarterly Review of Biology* 52:137-154.

- RACEY, P. A. 1973. Environmental factors affecting the length of gestation in heterothermic bats, *Journal of Reproduction and Fertility* 19:175-189.
- R CORE TEAM. 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- RACEY, P. A. 1988. Reproductive assessment in bats, Pp. 31-43 in *Ecology and Behavioral Methods for the Study of Bats* (T. H. Kunz, ed.). Smithsonian Institution Press, Washington, DC.
- RACEY, P. A., AND J. R. SPEAKMAN. 1987. The energy costs of pregnancy and lactation in heterothermic bats, *Symposia of the Zoological Society of London* 57:107-125.
- RACEY, P. A., AND S. M. SWIFT. 1981. Variations in gestation length in a colony of pipistrelle bats (*Pipistrellus pipistrellus*) from year to year, *Journal of Reproduction and Fertility* 61:123-129.
- RANCOURT, S. J., M. I. RULE, AND M. A. O'CONNELL. 2007. Maternity roost site selection of big brown bats in ponderosa pine forests of the Channeled Scablands of northeastern Washington State, USA, *Forest Ecology and Management* 248:183-192.
- RANDOLPH, P. A., J. C. RANDOLPH, K. MATTINGLY, AND M. M. FOSTER. 1977. Energy costs of reproduction in the cotton rat, *Sigmodon Hispidus*, *Ecology* 58:31-45.
- REYNOLDS, S. D., AND T. H. KUNZ. 2000. Changes in body composition during reproduction and postnatal growth in the little brown bat, *Myotis lucifugus* (Chiroptera: Vespertilionidae), *Ecoscience* 7:10-17.
- RIEK, A., G. KÖRTNER, AND F. GEISER. 2010. Thermobiology, energetics and activity patterns of the Eastern tube-nosed bat (*Nyctimene robinsoni*) in the Australian tropics: effect of temperature and lunar cycle, *Journal of Experimental Biology* 213:2557-2564.
- RYDELL, J. 1993. Variation in foraging activity of an aerial insectivorous bat during reproduction, *Journal of Mammalogy* 74:503-509.
- SANO, A. 2000. Postnatal growth and development of thermoregulative ability in the Japanese greater horseshoe bat, *Rhinolophus ferrumequinum nippon*, related to maternal care, *Mammal Study* 25:1-15.
- SCHMID, J., N. A. ANDERSON, J. R. SPEAKMAN, AND S. C. NICOL. 2003. Field energetics of free-living, lactating and non-lactating echidnas (*Tachyglossus aculeatus*), *Comparative Biochemistry and Physiology* 136A:903-909.

- SEVICK, S. H., AND E. H. STUDIER. 1992. Change in forearm curvature throughout the summer in female big brown bats, *Journal of Mammalogy* 73:866-870.
- SHELTON, M., AND J. E. HUSTON. 1968. Effects of high temperature stress during gestation on certain aspects of reproduction in the ewe, *Journal of Animal Science* 27:153-158.
- SMIT, B., J. G. BOYLES, R. M. BRIGHAM, AND A. E. MCKECHNIE. 2011. Torpor in dark times: Patterns of heterothermy are associated with the lunar cycle in a nocturnal bird, *Journal of Biological Rhythms* 26:241-248.
- SOLICK, D. I., AND R. M. R. BARCLAY. 2006. Thermoregulation and roosting behaviour of reproductive and nonreproductive female western long-eared bats (*Myotis evotis*) in the Rocky Mountains of Alberta, *Canadian Journal of Zoology* 84:589-599.
- SOLICK, D. I., AND R. M. R. BARCLAY. 2007. Geographic variation in the use of torpor and roosting behaviour of female western long-eared bats, *Journal of Zoology* 272:358-366.
- SPEAKMAN, J. R. 2000. The Cost of Living: Field Metabolic Rates of Small Mammals, Pp. 177-297 in *Advances in Ecological Research* (A. H. Fitter and D. G. Raffaelli, eds.). Academic Press, Toronto.
- SPEAKMAN, J. R. 2008. The physiological costs of reproduction in small mammals, *Philosophical Transactions of the Royal Society B: Biological Sciences* 363:375-398.
- SPEAKMAN, J. R., AND P. A. RACEY. 1987. The energetics of pregnancy and lactation in the brown long-eared bat, *Plecotus auritus*, Pp. 367-393 in *Recent Advances in the Study of Bats* (M. B. Fenton, P. A. Racey and J. M. V. Rayner, eds.). Cambridge University Press, New York, NY.
- SPEAKMAN, J. R., AND D. W. THOMAS. 2003. Physiological ecology and energetics of bats, Pp. 430-490 in *Bat Ecology* (T. H. Kunz and M. B. Fenton, eds.). The University of Chicago Press, Chicago.
- STUDIER, E. H. 1981. Energetic advantages of slight drops in body temperature in little brown bats, *Myotis lucifugus*, *Comparative Biochemistry and Physiology* 70A:537-540.
- STUDIER, E. H., AND M. J. O'FARRELL. 1972. Biology of *Myotis thysanodes* and *M. lucifugus* (Chiroptera: Vespertilionidae) - I. Thermoregulation, *Comparative Biochemistry and Physiology* 41A:567-595.

