

Signature page

Combinations of Reproductive, Individual, and Weather Effects Explain Torpor Patterns

Among Female Little Brown Bats (*Myotis lucifugus*)

By  
Nicole K. Besler

A Thesis Submitted to  
Saint Mary's University, Halifax, Nova Scotia  
in Partial Fulfillment of the Requirements for  
the Degree of Master of Science in Applied Science.

April, 2018, Halifax, Nova Scotia

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**ABSTRACT**

Torpor is a thermoregulatory strategy used by some small mammals to, in part, conserve energy during poor weather conditions and limited food. Some mammalian females may use torpor throughout reproduction, however, there are associated physiological and ecological costs and benefits. Torpor use may vary among individuals and result in different fitness consequences. The objective of my study was to identify and quantify variables that best explain variation in torpor patterns among individual female little brown bats (*Myotis lucifugus*). I used an information-theoretic approach to rank Bayesian models containing reproductive condition, individual, and weather variables based on their probability of explaining variation in torpor. Precipitation and wind were the most influential predictors of torpor frequency, whereas reproductive condition and individual were the best predictors of torpor duration, depth, and the heterothermy index. These results highlight the importance of including multiple intrinsic and extrinsic variables when evaluating thermoregulatory patterns.

April 30, 2018

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## **DEDICATION**

To the bats of Newfoundland, who endured unwanted handling to provide data for this thesis. I hope that white-nose syndrome never reaches you.

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## 1. INTRODUCTION

Thermoregulatory strategies are hypothesized to have evolved to help individuals maintain a net positive energy balance and sustain physiological function (Dell et al. 2011, Dowd et al. 2015). However, there are costs and benefits associated with different thermoregulatory strategies (Huey and Slatkin 1976, Humphries et al. 2003). Homeothermic endothermy, for example, involves endogenous (internal) heat produced metabolically to maintain body temperature (Scholander 1955, Guppy and Withers 1999). Internal heat production allows endotherms, such as mammals and birds, to sustain foraging and reproduction, despite environmental conditions (e.g., cold ambient temperatures) (Heinrich 1977, Kurta 1986, Dell et al. 2011). However, it is energetically costly to produce metabolic heat (McNab 2002, Angilletta et al. 2010), especially for small-bodied animals that have a high surface area to volume ratio which lose heat more rapidly to the environment than larger-bodied animals (Aschoff 1981). Additionally, reproduction further increases energetic demands (Bronson 1985, Gittleman and Thompson 1988, Daan et al. 1990), particularly for female mammals as pregnancy and lactation require more energy and nutrients than non-reproductive females (Millar 1978, Barclay 1994, Speakman 2008). To cope with high energetic demands, female mammals can either increase energy uptake or conservation (Bronson 1985, Gittleman and Thompson 1988), which can have direct implications for the fitness of individuals (Millar 1978, Speakman 2008).

Heterothermy is a thermoregulatory strategy employed by some small-bodied endotherms to conserve energy (Wang and Wolowyk 1988, Geiser and Ruf 1995, Geiser 2004). Heterothermic animals reduce energetic expenditure by entering a physiological state, referred to as torpor, where metabolic rate is lowered and consequently body

temperature is adjusted towards ambient temperature (Wang and Wolowyk 1988, Geiser and Ruf 1995, Geiser 2004). There are two forms of torpor found among mammals: daily torpor and hibernation (Wang and Wolowyk 1988, Geiser and Ruf 1995, Wilz and Heldmaier 2000, Geiser 2004). Typically, daily torpor is characterized as a heterothermic bout lasting less than 24 hours and hibernation is characterized as a heterothermic bout lasting several days to weeks (Wang and Wolowyk 1988, Geiser and Ruf 1995, Wilz and Heldmaier 2000). Daily torpor can result in substantial energy savings during times of inactivity, limited food, cold conditions, and hot and arid conditions (Wang and Wolowyk 1988, Song and Geiser 1997, Brice et al. 2002, Christian and Geiser 2007, Wojciechowski et al. 2007, Turbill and Geiser 2008, Brigham et al. 2012, Doucette et al. 2012, Smit et al. 2013). The energy savings accrued through daily torpor can facilitate fat storage for migration (Carpenter and Hixon 1988; Hiebert 1993), hibernation (Kunz et al. 1998, Sheriff et al. 2013), or reproduction (Hamilton and Barclay 1994, Grinevitch et al. 1995, Speakman 2008, Geiser and Brigham 2012).

Despite the energy-conserving advantage of torpor use, there are also costs associated with this thermoregulatory strategy (Racey and Swift 1981, McNab 1982, Kurta et al. 1987, Wilde et al. 1999). While reproduction is an energetically demanding period for female mammals (Millar 1978, Bronson 1985, Gittleman and Thompson 1988, Speakman 2008), the lowered metabolic rate during torpor slows fetal development and milk production, potentially delaying parturition and weaning (Racey and Swift 1981, McNab 1982, Kurta et al. 1987, Wilde et al. 1999). An extended gestation and weaning period may negatively impact juvenile development and survival (Racey and Swift 1981, Kunz et al. 1998, Wilde et al. 1999, Frick et al. 2010*b*). As such, females must balance the immediate energetic advantages of torpor use with the costs on their reproductive

output (Racey and Swift 1981, Grindal et al. 1992, Wilde et al. 1999). In response, heterothermic female mammals typically either forego torpor use or use shallow bouts of torpor for short durations during pregnancy and lactation (Geiser and Masters 1994, Lausen and Barclay 2003, Dzal and Brigham 2013, Rintoul and Brigham 2014).

Insectivorous bats in temperate regions (Chiroptera: Vespertilionidae) are good model organisms for understanding how heterothermic strategies can be used to increase survival and reproduction. These animals have high energetic demands due to their small size (typically 5-35 g), rely on fluctuating food sources (i.e., insects) (Black 1974, Anthony and Kunz 1977), and employ flight as locomotion (Schmidt-Nielsen 1972, Thomas and Suthers 1972). Flight is an energetically expensive mode of locomotion and requires a metabolic rate greater than that of a non volant mammal of similar body mass during exercise (Schmidt-Nielsen 1972, Thomas and Suthers 1972). Additionally, flight limits the amount of fat that can be stored as a higher body mass results in a higher wing loading (Kalcounis and Brigham 1995), which requires more power and energy to sustain flight (Norberg and Rayner 1987). Given the high energetic demands and physical limitations on fat storage (Schmidt-Nielsen 1972, Thomas and Suthers 1972, Norberg and Rayner 1987, Kalcounis and Brigham 1995), temperate insectivorous bats may need to employ a variety of heterothermic responses to survive and reproduce (Audet and Fenton 1988, Hamilton and Barclay 1994, Angilletta et al. 2010). Despite the physiological costs of torpor, temperate bat species are among the few heterothermic groups that use torpor during both pregnancy and lactation in the wild (Audet and Fenton 1988, Chruszcz and Barclay 2002, Lausen and Barclay 2003, Solick and Barclay 2006, Dzal and Brigham 2013, McAllan and Geiser 2014, Rintoul and Brigham 2014), with the other group being small marsupials (Geiser et al. 2008, McAllan and Geiser 2014). To our knowledge, there

have been no studies to date that have supported this finding in free-ranging populations of subtropical and tropical species, despite the use of torpor among non-reproductive individuals and during non-reproductive periods in these regions (Bartels et al. 1998, Coburn and Geiser 1998, Geiser and Brigham 2000, Stawski and Geiser 2010, Geiser and Stawski 2011, Stawski et al. 2014). Differences in torpor use in temperate vs subtropical and tropical bat species suggests that unpredictable environments may be an important selective pressure on thermoregulatory strategies (McAllan and Geiser 2014).

The effect of reproductive condition and weather on torpor use by females of temperate bat species have been extensively characterized (Audet and Fenton 1988, Hamilton and Barclay 1994, Chruszcz and Barclay 2002, Willis et al. 2006, Solick and Barclay 2007, Dzal and Brigham 2013, Johnson and Lacki 2014, Rintoul and Brigham 2014, Czenze et al. 2017). However, these patterns are inconsistent for pregnant and lactating females (Audet and Fenton 1988, Chruszcz and Barclay 2002, Lausen and Barclay 2003, Dzal and Brigham 2013, Rintoul and Brigham 2014) and there are discrepancies about the importance of weather variables in explaining torpor patterns (Dzal and Brigham 2013, Johnson and Lacki 2014, Rintoul and Brigham 2014, Czenze et al. 2017). The inconsistencies can, in part, be explained by differences among species and geography (Solick and Barclay 2007). For example, lactating hoary bats (*Lasiurus cinereus*) maintain lower body temperatures than lactating big brown bats (*Eptesicus fuscus*), and the variation between the species may be due to their different roosting behaviours (Lausen and Barclay 2003, Klug and Barclay 2013). Individuals of populations of female western long-eared bats (*Myotis evotis*) roosting in the mountains used torpor to less of an extent than populations in the prairies, and the variation might be explained by differences in climate (e.g., aridity) and roost types available between the

locations (Solick and Barclay 2007). While variation among species and study sites have been noted, differences in energy acquisition among individuals within a reproductive condition may be important for explaining variation in torpor use. The costs and benefits of torpor use may depend on the multiplicative effects of reproductive condition, inter-individual variation, and weather (Dzal and Brigham 2013, Johnson and Lacki 2014, Rintoul and Brigham 2014).

Reproductive condition may explain variation in thermoregulatory strategies among bats. Energetic demands for female mammals varies throughout reproduction, with lactation being the most energetically costly stage (Millar 1978, Racey and Swift 1981, Wilde et al. 1999, McNab 2002, Speakman 2008), and offspring survival is dependent on the timing of parturition and weaning as juveniles need to accumulate sufficient fat reserves for winter (Kunz et al. 1998, Frick et al. 2010*b*). Therefore, torpor use in each reproductive stage may depend on the fitness consequences (Millar 1978, Racey and Swift 1981, Wilde et al. 1999, McNab 2002, Speakman 2008). For example, pregnant little brown bats (*Myotis lucifugus*) in New York and New Mexico, USA have been found to use torpor at shallower depths and for shorter durations than lactating females (Studier and O'Farrell 1972, Dzal and Brigham 2013). This suggests that, for this species in those study systems, the high energetic demands during lactation necessitates greater reliance on torpor use than during pregnancy and that the cost of delaying parturition is higher than reduced milk production (Studier and O'Farrell 1972, Dzal and Brigham 2013). However, in western long-eared bats (*Myotis evotis*) in Alberta, Canada, torpor in lactating females was at shallower depths than pregnant females (Chruszcz and Barclay 2002). This suggests that for this species deep torpor during lactation may be avoided to maximize juvenile growth at a cost to maternal energy status (Chruszcz and



Barclay 2002). Torpor patterns also vary intraspecifically. For example, in big brown bats (*Eptesicus fuscus*) in Alberta and Saskatchewan, Canada, lactating females used torpor for shorter durations and greater depths than pregnant females in some cases (Audet and Fenton 1988, Lausen and Barclay 2003), whereas other cases the opposite was true (Rintoul and Brigham 2014). Inter- and intra-specific variation in torpor use may be due to the confounding influence of individual physiology and weather (Chruszcz and Barclay 2002, Dzal and Brigham 2013, Johnson and Lacki 2014, Czenze et al. 2017).

Inter-individual variation in energy acquisition may, in part, explain the differences in thermoregulatory strategies found among female bats in the same reproductive condition (White and Kearney 2013, Dammhahn et al. 2016). For example, genetically determined differences in basal metabolic rates and behaviour, such as boldness and aggression, influences energetic expenditure and intake (Biro and Stamps 2008, White and Kearney 2013). The energy balance of an individual influences its body condition, which may affect torpor use in heterothermic species (Rambaldini and Brigham 2008, Stawski and Geiser 2010, Kobbe et al. 2011, Vuarin et al. 2013). In some cases, torpor is used in response to energetic constraints imposed by having a low body mass (Christian and Geiser 2007, Rambaldini and Brigham 2008). However, energy may be required to return to normal body temperature, therefore, individuals in poor body condition may be limited in torpor use (Terrien et al. 2009, Stawski and Geiser 2010, Kobbe et al. 2011, Vuarin et al. 2013). Furthermore, individuals may use different thermoregulatory strategies in response to environmental fluctuations (Hickey and Fenton 1996). For example, individual female hoary bats (*Lasiurus cinereus*) varied the frequency of torpor use when ambient temperature was between 13 and 21°C, but consistently used torpor at lower temps and never did at higher ones (Hickey and Fenton

1996). The differences in torpor frequency may be due to variation in body condition and foraging strategies, in which individuals with low fat reserves may forego torpor use to increase time spent foraging (Hickey and Fenton 1996, Kobbe et al. 2011, Vuarin et al. 2013). Therefore, differences in energy acquisition among individuals may result in variation in torpor use within the same reproductive condition, with some individuals employing different thermoregulatory strategies in response to fluctuations in weather (Hickey and Fenton 1996, White and Kearney 2013, Dammhahn et al. 2016).

Weather conditions may increase energetic demands and influence torpor use among reproductive female bats in regions with cool climates (Grindal et al. 1992, Dzal and Brigham 2013, Klug and Barclay 2013, Johnson and Lacki 2014). Low ambient temperatures and wind increase heat loss (Scholander et al. 1950, Aschoff 1981) while precipitation reduces the insulation of fur (Tuttle and Stevenson 1982, Schmidt-Nielsen 1997, Voigt et al. 2011). In addition to thermoregulatory costs, low ambient temperatures (<10°C) and rainfall reduces insect (i.e., prey) activity and, therefore, the potential for energy acquisition (Taylor 1963, Anthony et al. 1981, Racey et al. 1987). The interactive effects of low ambient temperatures, wind, and precipitation may have a stronger influence on energetic expenditure than each variable has on their own (Klug and Barclay 2013, Klug-Baerwald et al. 2016). For example, the interaction of wind and ambient temperature influenced torpor duration and depth and was associated with reduced foraging in hoary bats (*Lasiurus cinereus*) in Manitoba, Canada (Klug and Barclay 2013). Some authors have found weather variables (minimum ambient temperature, wind, and precipitation) to be an important predictor for the duration of torpor and drop in body temperature in temperate bats (depth) (Dzal and Brigham 2013, Klug and Barclay 2013, Johnson and Lacki 2014). However, other authors found that ambient temperature did not

explain torpor patterns (Rintoul and Brigham 2014, Czenze et al. 2017). The discrepancies of weather variables influence on torpor patterns may be due to the inconsistencies of weather variables measured among studies and the effects of multiple weather conditions may need to be considered (Klug and Barclay 2013, Klug-Baerwald et al. 2016). Additionally, weather conditions may vary among reproductive stages (Chruszcz and Barclay 2002) and torpor use may be necessary for surviving poor weather conditions and optimizing reproductive timing (Willis et al. 2006). For example, in regions with cold spring weather, torpor use during pregnancy may be advantageous as females can conserve energy and time parturition to coincide with the most favourable environmental conditions for offspring survival (Willis et al. 2006). In this case, torpor may be used less during lactation than pregnancy to ensure juvenile growth before hibernation (Audet and Fenton 1988, Kunz et al. 1998, Lausen and Barclay 2003, Solick and Barclay 2007, Frick et al. 2010b). Thus, the costs and benefits of torpor use for reproductive females likely depend on energetic demands, with below average weather conditions and cold climates potentially increasing the necessity of torpor use (Audet and Fenton 1988, McNab 2002, Lausen and Barclay 2003, Willis et al. 2006).

Newfoundland is on the eastern edge of the range of little brown bats (*Myotis lucifugus*) (Fenton and Barclay 1980), where the climatic conditions may place greater selection pressure on thermoregulatory and reproductive strategies relative to populations at the core of the species' range (Boyles et al. 2016). The climate is cold and wet, making it a good study system for understanding how heterothermic species respond to energetic constraints from environmental conditions. The daily average summer temperature is 14 °C (Banfield 1983), which is below the summer averages found at the core of the range of *M. lucifugus* (Schweingruber et al. 1991, Curriero et al. 2002). Annual precipitation is

1200-1700 mm (Banfield 1983) and the average wind speed is 20 km/hr (Khan and Iqbal 2004), which are above the averages typically found at the core of the range of *M. lucifugus* (Karl et al. 1993, National Climatic Data Center 1998). Additionally, the last frost day typically occurs in mid to late May (Banfield 1983), resulting in a delay to the onset of warm temperatures. The cold spring weather in Newfoundland compared to locations at the core of the range of *M. lucifugus* may result in these populations employing different thermoregulatory strategies than other populations of *M. lucifugus*.

Given the lack of consensus and the knowledge that multiple factors may influence torpor use in free-ranging bats (Dzal and Brigham 2013, Johnson and Lacki 2014, Rintoul and Brigham 2014), the objective of this study was to identify and quantify intrinsic and extrinsic variables that best explain variation in torpor use among female little brown bats (*Myotis lucifugus*). Most studies include reproductive condition and weather as variables in studying torpor in temperate bat species (Dzal and Brigham 2013, Johnson and Lacki 2014, Rintoul and Brigham 2014), however, the effect of belonging to an individual has yet to be examined as an explanatory variable for torpor use. Therefore, I hypothesized that (1) reproductive condition, (2) inter-individual variation, and (3) weather variables would explain differences in torpor frequency, duration, depth, and heterothermy index. Thermoregulation is not a bi-modal phenomenon but is better described as a continuum, which makes explaining a cut-off between normal body temperature and torpid temperature challenging (Boyles et al. 2011). Therefore, I measured the heterothermy index (HI), a metric that quantifies variation in body temperature, as it accounts for all measured temperature data and not only values below an arbitrary cut-off (Boyles et al. 2011). Given that torpor use may delay parturition and weaning (Racey and Swift 1981, McNab 1982, Kurta et al. 1987, Wilde et al. 1999), I

predicted that pregnant and lactating females would use torpor less frequently, for shorter durations, at shallower depths, and have a lower HI than post-lactating and non-reproductive. I expected greater torpor use during pregnancy compared to lactation as delaying parturition may not be as costly as delaying weaning in this study system, given the delayed onset to warm ambient temperatures, and likely higher insect activity, in Newfoundland. Therefore, I predicted that pregnant females would use torpor more frequently, for longer durations, at greater depths, and have a higher HI than lactating females. Given that physiological variation exists among individuals (e.g., metabolic rate) and likely affects energy acquisition (Hickey and Fenton 1996, White and Kearney 2013, Dammhahn et al. 2016), I predicted inter-individual variation in torpor use under the same reproductive conditions. Based on my prediction, I further hypothesized that body condition would explain differences in torpor patterns among individuals. I predicted that the body condition index would be positively correlated with torpor duration, depth, and HI as energy may be essential to arouse from torpor (Terrien et al. 2009, Stawski and Geiser 2010, Kobbe et al. 2011, Vuarin et al. 2013). Due to environmental conditions affecting energetic demands (Scholander et al. 1950, Tuttle 1976, Aschoff 1981), I predicted that low ambient temperatures, high wind speed, and precipitation would be associated with increased torpor frequency, duration, depth, and HI values by individuals.

## **2. METHODS**

### **2.1 Study Species**

Little brown bats (*Myotis lucifugus*) are well-studied insectivorous bats found across North America, from Newfoundland to British Columbia in Canada and Alaska to Mexico (Fenton and Barclay 1980, Crampton and Barclay 1998). *Myotis lucifugus*

hibernates over winter in caves and abandoned mines and the length of the hibernation season is dependent on geographic location and weather (Fenton and Barclay 1980). Mating occurs in autumn, however, ovulation and fertilization are delayed until arousal from hibernation in the following spring (Fenton and Barclay 1980). After hibernation, reproductive females frequently make use of anthropogenic structures, such as bat boxes and buildings, where they congregate in large maternity groups (Davis and Hitchcock 1965, Fenton and Barclay 1980, Anthony et al. 1981). Males and non-reproductive females typically roost alone or in small groups, separate from reproductive females (Fenton and Barclay 1980, Broders and Forbes 2004). Females give birth to one pup per year typically from late May to early July, although there is variation in the timing of parturition based on geographic location (Fenton and Barclay 1980, Barclay et al. 2004, Frick et al. 2010b). Reproductive rates also vary depending on geographical location and range from 49-95% (Slough and Jung 2008, Frick et al. 2010b, Reimer 2013, Kaupas 2016).

*Myotis lucifugus* has recently been listed as endangered in Canada under the Species At Risk Act (COSEWIC 2014) due to the effects of white-nose syndrome. White-nose syndrome is a fungal disease caused by *Pseudogymnoascus destructans* that disrupts the depth and duration of torpor during hibernation, causing bats to deplete fat stores more rapidly than they normally would (Blehert et al. 2009, Reeder et al. 2012). From 2005-2011, over one million *M. lucifugus* in North America have succumbed to the disease and a 78% reduction in bat activity has been observed (Blehert et al. 2009, Frick et al. 2010a, Dzal et al. 2011). Populations in Newfoundland have not yet been affected and this study system provides an opportunity to collect thermoregulatory data on uninfected individuals.

## 2.2 Study Site

The research took place in and around Salmonier Nature Park, Newfoundland (47°15'53.28"N, 53°17'2.04"W) which is a 14.6 km<sup>2</sup> protected area comprised of peatland and boreal forest (Roberts 1983). One major road runs north-south along the west side of the park, with cabins and homes along on the west side. There are 11 bat boxes distributed across 3 zones (with 4, 4 and 3 boxes per zone) that are used by free-ranging female *M. lucifugus* (Figure 1). The zones were linearly distributed with the first zone being about 170 m from the second zone and 1200 m from the third zone. The bat boxes were located in openings alongside forest edges or buildings. The height of the bat box opening from the ground was 3.6 m for zone 1, 2.4 or 2.5 m for zone 2, and 2.5m for zone 3.

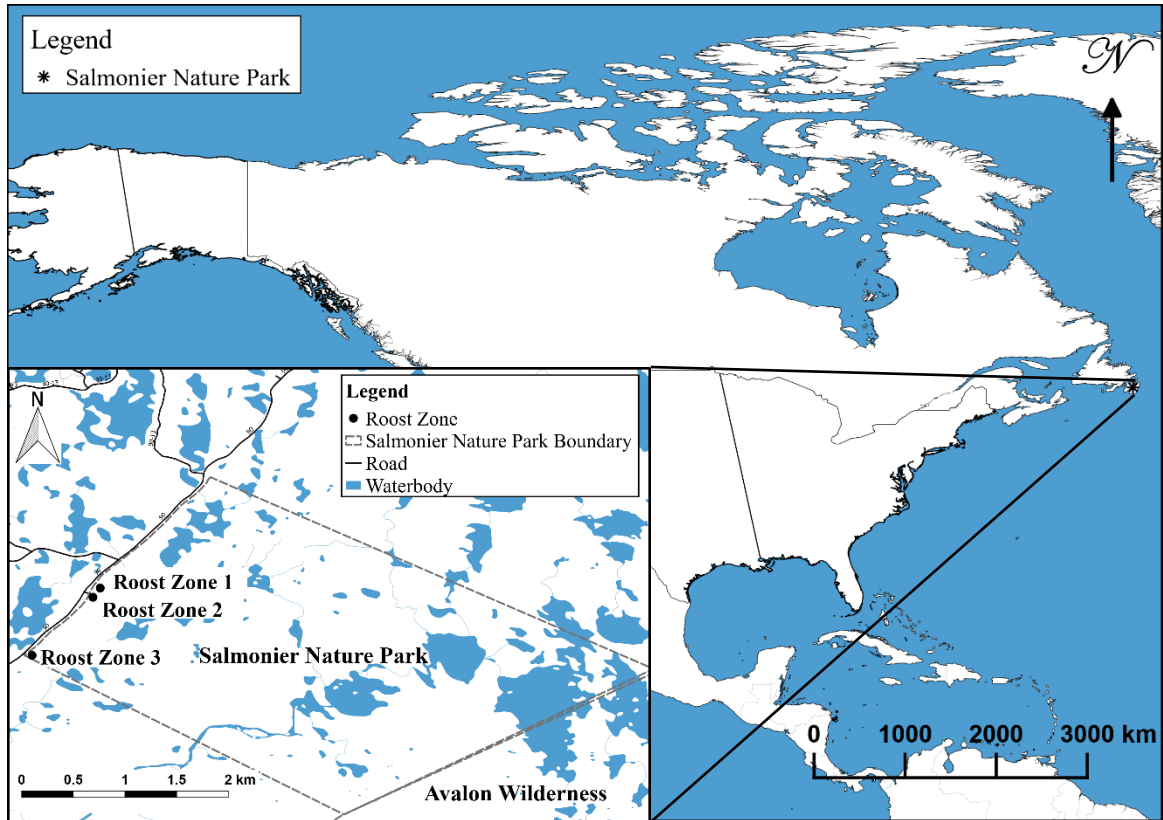


Figure 1. Study site at Salmonier Nature Park, Newfoundland where 11 bat boxes are located within three roost zones. The black circles in the inset represent each roost zone and the dashed grey line represents the park boundary.

### 2.3 Data Collection

Mist nets (Avinet Inc., Dryden, New York, U.S.A.) were used to capture *M. lucifugus* from June 11 to August 13, 2016 and May 20 to August 01, 2017. Upon capture, mass and forearm length were measured and individuals were assigned to a reproductive class. Pregnancy was determined by gently palpating the abdomen to detect a fetus. Bats were considered lactating if bare patches around the nipples were present and milk could be expressed and post-lactating if there was hair regrowth around the



nipples and milk could not be expressed (Racey and Swift 1981, Racey 1988). For non-pregnant individuals captured less than an hour after emergence, a body condition index (BCI) was calculated by dividing body mass by forearm length (average of three measurements) (Pearce et al. 2008). Pregnant individuals and individuals that potentially had food in their stomach were not included in body condition index calculations due to the fetus and stomach contents overestimating BCI (Jonasson and Willis 2011).

Additionally, a passive integrated transponder (PIT) tag (Trovan Micro Transponder; Dorset Group, Weverij 26, Aalten, The Netherlands) was inserted sub-dermally between the scapulae for individual identification (Patriquin et al. 2010, Burns and Broders 2015). Pre-calibrated temperature-sensitive radio-transmitters (Pip31; Lotek Wireless Inc., Newmarket, ON, Canada), weighing 0.37 g, were used to measure skin temperature ( $T_{sk}$ ) as an indicator of body temperature ( $T_b$ ) (Barclay et al. 1996). Transmitters were attached between the scapulae of bats using surgical cement (Torbot Group Inc., Cranston, Rhode Island, U.S.A.) after trimming the fur. I glued transmitters to 60 females, including two non-reproductive, 17 pregnant, 19 lactating, and 18 post-lactating females. Six other transmitters were glued on individuals that could not be confidently assigned as pregnant (not-obviously pregnant category) because in mid June, it was not possible to detect the presence of a fetus. The not-obviously-pregnant category was used to determine torpor patterns of females in early spring and potentially during early pregnancy. All handling procedures were done in accordance with the Canadian Council on Animal Care, approved by Saint Mary's University Animal Care Committee and under a permit from the province of Newfoundland and Labrador (permit # WLR2016-12 and WLR2017-16).

In each roost zone, ambient temperature ( $T_a$ ) and relative humidity (%rh) was recorded every 10 minutes using temperature and humidity data loggers ( $\pm 0.5^\circ\text{C}$ ,

Hygrochron iButton, DS1923, Embedded Data Systems, Lawrenceburg, KY, U.S.A.) placed in the shade, 2 m above the ground and within 5 m of the bat boxes. Daily maximum wind speed (km/hr) and total precipitation (mm) data was taken from the nearest weather station that logs data (St. John's; 47°37' N, 52°45' W; Environment Canada 2016, 2017; 57 km from Salmonier Nature Park). In 2017, maximum wind speed (km/hr) and total precipitation (mm) data were recorded daily from a weather station closer to the study site (Brigus Junction; 47°26' N, 53°33' W; Weather Underground, 2017; 26 km from Salmonier Nature Park), however, this weather station does not log data for >1 day and could not be used for 2016. Bat box temperature was logged every 10 minutes using temperature data loggers ( $\pm 0.5^{\circ}\text{C}$ , Thermochron iButton, DS1921G-F5, Embedded Data Systems) placed two inches inside each bat box throughout the study period. The iButtons were wrapped in plastic wrap to reduce the intensity of ultrasound emitted (Willis et al. 2009).