- STUDIER, E. H., S. H. SEVICK, J. O. KEELER, AND R. A. SCHENCK. 1994. Nutrient levels in guano from maternity colonies of big brown bats, *Journal of Mammalogy* 75:71-83.
- SYME, D. M., M. B. FENTON, AND J. ZIGOURIS. 2001. Roosts and food supplies ameliorate the impact of a bad summer on reproduction by the bat, *Myotis lucifugus* LeConte (Chiroptera: Vespertilionidae), *Ecoscience* 8:18-25.
- TRUNE, D. R., AND C. N. SLOBODCHIKOFF. 1976. Social effects of roosting on the metabolism of the pallid bat (*Antrozous pallidus*), *Journal of Mammalogy* 57:656-663.
- TURBILL, C., AND F. GEISER. 2006. Thermal physiology of pregnant and lactating female and male long-eared bats, *Nyctophilus geoffroyi* and *N. gouldi*, *Journal of Comparative Physiology B* 176:165-172.
- TURBILL, C., G. KÖRTNER, AND F. GEISER. 2003. Natural use of heterothermy by a small, tree-roosting bat during summer, *Physiological and Biochemical Zoology* 76:868-876.
- VAUGHAN, T. A., AND T. J. O'SHEA. 1976. Roosting ecology of the pallid bat, *Antrozous pallidus*, *Journal of Mammalogy* 57:19-42.
- VERBOOM, B., AND K. SPOELSTRA. 1999. Effects of food abundance and wind on the use of tree lines by an insectivorous bat, *Pipistrellus pipistrellus*, *Canadian Journal of Zoology* 77:1393-1401.
- VONHOF, M. J., AND R. M. R. BARCLAY. 1996. Roost-site selection and roosting ecology of forest-dwelling bats in southern British Columbia, *Canadian Journal of Zoology* 74:1797-1805.
- WANG, L. C. H. 1989. Ecological, physiological, and biochemical aspects of torpor in mammals and birds, Pp. 361-401 in *Animal Adaptations to Cold* (L. C. H. Wang, ed.). Springer-Verlag, New York.
- WANG, L. C. H., AND M. W. WOLOWYK. 1988. Torpor in mammals and birds, *Canadian Journal of Zoology* 66:133-137.
- WARNES, G. R. 2012. gmodels: Various R programming tools for model fitting. Version R package version 2.15.3.
- WEBB, P. I., J. R. SPEAKMAN, AND P. A. RACEY. 1993. The implication of small reductions in body temperature for radiant and convective heat loss in resting endothermic brown long-eared bats (*Plecotus auritus*), *Journal of Thermal Biology* 18:131-135.