Skin temperature data were collected each day a transmitter was active or until it fell off. Data logging receivers (SRX800-D1 and SRX400; Lotek Wireless Inc.) and three- and five-element Yagi antennas were placed below bat boxes to record the inter-pulse intervals of the transmitters every 10 minutes. The inter-pulse intervals of the transmitters were converted to temperature based on the transmitter-specific calibration curve. In some cases, logging receivers were not able to log the inter-pulse interval of a transmitter and a voice recorder (HTC One M8; HTC, New Taipei City, Taiwan) was used to record the transmitter beeps from a manual receiver (SRX800; Lotek Wireless Inc.) (Kaupas 2016). The number of beeps per minute were manually counted from the recordings at 10 minute intervals and from these I calculated interpulse interval.

## 2.4 Defining Torpor

Current methods for defining torpor based on  $T_{sk}$  are biased for at least some individuals, as  $T_{sk}$  can be unreliable for measuring  $T_b$  (body temperature) and may be influenced by environmental variables (e.g., temperature), resulting in differences from  $T_b$  up to 6 °C (McKechnie et al. 2007, Willis 2007). Additionally, metabolically determined thresholds cannot be inferred from skin temperature without  $T_b$  measurements (Willis 2007). The active temperature, defined as the  $T_{sk}$  10 minutes before emergence (Barclay et al. 2001), was not reliable as bats may emerge torpid (Willis and Brigham 2003). The modal method, defined as a threshold of 3 °C less than the mode of recorded  $T_{sk}$  (McKechnie et al. 2007), was unreliable for individuals that spent a day, or consecutive days, in torpor. The modal method, however, provided the most reasonable threshold for individuals using torpor for less than a day. Therefore, I used a method similar to the modal method, with a threshold set at 3 °C less than the 80<sup>th</sup> percentile of  $T_{sk}$  for all days for each individual, to get a conservative estimate of torpor frequency, duration, and depth. This resulted in a similar threshold as the modal method for most individuals but had a more reasonable threshold for individuals who maintained low temperatures for prolonged periods.

A bat was classified as torpid anytime  $T_{sk}$  fell below the temperature threshold ( $T_{onset}$ ) for  $\geq 2$  consecutive readings (20 min). In cases where a bat was not present at a roost over-night, a bat-day was defined as the final time a bat arrived at a roost until it emerged the following night. If a bat did not leave the roost overnight, then a bat-day was defined as starting at midnight and ending at 23:50 on the same day. Bat days missing  $>5$  consecutive  $T_{sk}$  readings (50 min) were not used in the analysis. Torpor frequency was calculated for each individual and was measured as the proportion of bat days for which

$T_{sk}$  dropped below the threshold. Torpor duration was measured as the number of minutes per day for which  $T_{sk}$  was below  $T_{onset}$ . Depth of torpor was defined as the maximum number of degrees ( $^{\circ}\text{C}$ ) that  $T_{sk}$  was below  $T_{onset}$ . The heterothermy index (HI) is the degree that  $T_{sk}$  fluctuates around the modal  $T_{sk}$  (Boyles et al. 2011) and was calculated for each bat day. Given that the  $T_{onset}$  used may potentially over- or under-estimate torpor use,  $T_{sk}$  patterns were qualitatively identified based on the magnitude of  $T_{sk}$  drop and length of low  $T_{sk}$ . The  $T_{sk}$  patterns were used to evaluate the accuracy of the torpor threshold in identifying torpor patterns.

## 2.5 Statistical Analysis

Statistical analyses were conducted in R version 3.4.2 (R Core Team 2016). The R package runjags version 2.0.4-2 (Denwood and Plummer 2016) was used to interface JAGS version 4.2.0 (Plummer 2003). I used a multi-model inference and information-theoretic approach (Burnham and Anderson 2002) to determine which variable hypothesized to be important (individual, reproductive condition, and weather variables), or combinations of these variables best explain variation in torpor patterns (frequency, depth, duration, and HI). Analyses were conducted using a Bayesian approach. Bayesian inference estimates the probability of a model parameter being a certain value given the data (Ellison 2004, Gelman et al. 2014, Kruschke 2014). Prior probability distributions are made to represent the range of potential values each model parameter can take, and the associated likelihoods (Ellison 2004, Gelman et al. 2014, Kruschke 2014). These priors are then used to reassign probabilities across possibilities for each parameter (Ellison 2004, Gelman et al. 2014, Kruschke 2014). Markov chain Monte Carlo (MCMC) methods randomly sample parameter values from a probability distribution to

approximate the posterior estimate distribution of a parameter (Gelman et al. 2014, Kruschke 2014). The resulting distribution of posterior estimates within the 95% highest density interval (HDI), where points within the interval have a higher probability density than points outside the interval, were used to determine the likelihood of model posterior estimates (Ellison 2004, Gelman et al. 2014, Kruschke 2014). The mean distribution value of the posterior estimates indicates the most likely value based on the collected data and specified prior beliefs (Gelman et al. 2014, Kruschke 2014). Hierarchical models account for parameters that have values that are not independent from one another by having each category within a parameter come from a single distribution (hyperprior) (Gelman et al. 2014, Kruschke 2014). My study used weakly informed prior distributions (relatively uniform) as I assumed no effect of the predictor variables on the predicted variable, which avoids bias on the resulting posterior distributions (Gelman et al. 2014, Kruschke 2014).

First, I compared weather variables and torpor characteristics between 2016 and 2017 to determine the effects of year on torpor patterns and whether data from both years could be combined. To compare the differences in mean weather variables (temperature, humidity, wind, and precipitation) between 2016 and 2017, I conducted a one-metric predicted variable with one-nominal variable analysis that had the following equation:

$$\mu_i = \beta_0 + \sum_j \beta_{1[j]} x_{[j]}$$

Where  $\beta_0$  is the mean value of  $y$  across all groups and  $\beta_1$  is the deflection above or below the mean value for each group within the predictor variable (Gelman et al. 2014, Kruschke 2014). The predicted values ( $\mu_i$ ) for each weather variable ( $y$ ) came from a normal distribution with a mean ( $\mu$ ) of zero and a standard deviation that came from a

gamma distribution. The prior distributions of  $\beta_0$ , and  $\beta_1$  (year) were came from a normal distribution with a mean ( $\mu$ ) of zero and a high standard deviation, thereby assuming equal probabilities across possible values (Gelman et al. 2014, Kruschke 2014). Year was considered a nominal variable as I was only interested in the difference between two groups and not the order that they occurred in. The model was made hierarchical with each year coming from a normal distribution centered over zero.

To test if torpor duration, depth, and HI depended on year for individuals in each reproductive condition (lactating, post-lactating, and not-obviously pregnant), I conducted a one-metric predicted variable with multiple nominal predictor variables analysis that had the following equation:

$$\mu_i = \beta_0 + \sum_j \beta_{1[j]} x_{1[j]} + \sum_k \beta_{2[k]} x_{2[k]} + \sum_l \beta_{3[l]} x_{3[l]}$$

Where  $\beta_0$  is the mean value of  $y$  across all groups for all predictor variables and  $\beta_1$  (year),  $\beta_2$  (reproductive condition), and  $\beta_3$  (individual) are the deflections above or below the mean value for each group within each predictor variable (Gelman et al. 2014, Kruschke 2014). The predicted values ( $\mu_i$ ) for the dependent variables torpor duration, depth, and HI came from a normal distribution with a mean ( $\mu$ ) of zero and a standard deviation that came from a gamma distribution. The prior distributions for  $\beta_0$ ,  $\beta_1$  (year),  $\beta_2$  (reproductive condition), and  $\beta_3$  (individual) came from a normal distribution with a mean ( $\mu$ ) of zero and a high standard deviation, thereby assuming equal probabilities across possible values (Gelman et al. 2014, Kruschke 2014). Repeated measures were taken from most individuals; therefore, the models were made hierarchical with each year, each reproductive condition, and each individual coming from a normal distribution centered

over zero. Pregnant and non-reproductive females were not used in this comparison as useable data was not present from these groups in both years.

Next, I tested if weather conditions (mean and minimum ambient temperature, maximum wind speed, and precipitation) were independent of reproductive (sampling) period. For each weather variable, I conducted a one-metric predicted variable and one nominal predictor variable (see equation on page 18). The predicted values ( $\mu_i$ ) for each weather variable ( $y$ ) came from a normal distribution with a mean ( $\mu$ ) of zero and a standard deviation that came from a gamma distribution. The prior distributions of  $\beta_0$ , and  $\beta_{1[j]}$  (reproductive period) came from a normal distribution with a mean ( $\mu$ ) of zero and a high standard deviation, thereby assuming equal probabilities across possible values (Gelman et al. 2014, Kruschke 2014). Reproductive period was made a nominal predictor variable as I was only interested in the differences among periods, not the order that they occurred in. The models were made hierarchical with each reproductive period coming from a normal distribution centered over zero.

After determining the sample characteristics, multi-model selection using information-criterion was conducted for each torpor pattern (frequency, duration, depth, and HI). I generated a set of 14 *a priori* models that included each predictor variable (individual, reproductive condition, and weather variables) on their own and in combinations (Table 1). Maximum wind speed (km/hr) was combined with daily minimum ambient temperature ( $^{\circ}\text{C}$ ) and total daily precipitation (mm), given the effects of the interactions of these variables on torpor use and bat activity (Stawski et al. 2009, Dzal and Brigham 2013, Klug and Barclay 2013, Johnson and Lacki 2014, Klug-

Baerwald et al. 2016). I ran the models for torpor frequency (torpid/not torpid) as logistic regressions with the global model having the following equation:

$$\mu_i = \text{ilogit}(\alpha_0 + \sum_j \alpha_1 x_{1[i,j]} + \alpha_2(x_{2[j]} - \bar{x}) + \sum_k \alpha_3 x_{3[i,k]} + \alpha_4(x_{4[j]} - \bar{x}) + \alpha_4(x_{4[j]} - \bar{x}))$$

I ran the models for torpor duration (minutes), depth (°C), and HI (°C) as multiple linear regressions with the global model having the following equation:

$$\mu_i = \alpha_0 + \sum_j \alpha_1 x_{1[i,j]} + \alpha_2(x_{2[j]} - \bar{x}) + \sum_k \alpha_3 x_{3[i,k]} + \alpha_4(x_{4[j]} - \bar{x}) + \alpha_4(x_{4[j]} - \bar{x})$$

The predicted values ( $\mu_i$ ) for torpor frequency came from a Bernoulli distribution and the values for torpor duration, depth, and HI came from a normal distribution with a mean ( $\mu$ ) of 0 and a standard deviation that came from a gamma distribution. These equations use  $\alpha$  instead of  $\beta$  because the coefficients need to be standardized due to the predictor variables being different data types (i.e. metric and nominal) (Gelman et al. 2014, Kruschke 2014).

The metric predictor variables are re-centered at their mean, allowing the value of  $\alpha_0$  to represent the mean predicted value for all predictor variables (Gelman et al. 2014, Kruschke 2014). The prior probabilities of  $\alpha$  (reproductive condition, individual, and weather variables) for the logistic regression model came from a normal distribution with a mean ( $\mu$ ) of 0 and a standard deviation that came from a gamma distribution. The prior probabilities of  $\alpha$  for the linear regression model came from a normal distribution with a mean ( $\mu$ ) of 0 and a high standard deviation, thereby assuming equal probabilities across possible values (Gelman et al. 2014, Kruschke 2014). Repeated measures were taken from most individuals; therefore, the models were made hierarchical. Each reproductive



condition came from a normal distribution containing individuals and each individual came from a normal distribution containing days.

I ranked models using the deviance information criterion (DIC), with the lowest DIC value indicating the model that best explains the variation in the data (Spiegelhalter et al. 2002). DIC is based on the posterior distribution of the deviance (log-likelihood) and is a useful model selection criterion for hierarchical Bayesian models where the posterior distributions are obtained from MCMC methods (Spiegelhalter et al. 2002, Berg et al. 2004). For each model, I took the difference between the DIC value and that of the best model ( $\Delta_i$ ). Using  $\Delta_i$ , I calculated the DIC weights ( $w_i$ ), the likelihood that the  $i$ th model is the best model, for each candidate model using the same equation as Akaike weights (Burnham and Anderson 2002). I then calculated the sum of the weights ( $\sum w_i$ ) for the  $i$ th model up to the highest ranking model for models constituting  $\geq 95\%$  of the weights (Burnham and Anderson 2002). Not all variables within models may be important, therefore, I calculated the normalized weight for each variable in the 95% confidence set (Burnham and Anderson 2002). A normalized variable weight ( $Nw_i$ ) greater than 0.60 was arbitrarily selected to indicate important effects (Garroway and Broders 2005). For variables considered to have important effects, I calculated the model-averaged posterior estimates, unconditional standard deviations (Burnham and Anderson 2002), and the model averaged  $\beta_0$ . For torpor frequency, the model averaged posterior estimates were used to determine the odds ratio ( $\exp(\text{posterior estimate} \times \text{unit of increase})$ ) (Hosmer and Lemeshow 2013).

I hypothesized that body condition may be an explanatory variable for inter-individual variation in torpor use. Since the body condition index (BCI) can not be

accurately determined in pregnant females, BCI was not included as a variable within the multi-model inference. However, the relationship between BCI and torpor duration, depth, and HI in non-pregnant females was determined using the Pearson's correlation coefficient. Additionally, I conducted a one-metric predicted variable with multiple-nominal predictor variables analysis (see equation on page 18) to determine if BCI varied among reproductive condition. The predicted values ( $\mu_i$ ) for BCI ( $y$ ) came from a normal distribution with a mean ( $\mu$ ) of zero and a standard deviation that came from a gamma distribution. The prior distributions for  $\beta_0$ ,  $\beta_1$  (reproductive condition), and  $\beta_2$  (individual) came from a normal distribution with a mean ( $\mu$ ) of zero and a high standard deviation, thereby assuming equal probabilities across possible values (Gelman et al. 2014, Kruschke 2014). The models were made hierarchical with each reproductive condition and individual coming from a normal distribution centered over zero.

Table 1. Logistic regression and multiple linear regression candidate models for predicting torpor frequency (i.e., the probability of using torpor on a given day) and the average duration, depth, and HI of torpor for female *Myotis lucifugus* in Newfoundland.

MinTa = minimum ambient temperature.