- WILDE, C. J., M. A. KERR, C. H. KNIGHT, AND P. A. RACEY. 1995. Lactation in vespertilionid bats, *Symposia of the Zoological Society of London* 67:139-149.
- WILDE, C. J., C. H. KNIGHT, AND P. A. RACEY. 1999. Influence of torpor on milk protein composition and secretion in lactating bats, *Journal of Experimental Zoology* 284:35-41.
- WILKINSON, L. C., AND R. M. R. BARCLAY. 1997. Differences in the foraging behaviour of male and female big brown bats (*Eptesicus fuscus*) during the reproductive period, *Ecoscience* 4:279-285.
- WILLIAMS, C., L. SALTER, AND G. JONES. 2011. The winter diet of the lesser horseshoe bat (*Rhinolophus hipposideros*) in Britain and Ireland, *Hystrix, the Italian Journal of Mammalogy* 22:159-166
- WILLIS, C. K. R. 2007. An energy-based body temperature threshold between torpor and normothermia for small mammals, *Physiological and Biochemical Zoology* 80:643-651.
- WILLIS, C. K. R., AND R. M. BRIGHAM. 2003. Defining torpor in free-ranging bats: experimental evaluation of external temperature-sensitive radiotransmitters and the concept of active temperature, *Journal of Comparative Physiology B* 173:379-389.
- WILLIS, C. K. R., AND R. M. BRIGHAM. 2007. Social thermoregulation exerts more influence than microclimate on forest roost preferences by a cavity-dwelling bat, *Behavioral Ecology and Sociobiology* 62:97-108.
- WILLIS, C. K. R., R. M. BRIGHAM, AND F. GEISER. 2006. Deep, prolonged torpor by pregnant, free-ranging bats, *Naturwissenschaften* 93:80-83.
- WILLIS, C. K. R., J. E. LANE, E. T. LIKNES, D. L. SWANSON, AND R. M. BRIGHAM. 2005. Thermal energetics of female big brown bats (*Eptesicus fuscus*), *Canadian Journal of Zoology* 83:871-879.
- WIMSATT, W. A. 1944. Further studies on the survival of spermatozoa in the female reproductive tract of the bat, *Anatomical Record* 88:193-204.
- WOJCIECHOWSKI, M. S., M. JEFIMOW, AND E. TEGOWSKA. 2007. Environmental conditions, rather than season, determine torpor use and temperature selection in large mouse-eared bats (*Myotis myotis*), *Comparative Biochemistry and Physiology* 147A:828-840.
- WOODS, C. P. 2002. Ecological aspects of torpor use and inactivity during winter by common poorwills, University of Regina.

ZAHN, A. 1999. Reproductive success, colony size and roost temperature in attic-dwelling bat *Myotis myotis*, *Journal of Zoology*, London 247:275-280.

ZHAO, Z.-J., AND J. CAO. 2009. Effect of fur removal on the thermal conductance and energy budgets in lactating Swiss mice, *Journal of Experimental Biology* 212:2541-2549.

ZUUR, A. F., E. N. IENO, AND C. S. ELPHICK. 2010. A protocol for data exploration to avoid common statistical problems, *Methods in Ecology and Evolution* 1:3-14.

APPENDIX A: CAPTURES

Table A1. Capture data of big brown bats (*Eptesicus fuscus*) tracked in 2011 and 2012. Body mass and reproductive condition was assessed within 1 hour of capture. Number of days with complete data (n) does not represent number of days an individual carried an active transmitter because not all bats were tracked every day.