Model	Predictor Variables
1	Reproductive
2	Individual
3	MinTa
4	Wind
5	Precipitation
6	MinTa + Wind
7	Wind + Precipitation
8	Reproductive + MinTa + Wind + Precipitation
9	Reproductive + Individual
10	Individual + MinTa + Wind + Precipitation
11	Reproductive + Individual + MinTa
12	Reproductive + Individual + Wind
13	Reproductive + Individual + Precipitation
14	Reproductive + Individual + MinTa + Wind + Precipitation

### **3. RESULTS**

#### **3.1 Sample Characteristics**

I collected usable skin temperature data from 12 pregnant, 11 lactating, eight post-lactating, two non-reproductive, and four not-obviously pregnant females for total 153 bat days. Data from not-obviously pregnant females were collected from June 16-20, 2016 and June 12-26, 2017. Data were collected from pregnant females between June 26 and July 8, 2017. Data from pregnant females in 2016 were not used in the analysis due to incomplete data days from transmitter failure. The data collection period for non-reproductive females occurred between June 29 and July 4, 2016 and were not sampled in 2017 as my supply of transmitters were allocated to pregnant females. Data were collected from lactating females from July 18-24 and on August 12, 2016 and from July 17-28, 2017. Data on post-lactating females were collected from August 02-04, 2016 and August 04-16, 2017. Some pregnant females roosted in a cabin and those bat days were removed from analysis due to the possible effects of roost type on torpor use, particularly the difference in lowest skin temperature between bats roosting in a cabin (4.30 °C) compared to bat boxes (14.22 °C) (Appendix A). Additionally, one individual was captured as pregnant and tracked again during lactating (Appendix B).

Capture data was used to approximate the timing of parturition and juvenile development period, which was determined as the difference between the first lactating female caught and the first volant juvenile caught. The first lactating female caught was on July 16 in 2016 and July 14 in 2017 and the latest a pregnant female was caught in 2017 was July 24 (there was not enough capture data in 2016). The first volant juvenile caught was July 29 in 2016 and July 28 in 2017, resulting in a juvenile development

period of approximately 13-14 days. The greatest mean ambient temperatures during my study occurred on July 17 for 2016 (24.29 °C) and 2017 (19.88 °C) (Appendix C), shortly after the dates of the approximated first parturition.

Environmental conditions were consistent between 2016 and 2017 (Appendix C). The difference in posterior estimates between 2016 and 2017 for daily mean ambient temperature, relative humidity, maximum wind speed, and precipitation were small and close to zero. This demonstrates little effect of year on weather variables for 2016 and 2017. Further, torpor patterns were similar between years (Appendix C). The posterior estimates of year for torpor duration, depth, and HI were small and close to zero. This suggests that year had little effect on torpor patterns for not-obviously pregnant, lactating, and post-lactating. Given that year had little effect on weather and torpor patterns, data from both years were pooled.

The weather during each sampling period varied (Table 2) and were not entirely independent for some reproductive periods (Appendix D). For mean and minimum ambient temperature, the posterior distributions of the non-reproductive, lactating, and post-lactating periods had a positive range, while the not-obviously pregnant and pregnant periods were negative. The 95% HDI of posterior distributions for all sampling periods did not overlap zero, indicating a strong certainty in the posterior estimates. For maximum wind speed, the greatest difference occurred between the not-obviously pregnant and post-lactating periods, in which there was strong certainty (95% HDI did not overlap zero) that there were higher wind speeds in early spring compared to late summer. There was little difference (almost zero) in wind speed between the lactating period and other sampling periods. For precipitation, the greatest difference occurred

between the pregnant and lactating periods, in which there was more precipitation during the pregnant period, however, there was a greater amount of uncertainty in these estimates (95% HDI overlapped zero). There were small differences (almost zero) in precipitation between the not-obviously pregnant, non-reproductive, and post-lactating periods.

Table 2. Mean  $\pm$  SD of the daily mean ambient temperature, minimum ambient temperature, maximum wind speed, and precipitation for each reproductive period in 2016 and 2017. Temperature and humidity were recorded using iButtons at Salmonier Nature Park, Newfoundland. Wind speed and precipitation data were taken from Environment Canada’s weather station in St. John’s, Newfoundland. n refers to the number of days. Ta = ambient temperature.

<b>2016</b>				
Reproductive Period	Mean Ta (°C)	Minimum Ta (°C)	Wind (km/hr)	Precipitation (mm)
<b>Not-obviously pregnant</b> (June 16-20)	10.21 $\pm$ 3.48	5.10 $\pm$ 2.41	60.40 $\pm$ 15.19	1.24 $\pm$ 1.87
<b>Non-reproductive</b> (June 29-July 4)	16.26 $\pm$ 2.47	11.38 $\pm$ 2.62	59.50 $\pm$ 16.33	1.64 $\pm$ 2.32
<b>Lactating</b> (July 18-24)	17.38 $\pm$ 1.37	12.92 $\pm$ 1.61	55.86 $\pm$ 8.17	0.63 $\pm$ 1.22
<b>Post-lactating</b> (August 2-4)	13.96 $\pm$ 1.24	8.77 $\pm$ 1.76	31.00 $\pm$ 0.00	0.07 $\pm$ 0.12
<b>2017</b>				
Reproductive Period	Mean Ta (°C)	Minimum Ta (°C)	Wind (km/hr)	Precipitation (mm)
<b>Not-obviously pregnant</b> (June 12-26)	12.72 $\pm$ 2.20	7.40 $\pm$ 2.45	59.20 $\pm$ 12.02	2.15 $\pm$ 6.47
<b>Pregnant</b> (June 23-July 2)	13.56 $\pm$ 2.55	8.08 $\pm$ 1.40	54.20 $\pm$ 10.39	8.70 $\pm$ 11.29
<b>Lactating</b> (July 17-28)	16.80 $\pm$ 2.00	11.81 $\pm$ 2.01	45.83 $\pm$ 10.74	1.35 $\pm$ 3.13
<b>Post-lactating</b> (August 4-16)	17.28 $\pm$ 1.52	12.79 $\pm$ 1.43	50.00 $\pm$ 12.50	6.04 $\pm$ 10.56

### 3.2 Skin Temperature Patterns and Trends

Torpor was used by females in all reproductive conditions. Six skin temperature ( $T_{sk}$ ) patterns were identified and the most frequently used patterns differed among reproductive groups (Appendix E). Maintaining a constant  $T_{sk}$  at normothermia (Figure 2a) was the most frequently occurring pattern for lactating (19 out of 43 bat days) and non-reproductive females (4 out of 7 bat days). Pregnant females typically exhibited frequent and shallow drops (difference in  $T_{sk}$  of 5-10 °C) in  $T_{sk}$  (16 out of 30 bat days) (Figure 2b). Medium drops (difference in  $T_{sk}$  of 10-15 °C) in  $T_{sk}$  was the pattern most typically used among post-lactating females (14 out of 37 bat days) (Figure 2c). Not-obviously pregnant females most frequently maintained long and deep drops in  $T_{sk}$  (14 out of 22 bat days) (Figure 2d). Not-obviously pregnant females and post-lactating females were the only reproductive groups to maintain low  $T_{sk}$  for the duration of one day (Figure 2e) and not-obviously pregnant females were the only group to exhibit low  $T_{sk}$  (> 10 °C below maximum  $T_{sk}$ ) over multiple days (Figure 2f).



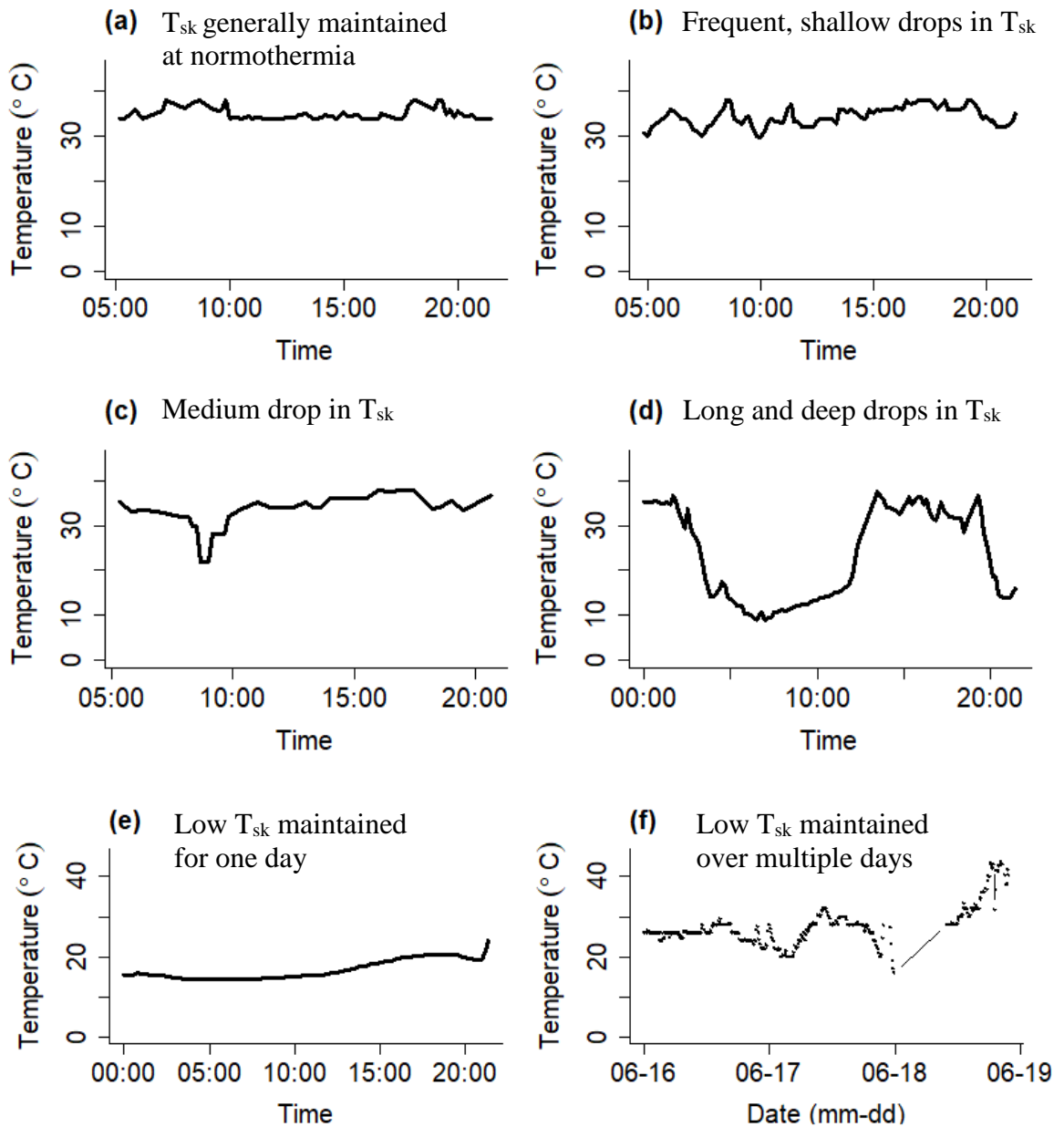


Figure 2. Examples of skin temperature ( $T_{sk}$ ) patterns (a) 1, (b) 2, (c) 3, (d) 4, (e) 5, and (f) 6 in female *Myotis lucifugus* roosting in bat boxes in Newfoundland from June to August 2016 and 2017. The black line represents  $T_{sk}$ . Straight lines indicate missing data.

### 3.3 Model Selection and Posterior Estimates

For predicting torpor frequency (i.e., the probability of torpor being used on a given day) in female *Myotis lucifugus*, the highest ranked model ( $w_i = 0.33$ ) contained two weather variables (maximum wind speed and precipitation) (Table 3). Reproductive condition and individual occurred in the highest ranked models for predicting torpor duration (min/day) ( $w_i = 0.48$ ), depth (°C) ( $w_i = 0.32$ ), and HI (°C) ( $w_i = 0.55$ ) (Tables 4-6). The 95% confidence sets included five models for torpor duration and depth and four models for HI. This suggests some certainty in the importance of the predictor variables reproductive condition and individual in explaining torpor duration, depth, and HI. Minimum ambient temperature also occurred in the highest ranked model for torpor depth (Table 5) and all weather variables (minimum ambient temperature, maximum wind speed, and precipitation) occurred in the highest ranked model for HI (Table 6).

Although minimum ambient temperature occurred in the highest ranked model for torpor depth and HI (Tables 5 and 6), the normalized variable weight was  $<0.60$  (Table 7) and was not considered to have important effects. However, the 95% HDI of the posterior distribution of minimum ambient temperature for torpor depth did not overlap zero (Appendix F). This indicates strong certainty in the effect of minimum ambient temperature on torpor depth, however, it is not as important as the effects of reproductive condition and individual. Despite the inclusion of precipitation in the highest ranked model for HI (Table 6), it had a normalized variable weight  $<0.60$  (Table 7) and was not considered important. Therefore, the weather predictor variables were considered to have less important effects on torpor duration and depth than reproductive condition and

individual. Only maximum wind speed was considered important for explaining variation in HI.

### *3.3.1 Reproductive Condition*

Reproductive condition occurred in three of the five models that constituted the 95% confidence set for torpor duration (Table 4) and was in each of the models constituting the 95% confidence set for torpor depth and HI (Tables 5 and 6). The normalized variable weights were high for torpor duration ( $Nw_i = 0.85$ ), depth ( $Nw_i = 1.00$ ), and HI ( $Nw_i = 1.00$ ) (Table 7). The mean  $\pm$  SD torpor duration for pregnant ( $298.67 \pm 318.66$  min/day), lactating ( $243.50 \pm 191.84$  min/day), post-lactating ( $326.76 \pm 301.07$  min/day), and non-reproductive ( $251.43 \pm 247.08$  min/day) females were lower than not-obviously pregnant females ( $819.10 \pm 387.69$  min/day) (Figure 3a) (Appendix E). The model-averaged mean torpor duration across all predictor variables ( $\beta_0$ ) where reproductive condition occurred was 377.49 min/day (Table 8). The not-obviously pregnant condition was the only reproductive condition to result in a positive effect on duration with the greatest difference occurring between the lactating and not-obviously pregnant conditions (Table 8). Being in the lactating condition results in a decrease of torpor duration by 155.75 min/day below the mean across all predictor variables ( $\beta_0$ ), whereas being in the not-obviously pregnant condition results in an increase by 314.71 min/day. The 95% HDI of the posterior distributions of the highest ranked model (model #9) for lactating and not-obviously pregnant conditions did not overlap zero, suggesting strong certainty in the estimates (Figure 3a). Additionally, the longest torpor bout was recorded from a not-obviously pregnant female and was 1,290 minutes (21.5 hours).