Bat	Body Mass (g)	Transmitter Mass (g;% body mass)	Capture Time	Release Time	Date of Capture	n	Reproductive Condition
145	19.6	0.72 (3.7)	21:45	23:00	25-May-12	3	Pregnant
353	20.7	0.72 (3.5)	21:50	23:15	25-May-12	3	Pregnant
485-1	19.9	0.72 (3.6)	22:45	23:45	25-May-12	2	Pregnant
559-1	20.1	0.72 (3.6)	21:57	23:10	01-Jun-12	2	Pregnant
613	19.7	0.72 (3.7)	21:55	22:33	01-Jun-12	1	Pregnant
635	18.5	0.72 (3.9)	22:00	23:25	01-Jun-12	1	Pregnant
698	18.6	0.72 (3.9)	22:53	23:54	01-Jun-12	2	Pregnant
734	22.7	0.72 (3.2)	23:25	0:11	01-Jun-12	2	Pregnant
382	22.5	0.72 (3.2)	22:55	0:30	08-Jun-11	2	Pregnant
512	22.8	0.72 (3.2)	22:40	23:28	08-Jun-11	8	Pregnant
766	23	0.72 (3.1)	21:55	22:33	08-Jun-12	8	Pregnant
786	21.8	0.72 (3.3)	21:59	22:49	08-Jun-12	2	Pregnant
805	23.5	0.72 (3.1)	22:00	23:10	08-Jun-12	2	Pregnant
822	20.3	0.72 (3.5)	22:00	22:58	23-Jun-12	2	Lactating
842	19.3	0.72 (3.7)	22:05	23:23	23-Jun-12	1	Lactating
865	20	0.72 (3.6)	22:15	0:35	23-Jun-12	1	Lactating
885	19.5	0.72 (3.7)	22:20	22:56	24-Jun-12	0 *	Lactating
526	19.1	0.65 (3.4)	22:25	1:25	30-Jun-12	3	Lactating
566	17.3	0.65 (3.8)	22:20	1:05	30-Jun-12	3	Lactating
584	20.7	0.65 (3.1)	22:30	1:45	30-Jun-12	7	Lactating
904	17.8	0.72 (4.0)	22:10	22:10	30-Jun-12	1	Lactating
922	19.5	0.72 (3.7)	22:15	0:48	30-Jun-12	1	Lactating
944	18.8	0.72 (3.8)	22:05	23:56	30-Jun-12	1	Lactating
963	18.2	0.72 (4.0)	22:00	23:30	30-Jun-12	2	Lactating
462	20.2	0.65 (3.2)	22:05	23:25	06-Jul-12	5	Lactating
485-2	20.7	0.65 (3.1)	22:10	23:48	06-Jul-12	2	Lactating
557-2	16.9	0.72 (4.3)	22:05	23:05	06-Jul-12	3	Lactating
90	22.4	0.72 (3.2)	1:10	1:30	10-Jul-11	3	Lactating
162	22.5	0.72 (3.2)	1:30	1:47	10-Jul-11	3	Lactating
281	23.7	0.72 (3.0)	2:15	2:50	10-Jul-11	2	Lactating
571	24.8	0.72 (2.9)	2:10	3:13	10-Jul-11	1	Lactating
981	19	0.72 (3.8)	21:55	20:35	17-Jul-12	2	Lactating

*Dropped transmitter early morning next day.

APPENDIX B: MODEL SELECTION AIC_c TABLES

Table B1. Torpor depth ($T_{\text{onset}}-T_{\text{sk}}$) model selection. Bolded values above the dashed line make up the confidence set ($\sum w_i = 0.95$) used for model averaging. K is the number of parameters in each model, logLikelihood is the goodness of fit of the model, AIC_c is the penalized ranking score, and ΔAIC_c is the difference in AIC_c from the top model to each subsequent model. w_i is the Akaike weight and ER is the number of times more likely the top model is better than each model. The confidence set of models was averaged following Burnham and Anderson (2002); Model averaged parameter estimate (β) and unconditional standard error ($\hat{\text{se}}$) with associated upper and lower 95% confidence intervals calculated. For model description, see Table 1.

Model	K	logLikelihood	AICc	ΔAIC_c	w_i	ER
T3	6	-155.1	323.9	0.00	0.27	
T9	6	-155.2	324.3	0.40	0.22	1.22
T4	5	-156.7	324.5	0.67	0.19	1.40
T1	5	-157.4	326.1	2.27	0.09	3.12
T10	8	-153.9	326.9	3.08	0.06	4.67
T7	6	-156.6	327.1	3.20	0.05	4.95
T2	3	-159.3	327.1	3.22	0.05	5.00
T6	6	-157.4	328.6	4.70	0.03	10.49
T8	5	-158.8	328.8	4.97	0.02	12.03
T5	5	-159.9	331.1	7.27	0.01	37.99
Model Averaging						
Parameter	β	$\hat{\text{se}}$	Upper CI	Lower CI		
Intercept	4.31	1.11	6.48	2.13		
RC	1.31	1.79	4.82	-2.20		
RT	2.72	1.47	5.59	-0.16		
pnf	-0.84	0.63	0.40	-2.07		
mdt	0.02	0.22	0.45	-0.42		

Table B2. Torpor duration ($\ln(\text{Torpor duration} + 1)$) model selection. Bolded values above the dashed line make up the confidence set ($\sum w_i = 0.95$) used for model averaging. For model description, see Table 1. For table description, see Table B1.

Model	K	logLikelihood	AICc	ΔAICc	w_i	ER
T4	5	-81.6	174.3	0.00	0.55	
T3	6	-81.2	176.2	1.83	0.22	2.49
T2	4	-84.3	177.5	3.18	0.11	4.89
T1	5	-83.4	178.0	3.70	0.09	6.36
T6	6	-83.8	181.3	6.93	0.02	31.90
T5	5	-86.5	184.3	10.00	0.00	148.41
T9	6	-87.1	188.0	13.63	0.00	909.37
T8	5	-89.5	190.2	15.90	0.00	>1000
T7	6	-88.8	191.4	17.03	0.00	>1000
T10	8	-88.3	195.7	21.41	0.00	>1000
Model Averaging						
Parameter	β	\hat{se}	Upper CI	Lower CI		
Intercept	4.781	0.2	5.3	4.31		
RT	0.923	0.3	1.7	0.16		
RC	0.397	0.4	1.2	-0.40		

Table B3. Torpor or no torpor model selection. Bolded values above the dashed line make up the confidence set ($w_i = 0.95$) used for model averaging. For model description, see Table 1. For table description, see Table B1.

Model	K	logLikelihood	AICc	Δ AICc	w_i	ER
T2	3	-48.2	102.8	0.00	0.27	
T8	4	-47.7	103.9	1.12	0.16	1.75
T4	4	-47.8	104.0	1.22	0.15	1.84
T5	4	-48.1	104.6	1.82	0.11	2.48
T1	4	-48.1	104.8	2.02	0.10	2.75
T9	5	-47.5	105.8	3.00	0.06	4.49
T7	5	-47.7	106.2	3.40	0.05	5.48
T6	5	-47.7	106.3	3.50	0.05	5.76
T3	5	-47.8	106.3	3.50	0.05	5.76
T10	7	-47.5	110.5	7.66	0.01	46.00
Model Averaging						
Parameter	β	\hat{se}	Upper CI	Lower CI		
Intercept	1.22	0.58	2.36	0.09		
PNF	-0.01	0.01	0.01	-0.03		
RT	-0.57	0.64	0.68	-1.81		
MDT	-0.03	0.06	0.09	-0.16		
RC	-0.18	0.64	1.06	-1.43		

Table B4. Torpor degree minute model selection. Bolded values above the dashed line make up the confidence set ($\sum w_i = 0.95$) used for model averaging. For model description, see Table 1. For table description, see Table B1.

Model	K	logLikelihood	AICc	ΔAICc	w_i	ER
T2	4	-64.9	138.6	0.00	0.59	
T1	5	-64.9	140.9	2.32	0.18	3.20
T4	5	-65.0	141.2	2.62	0.16	3.7
T3	6	-65.0	143.9	5.25	0.04	13.80
T5	5	-67.2	145.5	6.92	0.02	31.89
T6	6	-67.3	148.4	9.75	0.00	130.97
T8	5	-70.8	152.9	14.32	0.00	>1000
T9	6	-70.3	154.3	15.65	0.00	>1000
T7	6	-70.6	155.0	16.35	0.00	>1000
T10	8	-72.3	163.8	25.23	0.00	>1000
Model Averaging						
Parameter	β	\hat{se}	Upper CI	Lower CI		
Intercept	0.09	0.18	0.26	-0.44		
RC	0.23	0.33	0.88	-0.42		
RT	0.30	0.23	0.74	-0.15		

Table B5 Heterothermy index model selection. Bolded values above the dashed line make up the confidence set ($\sum w_i = 0.95$) used for model averaging. For model description, see Table 1. For table description, see Table B1.