While this supports the evidence that not-obviously pregnant females had the greatest, positive effect on duration, it is inconsistent with the skin temperature patterns as some individuals had low skin temperatures for a minimum of 24 hours (Figure 2).

Additionally, the pregnant condition had the least negative effect on torpor duration compared to the lactating, post-lactating, and non-reproductive conditions (Table 8) (Figure 3a). However, the 95% HDI of the distributions for pregnant, post-lactating and non-reproductive females did overlap zero, indicating some uncertainty in the estimates.

For torpor depth and HI, the 95% HDI of the posterior distributions for the highest ranked model overlapped zero for all reproductive conditions, indicating uncertainty in the posterior estimates (Figures 3b and 3c). The mean  $\pm$  SD of torpor depth and HI for pregnant ( $6.61 \pm 6.98$  °C;  $3.92 \pm 4.09$  °C), lactating ( $4.24 \pm 3.97$  °C;  $2.68 \pm 1.54$  °C), post-lactating ( $7.09 \pm 6.04$  °C  $3.91 \pm 2.85$  °C), and non-reproductive ( $4.37 \pm 5.07$  °C;  $3.70 \pm 4.89$  °C) females were lower than the not-obviously pregnant females ( $8.63 \pm 5.63$  °C;  $5.78 \pm 3.14$  °C) (Figures 3b and 3c) (Appendix E). The model-averaged mean torpor depth and HI across all predictor variables ( $\beta_0$ ) where reproductive condition occurred was  $6.55$  °C and  $3.93$  °C, respectively (Table 8). The pregnant, post-lactating, and not-obviously pregnant conditions had a positive effect on depth and HI while the lactating and non-reproductive condition had a negative effect (Table 8) (Figures 3b and 3c). The greatest difference in the model-averaged posterior estimates occurred between the lactating and post-lactating conditions (Table 8). Being in the lactating condition most likely results in a decrease in maximum torpor depth and HI by  $2.24$  and  $1.00$  °C, respectively, from the mean across all predictor variables ( $\beta_0$ ) (Table 8). Being in the post-lactating condition likely results in an increase in depth by  $1.41$  °C and HI by  $0.67$

°C. These results are inconsistent with the skin temperature patterns of not-obviously pregnant females, as most individuals had skin temperatures that dropped to 10°C (Figure 2) (Appendix E). The lowest skin temperature recorded was 6 °C from a not-obviously pregnant female (Appendix E), however, the corresponding depth was 16 °C and likely does not reflect the actual depth. This suggests that the torpor threshold used underestimated torpor depth in not-obviously pregnant females.

### 3.3.2 *Individual*

The predictor variable individual occurred in each of the models constituting the 95% confidence set for torpor duration, depth, and HI (Tables 4, 5, and 6) and had a high normalized variable weight ( $Nw_i = 1.00$ ) (Table 7). The model-averaged mean across all predictor variables ( $\beta_0$ ) where individual occurred was 370.31 min/day for torpor duration, 6.55 °C for depth, and 3.93 °C for HI (Table 8). The individuals with the most positive and negative model-averaged posterior estimates were identified to demonstrate the extent of variation among the effect of individuals on torpor patterns. The greatest difference in estimates for torpor duration occurred between two pregnant individuals, #13 and #17 (Figure 4), that differed in body mass and forearm length (Figure 4). Individual #17 had a higher body mass and forearm (9.27 g and 39.64 mm) and most likely increases duration by 208.16 min/day from the mean across all predictor variables ( $\beta_0$ ), (Table 8). Individual #13 had a lower body mass and forearm (8.94 g and 36.95 mm) and most likely results in a decrease in torpor duration by 152.62 min/day (Table 8). The individual with the most negative estimate for torpor duration was the same for torpor depth and HI (individual #13), and likely results in a decrease in depth and HI by 3.67 °C,

and 1.43 °C, respectively (Table 8). Individual #23 had the most positive estimate for depth and HI (Figure 4) and was also a pregnant female with a smaller body mass (8.24 g) but larger forearm length (38.21 mm) than individual #13. Individual #23 likely results in an increase in depth and HI by 4.99 °C and 2.52 °C, respectively (Table 8). The variation among pregnant individuals in posterior estimates suggests inter-individual variation within reproductive condition has important effects on torpor patterns. Additionally, the difference in the most negative and positive posterior estimates of torpor depth and HI were higher for individual than reproductive condition (Table 8). This suggests that the effect of belonging to an individual was stronger than belonging to a reproductive condition for torpor depth and HI, despite the two predictor variables having the same normalized weight ( $Nw_i = 1.00$ ).

### 3.3.3 Weather

Maximum wind speed and precipitation occurred in five of the ten models that comprised the 95% confidence set for torpor frequency, with precipitation occurring in the top two models (Table 3). Maximum wind speed and precipitation had normalized variable weights of 0.62 and 0.81, respectively (Table 7), indicating that precipitation had more important effects than maximum wind speed. Despite a high normalized variable weight, individuals started with a high probability of using torpor when there was no wind or precipitation (Figure 5). However, the model-averaged posterior estimates suggest a stronger effect of precipitation on torpor frequency compared to maximum wind speed (Table 8). An increase in maximum wind speed from 0 to 10 km/hr most likely increases torpor frequency by 1.35 times ( $\exp(\text{posterior estimate} \times \text{unit of increase})$ ).

(Figure 5a), whereas an increase in precipitation from 0 to 10 mm increases torpor frequency by 22.20 times (Figure 5b) (Table 9). The 95% HDI of the posterior distributions for the highest ranked model overlap zero for maximum wind speed, however, they do not overlap zero for precipitation, which suggests more certainty in the estimates for precipitation. All individuals in the lactating, non-reproductive, and not-obviously pregnant conditions used torpor when maximum wind speed was  $>50$  km/hr (Figure 5a) (Appendix E). Pregnant and post-lactating females were not exposed to wind speeds over 50 km/hr. All individuals in the pregnant, lactating, post-lactating, and not-obviously pregnant conditions used torpor when precipitation was  $>4$  mm (Figure 5c) (Appendix E). Non-reproductive females were not exposed to precipitation over 4 mm.

Maximum wind speed occurred in the top two models for HI (Table 6) and had a normalized weight of 0.87 (Table 7). Despite having a high normalized weight, the posterior estimate was small, in which an increase in maximum wind speed from 0 to 10 km/hr most likely results in an increase in HI by  $0.6$  °C (Table 8). The 95% HDI of the posterior distribution for the highest ranked model of maximum wind speed overlapped zero and the shape of the distribution indicates that there is uncertainty in the estimate (Figure 6). Given the small effect and uncertainty of the posterior estimate, maximum wind speed was considered less important than individual and reproductive condition for explaining HI.

### 3.4 Body Condition Index

Variation in body condition index (BCI) may help explain the inter-individual differences in torpor duration, depth, and HI. There was a small, negative correlation between BCI and torpor duration ( $r = -0.42$ ,  $n = 102$ ,  $p < 0.05$ ) and HI ( $-0.30$ ,  $n = 102$ ,  $p < 0.05$ ) and a weak, negative relationship with torpor depth ( $-0.18$ ,  $n = 102$ ,  $p = 0.07$ ) (Figure 7). While there was a reduction in torpor use among individuals with the highest BCI, there was also a reduction among individuals with the lowest BCI (Figure 7). The data suggests that individuals on the extreme low and high end of BCI use torpor to a lesser extent than individuals within the mean range. BCI varied among reproductive conditions and the greatest difference occurred between lactating and non-reproductive females, with lactating females having a larger BCI (Appendix G). The 95% HDI for the lactating condition did not overlap zero, indicating a strong certainty in the estimates, however, it did slightly overlap zero for non-reproductive females, suggesting uncertainty in the estimate (Appendix G).



Table 3. Deviance information criterion (DIC) model results for explaining variation in torpor frequency among female *Myotis lucifugus* roosting in bat boxes in Newfoundland, Canada. Models were ranked based on DIC values, with lowest value explaining more of the variation in the data.  $\Delta i$  is the difference between the DIC weight ( $w_i$ ) of the model and that of the best model.  $\sum w_i$  is the sum of the DIC weights of the  $i$ th model and all higher-ranking models constituting  $\geq 95\%$  of the DIC weights. MinTa = minimum ambient temperature.

Model	Predictor Variables	DIC	$\Delta i$	$w_i$	$\sum w_i$
<b>7</b>	<b>Precipitation + Wind</b>	<b>89.12</b>	<b>0.00</b>	<b>0.33</b>	<b>0.33</b>
<b>5</b>	<b>Precipitation</b>	<b>89.88</b>	<b>0.75</b>	<b>0.23</b>	<b>0.56</b>
<b>8</b>	<b>Precipitation + Wind + MinTa + Reproductive</b>	<b>91.64</b>	<b>2.52</b>	<b>0.09</b>	<b>0.66</b>
<b>4</b>	<b>Wind</b>	<b>92.33</b>	<b>3.21</b>	<b>0.07</b>	<b>0.72</b>
<b>10</b>	<b>Precipitation + Wind + MinTa + Individual</b>	<b>92.35</b>	<b>3.23</b>	<b>0.07</b>	<b>0.79</b>
<b>13</b>	<b>Precipitation + Reproductive + Individual</b>	<b>92.67</b>	<b>3.54</b>	<b>0.06</b>	<b>0.85</b>
<b>6</b>	<b>Wind + MinTa</b>	<b>93.71</b>	<b>4.58</b>	<b>0.03</b>	<b>0.88</b>
<b>3</b>	<b>MinTa</b>	<b>93.92</b>	<b>4.80</b>	<b>0.03</b>	<b>0.91</b>
<b>2</b>	<b>Individual</b>	<b>94.21</b>	<b>5.09</b>	<b>0.03</b>	<b>0.94</b>
<b>1</b>	<b>Reproductive</b>	<b>94.46</b>	<b>5.34</b>	<b>0.02</b>	<b>0.96</b>
12	Wind + Reproductive + Individual	94.59	5.46	0.00	
9	Reproductive + Individual	96.12	6.99	0.00	
11	MinTa + Reproductive + Individual	97.57	8.45	0.00	
14	Precipitation + Wind + MinTa + Reproductive + Individual	99.58	10.45	0.00	

Table 4. Deviance information criterion (DIC) model results for explaining variation in torpor duration (min/day) among female *Myotis lucifugus* roosting in bat boxes in Newfoundland, Canada. Models were ranked based on DIC values, with lowest value explaining more of the variation in the data.  $\Delta i$  is the difference between the DIC weight ( $w_i$ ) of the model and that of the best model.  $\sum w_i$  is the sum of the DIC weights of the  $i$ th model and all higher-ranking models constituting  $\geq 95\%$  of the DIC weights. MinTa = minimum ambient temperature.

Model	Predictor Variables	DIC	$\Delta i$	$w_i$	$\sum w_i$
<b>9</b>	<b>Reproductive + Individual</b>	<b>343.10</b>	<b>0.00</b>	<b>0.48</b>	<b>0.48</b>
<b>11</b>	<b>Reproductive + Individual + MinTa</b>	<b>344.94</b>	<b>1.83</b>	<b>0.19</b>	<b>0.68</b>
<b>13</b>	<b>Reproductive + Individual + Precipitation</b>	<b>345.44</b>	<b>2.33</b>	<b>0.15</b>	<b>0.83</b>
<b>10</b>	<b>Individual + MinTa + Wind + Precipitation</b>	<b>346.02</b>	<b>2.92</b>	<b>0.11</b>	<b>0.94</b>
<b>2</b>	<b>Individual</b>	<b>348.19</b>	<b>5.08</b>	<b>0.04</b>	<b>0.98</b>
14	Reproductive + Individual + MinTa + Wind + Precipitation	350.67	7.56	0.01	
1	Reproductive	350.87	7.77	0.01	
3	MinTa	384.03	40.93	0.00	
4	Wind	398.94	55.84	0.00	
5	Precipitation	398.57	55.47	0.00	
6	MinTa + Wind	384.73	41.63	0.00	
7	Wind + Precipitation	399.86	56.76	0.00	
8	Reproductive + MinTa + Wind + Precipitation	360.89	17.79	0.00	
12	Reproductive + Individual + Wind	353.92	10.82	0.00	

Table 5. Deviance information criterion (DIC) model results for explaining variation in torpor depth (°C) among female *Myotis lucifugus* roosting in bat boxes in Newfoundland, Canada. Models were ranked based on DIC values, with lowest value explaining more of the variation in the data.  $\Delta i$  is the difference between the DIC weight ( $w_i$ ) of the model and that of the best model.  $\sum w_i$  is the sum of the DIC weights of the  $i$ th model and all higher-ranking models constituting  $\geq 95\%$  of the DIC weights. MinTa = minimum ambient temperature.

Model	Predictor Variables	DIC	$\Delta i$	$w_i$	$\sum w_i$
<b>11</b>	<b>Reproductive + Individual + MinTa</b>	<b>380.09</b>	<b>0.00</b>	<b>0.32</b>	<b>0.32</b>
<b>9</b>	<b>Reproductive + Individual</b>	<b>380.12</b>	<b>0.03</b>	<b>0.31</b>	<b>0.63</b>
<b>14</b>	<b>Reproductive + Individual + MinTa + Wind + Precipitation</b>	<b>380.92</b>	<b>0.83</b>	<b>0.21</b>	<b>0.84</b>
<b>13</b>	<b>Reproductive + Individual + Precipitation</b>	<b>383.09</b>	<b>3.00</b>	<b>0.07</b>	<b>0.91</b>
<b>12</b>	<b>Reproductive + Individual + Wind</b>	<b>383.19</b>	<b>3.10</b>	<b>0.07</b>	<b>0.98</b>
10	Individual + MinTa + Wind + Precipitation	386.87	6.78	0.01	
8	Reproductive + MinTa + Wind + Precipitation	389.15	9.06	0.00	
2	Individual	389.22	9.12	0.00	
6	MinTa + Wind	391.70	11.61	0.00	
3	MinTa	391.99	11.89	0.00	
1	Reproductive	393.96	13.86	0.00	
4	Wind	398.69	18.60	0.00	
5	Precipitation	399.14	19.04	0.00	
7	Wind + Precipitation	399.64	19.55	0.00	

Table 6. Deviance information criterion (DIC) model results for explaining variation in the heterothermy index (HI) (°C) for torpor among female *Myotis lucifugus* roosting in bat boxes in Newfoundland, Canada. Models were ranked based on DIC values, with lowest value explaining more of the variation in the data.  $\Delta i$  is the difference between the DIC weight ( $w_i$ ) of the model and that of the best model.  $\sum w_i$  is the sum of the DIC weights of the  $i$ th model and all higher-ranking models constituting  $\geq 95\%$  of the DIC weights. MinTa = minimum ambient temperature.