Model	K	logLikelihood	AICc	ΔAICc	w_i	ER
T1	5	-181.4	373.7	0.00	0.40	
T2	4	-183.1	374.8	1.12	0.23	1.75
T3	6	-181.0	375.2	1.44	0.19	2.06
T4	5	-182.5	375.9	2.20	0.13	3.00
T5	5	-184.2	379.1	5.40	0.03	14.88
T6	6	-183.6	380.5	6.74	0.01	29.15
T7	6	-185.6	384.5	10.74	0.00	215.38
T8	5	-187.8	386.4	12.70	0.00	572.50
T9	6	-186.9	387.0	13.24	0.00	751.73
T10	8	-186.1	390.4	16.64	0.00	>1000
Model Averaging						
Parameter	β	$\hat{s}e$	Upper CI	Lower CI		
Intercept	2.81	0.58	3.94	1.68		
RC	1.15	0.87	2.83	-0.53		
RT	0.28	0.61	1.48	-0.93		

Table B6. Relative insect abundance model selection. Bolded values above the dashed line make up the confidence set ($\sum w_i = 0.95$) used for model averaging. For model description, see Table 1. For table description, see Table B1.

Model	K	logLikelihood	AIC	ΔAIC_c	w_i	ER
I1	8	-192.4	401.7	0.00	0.64	
I2	5	-196.9	404.18	2.40	0.19	3.32
I3	5	-197.2	404.6	2.90	0.15	4.27
I4	4	-200	408.3	6.59	0.02	26.93
I5	3	-210.3	426.8	25.09	0.00	>1000
I6	3	-210.9	427.9	26.19	0.00	>1000
I7	3	-215.6	437.2	35.49	0.00	>1000
I8	3	-220.5	447.1	45.39	0.00	>1000
I9	2	-222.1	448.3	46.63	0.00	>1000
I10	3	-222.1	450.3	48.59	0.00	>1000
Model Averaging						
Parameter	β	\hat{se}	Upper CI	Lower CI		
Intercept	0.81	0.724	2.22	-0.62		
Temp*Wind	0.01	0.002	0.01	0.001		
Temp	0.05	0.039	0.12	-0.03		
Wind	-0.10	0.037	-0.03	-0.18		
Moon	-0.02	0.016	0.11	-0.15		
Time	0.01	0.005	0.02	0.004		
Precip	-0.2	0.144	0.09	-0.48		

Table B7. Foraging duration model selection. Bolded values above the dashed line make up the confidence set ($\sum w_i = 0.95$) used for model averaging. For model description, see Table 1. For table description, see Table B1.

Model	K	logLikelihood	AIC	ΔAICc	w_i	ER
F1	6	-94.1	201.4	0.00	0.54	
F2	5	-96.2	203.2	1.77	0.22	2.43
F3	5	-96.5	203.7	2.27	0.17	3.13
F4	4	-99.1	206.8	5.41	0.04	14.94
F5	7	-96.4	208.2	6.79	0.02	29.79
F6	5	-99.9	210.5	9.07	0.01	93.41
F7	5	-101.0	212.7	11.27	0.00	280.61
F8	5	-101.6	214.0	12.57	0.00	537.52
F9	7	-99.9	215.4	13.99	0.00	>1000
F10	6	-101.7	216.4	15.00	0.00	>1000
F11	9	-100.8	222.0	20.56	0.00	>1000
Model Averaging						
Parameter	β	\hat{se}	Upper CI	Lower CI		
Intercept	-0.7	0.34	-0.03	-1.37		
Bouts	0.29	0.10	0.49	0.09		
Repro_cond	0.66	0.24	1.13	0.19		