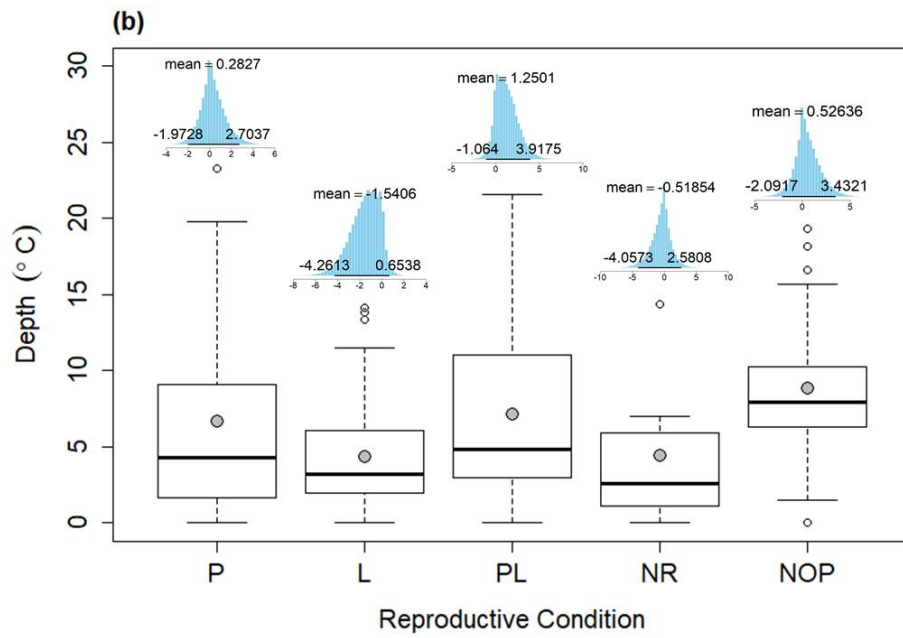
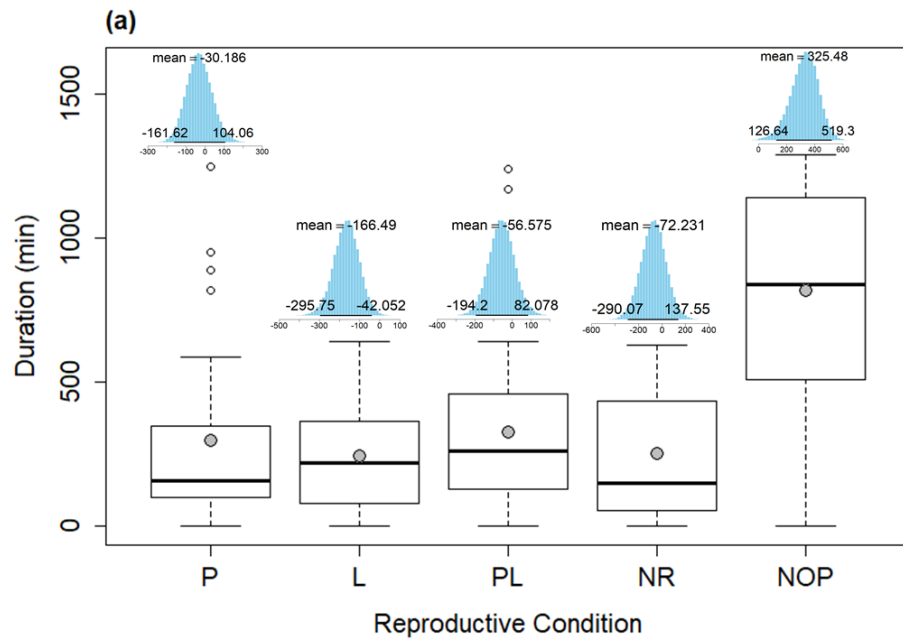
Model	Predictor Variables	DIC	$\Delta i$	$w_i$	$\sum w_i$
<b>14</b>	<b>Reproductive + Individual + Wind + MinTa + Precipitation</b>	<b>362.73</b>	<b>0.00</b>	<b>0.55</b>	<b>0.55</b>
<b>12</b>	<b>Reproductive + Individual + Wind</b>	<b>363.89</b>	<b>1.15</b>	<b>0.31</b>	<b>0.85</b>
<b>9</b>	<b>Reproductive + Individual</b>	<b>366.35</b>	<b>3.61</b>	<b>0.09</b>	<b>0.94</b>
<b>11</b>	<b>Reproductive + Individual + MinTa</b>	<b>368.33</b>	<b>5.59</b>	<b>0.03</b>	<b>0.97</b>
13	Reproductive + Individual + Precipitation	369.06	6.33	0.02	
10	Individual + Wind + MinTa + Precipitation	374.14	11.41	0.00	
2	Individual	375.07	12.34	0.00	
6	Wind + MinTa	386.38	23.65	0.00	
3	MinTa	388.59	25.86	0.00	
1	Reproductive	390.07	27.34	0.00	
8	Reproductive + Wind + MinTa + Precipitation	390.67	27.93	0.00	
4	Wind	396.78	34.05	0.00	
5	Precipitation	398.33	35.60	0.00	
7	Wind + Precipitation	399.00	36.27	0.00	

Table 7. Normalized weights for variables ( $Nw_i$ ) in the models constituting  $\geq 95\%$  of the DIC weights to explain variation in torpor frequency, duration, depth, and HI. Variables with normalized weights  $< 0.60$  were not considered to have a substantial effect. MinTa = minimum ambient temperature. Bolded values indicate variables that occurred in the highest-ranked model.

Torpor Characteristic	Reproductive	Individual	Min Ta	Wind	Precipitation
Frequency	0.18	0.16	0.23	<b>0.62</b>	<b>0.81</b>
Duration	<b>0.85</b>	<b>1.00</b>	0.31	0.11	0.27
Depth	<b>1.00</b>	<b>1.00</b>	<b>0.54</b>	0.28	0.29
HI	<b>1.00</b>	<b>1.00</b>	<b>0.59</b>	<b>0.87</b>	<b>0.56</b>

Table 8. The model averaged posterior estimates ( $\hat{\theta}$ ), unconditional standard deviations (SD), 95% HDI from the highest ranked model, and the model averaged  $\beta_0$  for variables with a normalized weight  $> 0.60$  for torpor frequency, duration, depth, and heterothermy index (HI). Only the posterior estimates for the individual with the most negative value and for the individual with the most positive value for duration, depth, and HI are displayed for brevity.

Variable	Posterior Estimate ( $\hat{\theta}$ )	SD	95% HDI	$\beta_0$
<b>Frequency</b>				
Wind	0.03	0.02	-0.01, 0.08	2.11
Precipitation	0.31	0.20	0.00, 0.74	1.78
<b>Duration</b>				
Pregnant	-36.50	69.51	-163.67, 102.39	377.49
Lactating	-155.75	67.52	-292.82, -44.06	377.49
Post-lactating	-50.86	70.82	-191.33, 81.79	377.49
Non-reproductive	-71.60	108.09	-289.35, 136.10	377.49
Not-obviously pregnant	314.71	105.16	123.31, 514.46	377.49
Individual #13	-152.62	103.80	-372.85, 30.75	370.31
Individual #17	208.16	165.52	-72.41, 533.47	370.31
<b>Depth</b>				
Pregnant	0.96	1.10	-1.88, 2.78	6.55
Lactating	-2.24	1.29	-4.47, 0.56	6.55
Post-lactating	1.41	1.33	-1.03, 3.84	6.55
Non-reproductive	-1.16	1.77	-3.99, 2.47	6.55
Not-obviously pregnant	1.03	1.37	-2.05, 3.58	6.55
Individual #13	-3.67	1.69	-7.49, 0.39	6.55
Individual #23	4.99	1.89	-0.71, 9.99	6.55
<b>HI</b>				
Pregnant	0.47	0.66	-0.92, 1.89	3.93
Lactating	-1.00	0.88	-2.46, 0.36	3.93
Post-lactating	0.67	0.76	-0.44, 3.16	3.93
Non-reproductive	-0.41	1.02	-3.32, 1.43	3.93
Not-obviously pregnant	0.28	1.10	-1.57, 1.91	3.93
Individual #13	-1.43	1.06	-4.38, -0.15	3.93
Individual #23	2.52	1.57	0.88, 7.33	3.93
Wind	0.06	0.04	-0.04, 0.11	3.82



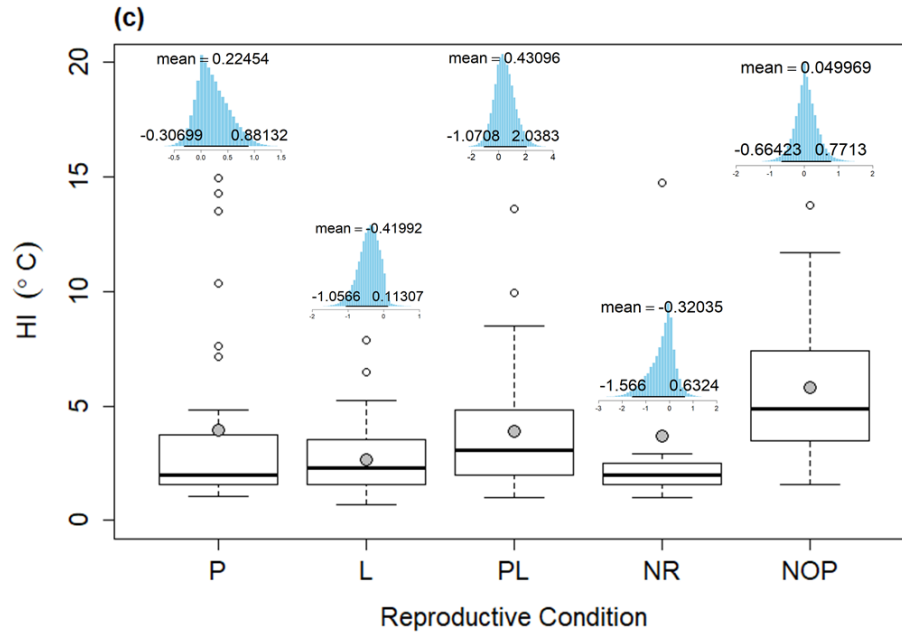
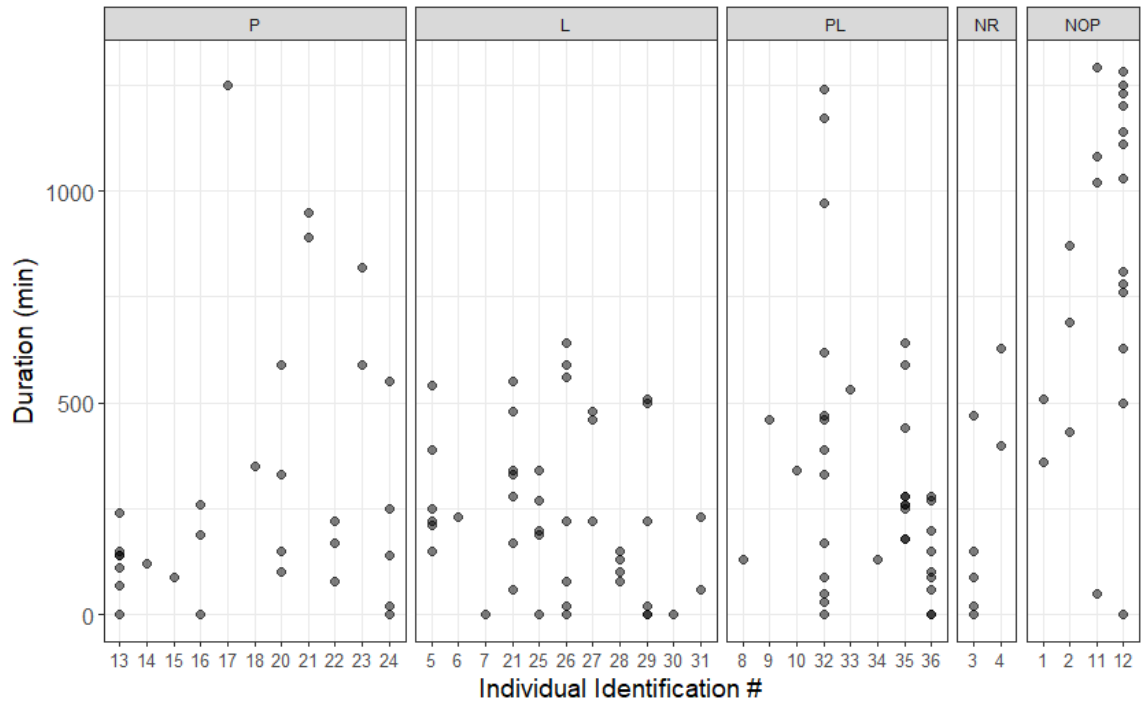


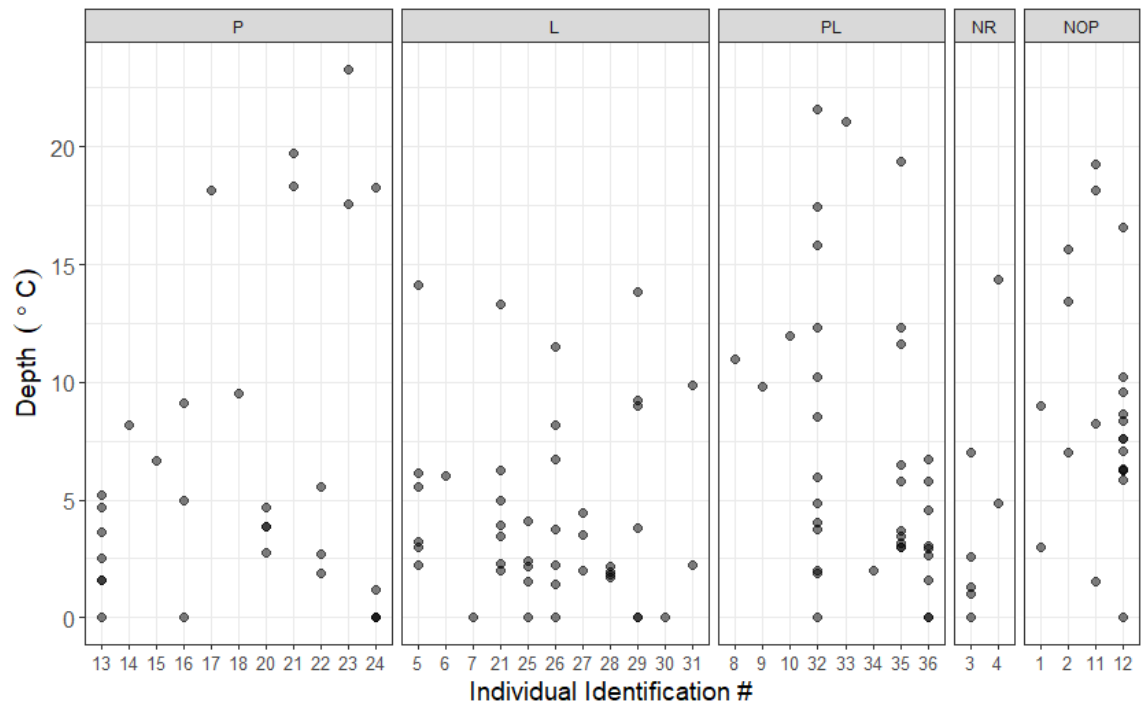
Figure 3. Difference in torpor (a) duration (total amount of time spent torpid in one day), (b) depth (maximum drop in skin temperature below the torpid threshold), and (c) the heterothermy index (skin temperature fluctuation) for pregnant ( $n = 11$ ,  $N = 30$ ), lactating ( $n = 11$ ,  $N = 43$ ), post-lactating ( $n = 8$ ,  $N = 37$ ), non-reproductive ( $n = 2$ ,  $N = 7$ ), and not-obviously pregnant ( $n = 4$ ,  $N = 22$ ) female *Myotis lucifugus* in Newfoundland from June to August 2016 and 2017. The top and bottom of each box show the upper and lower quartiles and the dashed vertical lines represent the maximum and minimum values. The black bars represent the median, the grey dots represent the mean, and open circles represent outliers. Above the boxes are the posterior distributions for the estimates of each reproductive condition from the highest ranked candidate models.  $n$  = number of individual bats,  $N$  = number of bat days, P = pregnant, L= lactating, PL = post-lactating, NR = non-reproductive, and NOP = not-obviously pregnant.



(a)



(b)



(c)

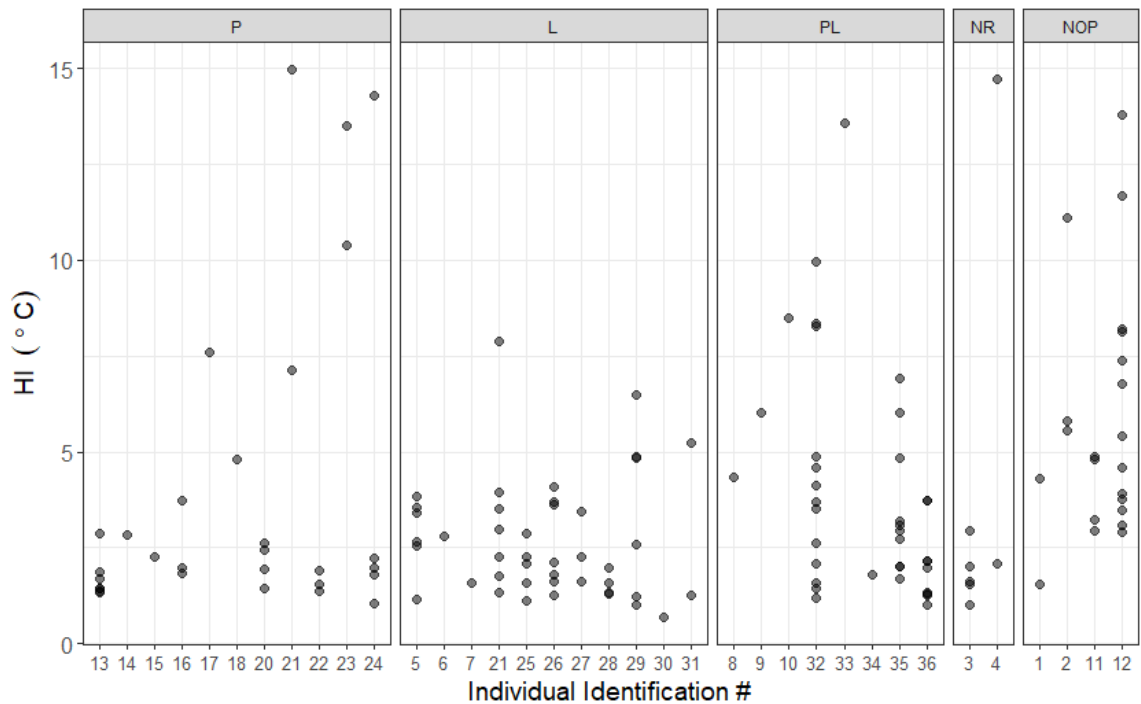


Figure 4. Torpor (a) duration (total amount of time spent torpid in one day), (b) depth (maximum drop in skin temperature below the torpid threshold), and (c) the heterothermy index (skin temperature fluctuation) among individual female *Myotis lucifugus* in pregnant (P), lactating (L), post-lactating (PL), non-reproductive (NR), and not-obviously pregnant (NOP) conditions. Data was collected at Salmonier Nature Park, Newfoundland from June to August, 2016 and 2017. Individual #21 was sampled when pregnant and lactating.

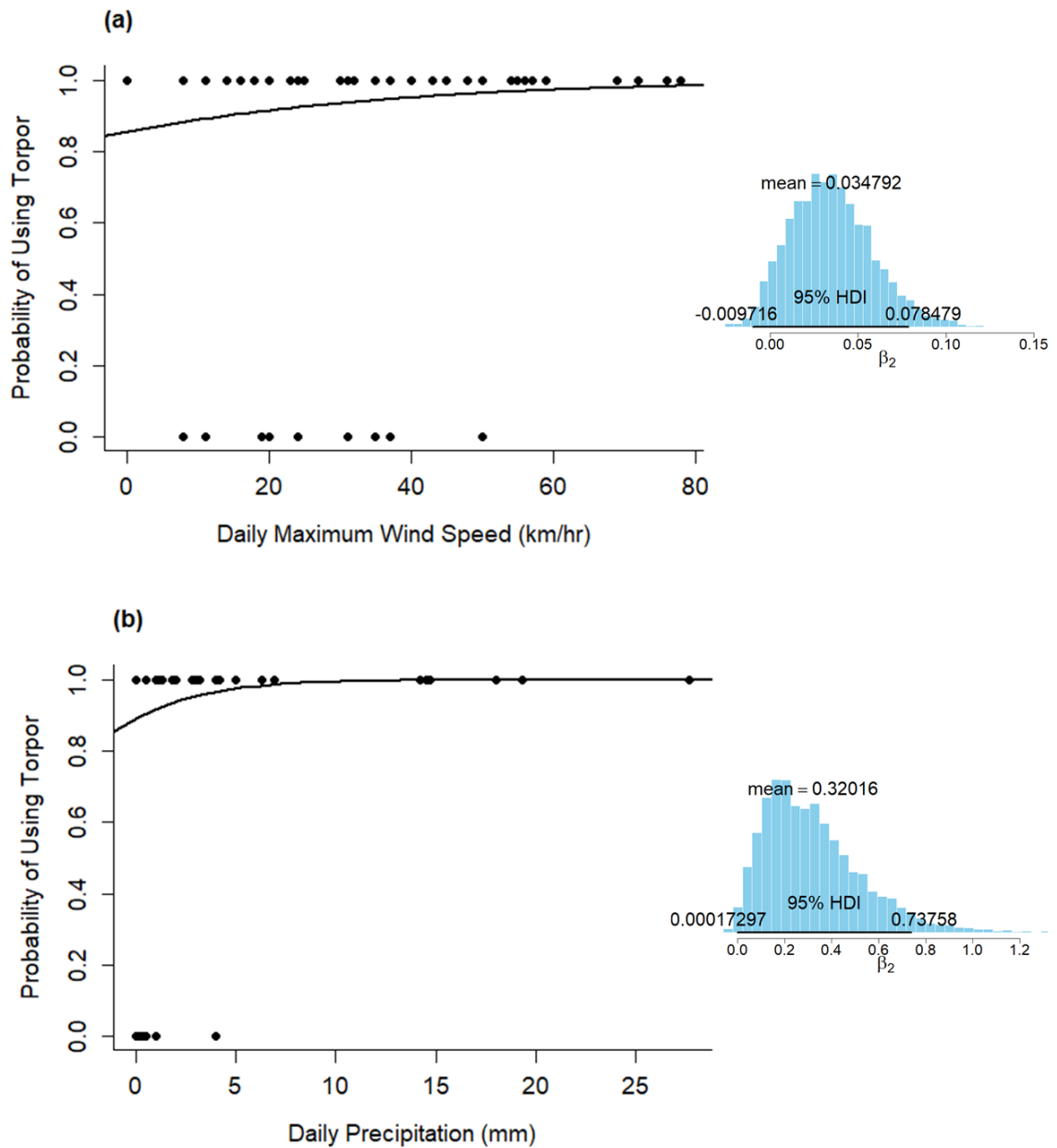


Figure 5. Torpor frequency (i.e., the probability of using torpor on a given day) for female *Myotis lucifugus* in Newfoundland as mean daily (a) maximum wind speed and (b) precipitation increase. Curves are logistic regressions ( $y = \exp(\beta_0 + \beta_1) / (1 + \exp(\beta_0 + \beta_1))$ ) based on the model averaged posterior estimates. The posterior distribution of each variable for the highest ranked model is adjacent to the plot.

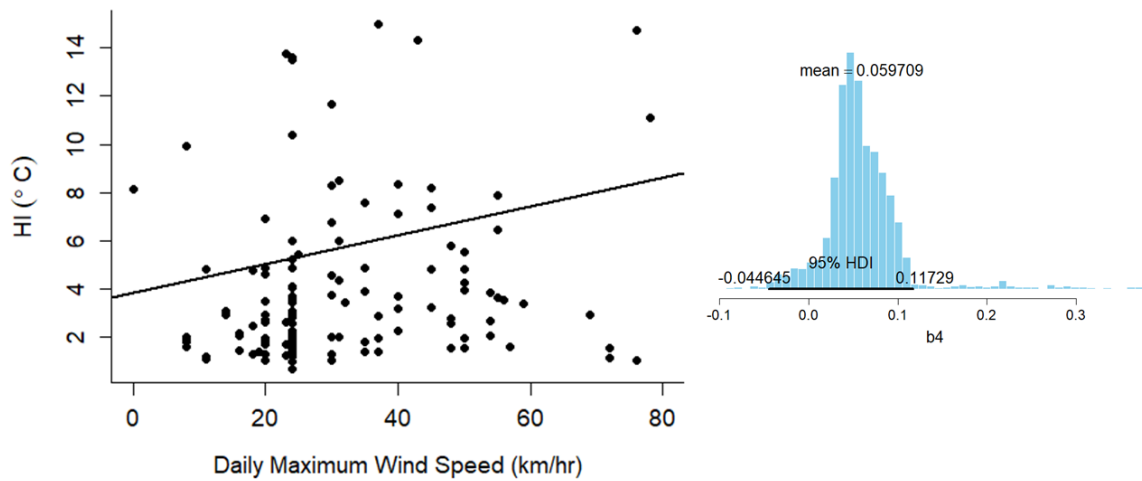


Figure 6. The effects of maximum wind speed on the heterothermy index (skin temperature fluctuation) in female *Myotis lucifugus* in Newfoundland from June to August 2016 and 2017. The black line is a linear regression based on the model averaged posterior estimates of the slope and intercept ( $y=0.06x+3.82$ ). The posterior distribution of maximum wind speed for the highest ranked model is adjacent to the plot.

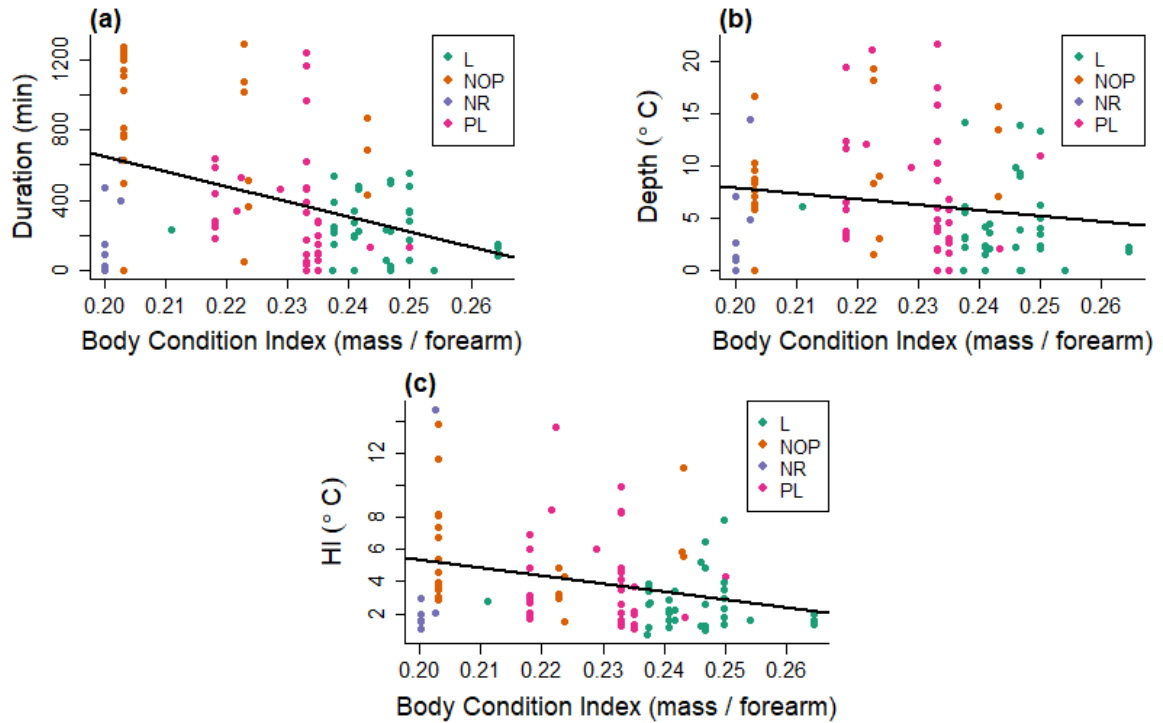


Figure 7. The relationship between body condition index (mass divided by forearm) and torpor (a) duration ( $y = -8570.80x + 2364.00$ ,  $R^2 = 0.16$ ), (b) depth ( $y = -54.62x + 18.85$ ,  $R^2 = 0.03$ ), and (c) HI ( $y = -49.82x + 15.32$ ,  $R^2 = 0.08$ ) among lactating ( $n = 10$ ), post-lactating ( $n = 8$ ), non-reproductive ( $n = 2$ ), and not-obviously pregnant ( $n = 4$ ) *Myotis lucifugus* at Salmonier Nature Park, Newfoundland. Bats were captured from 2 June to 5 August 2016 and 2017. Data points are coloured by reproductive condition.  $n$  = number of individual bats, L = lactating, PL = post-lactating, NR = non-reproductive, and NOP = not-obviously pregnant.

## **4. DISCUSSION**

Similar to other studies on bats (Dzal and Brigham 2013, Johnson and Lacki 2014), my results demonstrate that the combinations of extrinsic and intrinsic factors influence torpor use and that each predictor variable has different effects on torpor frequency, duration, depth, and the heterothermy index (HI). My hypothesis that weather conditions explain torpor patterns was supported for torpor frequency (i.e. the probability of using torpor on a given day) and HI. Precipitation and wind provided the most support when explaining torpor frequency and maximum wind speed was an important variable for explaining HI. My hypothesis that reproductive condition and individual explain torpor patterns was supported for torpor duration, depth, and HI as reproductive condition and individual provided the most support for these patterns. Additionally, the thresholds and metrics used to measure torpor may over-or under-estimate torpor use in some individuals. Finding a more accurate representation of torpor use for all individuals may allow for a better distinction of the effects among predictor variables on torpor patterns.

### **4.1 Reproductive Condition**

Reproductive condition was one of the most important predictors of torpor duration, depth, and HI. I had predicted that pregnant and lactating females would use torpor for shorter durations, at shallower depths, and have a lower heterothermy index (HI) than post-lactating, non-reproductive, and not-obviously pregnant females. Contrary to my prediction and other studies of temperate bats (Audet and Fenton 1988, Solick and Barclay 2006, Johnson and Lacki 2014), non-reproductive females had a lower mean torpor duration, depth, and HI than pregnant females. This may be because non-reproductive females in my study had the lowest body condition index among all

individuals and may not have had sufficient fat reserves to use torpor for long durations or at great depths (Terrien et al. 2009, Stawski and Geiser 2010, Kobbe et al. 2011, Vuarin et al. 2013) (see section 4.2 below). An additional explanation is that the non-reproductive females may have been yearlings that may have needed additional growing (Davis and Hitchcock 1965), which requires maintaining an elevated body temperature (Gillooly et al. 2002). The sample size of non-reproductive females was low and further investigation of the differences in torpor use among non-reproductive females would be useful in understanding the effects of body condition and age on torpor patterns.

As predicted, and similar to other research (Lausen and Barclay 2003, Dzal and Brigham 2013, Johnson and Lacki 2014), pregnant and lactating females had a greater decline in torpor depth and HI than post-lactating. This is not surprising given that torpor use delays parturition and weaning (Racey and Swift 1981, Kurta et al. 1987, Wilde et al. 1999), which may result in fitness consequences for females (Kunz et al. 1998, Frick et al. 2010*b*). The greater torpor depths in post-lactating females may be to conserve energy gained from foraging to prepare for hibernation and reproduction the following spring (Kunz et al. 1998, Jonasson and Willis 2011, Dzal and Brigham 2013). However, post-lactating females had a more negative effect on torpor duration than pregnant females, although there was some uncertainty in the posterior estimates. This may be explained by the torpor threshold used under-estimating torpor duration among post-lactating females (see section 4.4 below).

I expected the cold, wet spring weather in Newfoundland to place a selective pressure on greater torpor use among pregnant females compared to lactating females. As predicted, pregnant females had a higher mean torpor duration, depth, and HI than lactating females and the lactating condition had the most negative effect on torpor

duration, depth, and HI. These results differ from other studies of *M. lucifugus* (Dzal and Brigham 2013) that found greater torpor use during lactation than pregnancy. Weather conditions at the study site were colder, windier, and wetter during the pregnancy period than the lactation period. These conditions are also associated with lower insect availability and abundance (Taylor 1963, Anthony and Kunz 1977, Fouts 2018, in prep). Therefore, pregnant females in Newfoundland likely had higher energetic costs from the environment than lactating females, in which torpor was likely necessary for pregnant females to survive the environmental conditions in June and early July (Taylor 1963, Wojciechowski et al. 2007, Stawski et al. 2014). Additionally, females may maximize reproductive success in these environments by delaying parturition until temperatures are warmer for juvenile growth (Tuttle 1976, Gillooly et al. 2002, Willis et al. 2006) and when insect availability is higher to meet the energetic demands of lactation (Anthony and Kunz 1977, Millar 1978, Barclay 1994, Fouts 2018, in prep). In my study, the earliest approximated parturition date was later than that of other populations of *M. lucifugus* and occurred shortly before the maximum mean ambient temperature of the study (Appendix C). Parturition at the study site occurred in mid July, whereas parturition in other populations of *M. lucifugus*, range from the end of May to early July (Kunz 1971, Slough and Jung 2008, Frick et al. 2010b, Dzal and Brigham 2013, Kaupas 2016).

In response to the late parturition dates, lactating females may reduce torpor use compared to pregnancy to ensure juveniles are weaned in time to gain fat reserves before winter (Kunz et al. 1998, Frick et al. 2010b). The juvenile development period in my study was about 13-15 days, which is similar to studies of *M. lucifugus* at higher latitudes (e.g., Northwest Territories) (Kaupas 2016). However, it is shorter than studies at lower latitudes (e.g., Iowa), where volant juveniles were found 4-5 weeks after parturition



(Kunz 1971). The short juvenile development period in my study may be due to lactating females using torpor less in climates with cold spring weather compared to lactating females of *M. lucifugus* populations in other climates.

Pregnant females had the greatest amount of inter-individual variation in torpor duration, depth, and HI (see section 4.2 below) and this variation may be due to individuals being in different stages of pregnancy. Racey and Speakman (1987) (cited in Aldridge and Brigham 1991) found that energetic expenditure during early pregnancy was low, indicating torpor use, and energetic expenditure increased during late pregnancy, likely due to maintaining body temperature. Little is known about torpor patterns in early pregnancy, however, there were likely females in early pregnancy within the not-obviously pregnant group in my study's sample. If this was the case, then the greater torpor use in not-obviously pregnant females suggests that saving energy in early pregnancy likely outweighs the cost of deep and prolonged torpor on embryonic and early fetal development. The costs of torpor use on fetal development may become more pronounced in late pregnancy (Racey and Swift 1981, Racey et al. 1987, Aldridge and Brigham 1991). Saving energy during early pregnancy may be important for reproductive success because if energetic demands become too high, females may abort a fetus (Grindal et al. 1992, Lewis 1993). Aborted fetuses in various stages were observed underneath bat boxes at the study site and may be reflective of some individuals being unable to meet energetic demands.

#### **4.2 Individual and Body Condition Index**

Variation among individuals was one of the most important predictors of torpor duration, depth, and HI and as predicted, some individuals within the same reproductive

class used different torpor strategies. The individuals with the most negative and most positive posterior estimates for each of torpor duration, depth, and HI were pregnant, suggesting more inter-individual variation among pregnant individuals than lactating and post-lactating individuals. Parturition was asynchronous among females in my study and may be reflective of variation in torpor use among individuals during pregnancy. The different torpor use may have fitness implications as the timing of parturition can influence offspring survival (Kunz et al. 1998, Willis et al. 2006, Frick et al. 2010*b*). Potential explanations for inter-individual variation in torpor use include genetic variation in torpor-related traits and body condition. Given that the timing of hibernation emergence is heritable (Lane et al. 2011), there may be genetic variation among individuals associated with the expression of torpor (Ellison 1993). Additionally, basal metabolic rate is heritable and varies among intraspecific individuals (White and Kearney 2013), which may result in inter-individual variation in body condition.

I found small correlations between body condition index (BCI) and torpor duration, depth, and HI, which supports my hypothesis that body condition may explain at least some inter-individual variation in torpor use. I predicted that BCI would be positively correlated with torpor duration, depth, and HI given that a minimum amount of fat is required for arousal from torpor (Terrien et al. 2009, Stawski and Geiser 2010, Kobbe et al. 2011, Vuarin et al. 2013). Contrary to my predictions, but similar to some studies of heterothermic mammals (Christian and Geiser 2007, Rambaldini and Brigham 2008), BCI was negatively correlated with torpor duration, depth, and HI. This suggests that individuals in the best body condition can limit the negative consequences of torpor use due to sufficient fat reserves, which may reduce the necessity of torpor (Christian and Geiser 2007, Rambaldini and Brigham 2008). However, individuals with the lowest BCI

in my study used torpor to a lesser extent than individuals with an average BCI, indicating that the relationship between BCI and torpor use is nonlinear. This supports other studies that found individuals in very poor body condition to limit torpor use compared to individuals in better body condition (Terrien et al. 2009, Stawski and Geiser 2010, Kobbe et al. 2011, Vuarin et al. 2013). Individuals in poor body condition may limit torpor use to optimize foraging rather than conserve energy (Vuarin et al. 2013). BCI also varied among reproductive conditions, with lactating females having the highest values and non-reproductive females having the lowest. Reproductive females need to be in good body condition to successfully raise offspring (Barclay et al. 2004, Jonasson and Willis 2011) and may explain the differences in BCI between non-reproductive females and lactating and post-lactating females. Additionally, there may have been temporal changes in body mass as the availability of insects (prey) increases from spring to summer (Anthony and Kunz 1977, Fouts 2018, in prep). Warmer temperatures, and likely higher insect activity (Taylor, 1963, Fouts 2018, in prep), were present when lactating and post-lactating females were sampled compared to the others.

In addition to inter-individual variation, there was a large amount of intra-individual variation in torpor use. This is similar to other studies on daily torpor in mammalian heterotherms (Canale et al. 2011, Kobbe et al. 2011, Vuarin et al. 2013) and suggests that individual plasticity in response to environmental conditions may be an important factor. Additionally, the amount of phenotypic flexibility in daily torpor may differ among individuals (Canale et al. 2011, Kobbe et al. 2011, Vuarin et al. 2013) and further research on the causes of inter-individual variation will be useful for identifying the fitness implications of various thermoregulatory responses (Frick et al. 2010*b*, Lane et al. 2011).

### 4.3 Weather

Some weather variables had important effects on torpor frequency and the heterothermy index (HI). I predicted that low ambient temperatures, high wind speed, and precipitation would be associated with increased torpor frequency, duration, depth, and HI. As predicted, high wind speed and precipitation was associated with increased use of torpor and maximum wind speed was positively associated with HI. Given the effect of wind and precipitation on heat loss during flight (Voigt et al. 2011) and on insect (prey) activity (Racey et al. 1987), bats may forego foraging and use torpor. Therefore, the reduction in bat activity due to weather (Anthony et al. 1981, Kurta 1986, Klug-Baerwald et al. 2016) may affect torpor use. Despite wind and precipitation being the most important variables for explaining torpor frequency, individuals started with a high probability of using torpor when there was no wind or precipitation. This suggests that other variables not measured affected torpor frequency. The variation in torpor use across days may be better explained by weather conditions (Klug and Barclay 2013) and time spent foraging (Rintoul and Brigham 2014) the night before than by daily weather conditions. Further, previous weather conditions may influence insect (prey) availability the night before (Taylor 1963, Anthony and Kunz 1977, Racey et al. 1987) and may be more informative of torpor use the following day. My results demonstrate the importance of using a multivariate approach when including weather as a variable for explaining thermoregulatory patterns.

#### 4.4 Problems Associated with Torpor Thresholds

In general, the torpor threshold used resulted in a reliable estimate of torpor frequency, duration, and depth for pregnant, lactating, and non-reproductive females given the skin temperature patterns used among these individuals. However, my results demonstrate that current methods for torpor thresholds (e.g. modal and active temperature (Barclay et al. 2001, McKechnie et al. 2007)) under-estimate torpor use for individuals maintaining low body temperature over a day or multiple days and for individuals emerging torpid. Post-lactating and not-obviously pregnant females had skin temperature ( $T_{sk}$ ) patterns that involved maintaining low  $T_{sk}$  over one day, in which normothermia was never reached before emergence. Additionally, one not-obviously pregnant individual maintained  $T_{sk}$  below normothermia over multiple days. This resulted in a torpor threshold from 22-29 °C, which resulted in durations and depths inconsistent with the  $T_{sk}$  patterns. The measured torpor duration for individuals maintaining low  $T_{sk}$  over a day or multiple days was 6 hours instead of 24 hours. For example, the lowest  $T_{sk}$  for not-obviously pregnant females was 6 °C, however, the difference from the onset of torpor (depth) was 16 °C, which does not accurately reflect the magnitude of torpor depth.

The heterothermy index (HI) was likely under-estimated for post-lactating and not-obviously pregnant females. When modal values are used in place of optimum body temperature to measure HI, it underrepresents individuals maintaining low body temperatures for extended periods of time, as exhibited during hibernation (Boyles et al. 2011). However, individuals may continue to use torpor for extended periods after hibernation and during reproduction, which would result in HI being uninformative without a known optimal body temperature (Boyles et al. 2011, Brigham et al. 2011). A

more accurate threshold and metric may have resulted in more certainty in the parameter estimates among reproductive conditions in my study. The effect of the post-lactating and not-obviously pregnant conditions on torpor patterns were likely conservative estimates and do not reflect the extent to which torpor was used. My results demonstrate that the current methods used in defining torpor thresholds based on  $T_{sk}$  (Barclay et al. 2001, McKechnie et al. 2007) are probably not suitable for measuring torpor use during reproduction, given that extended periods of torpor may be used. An alternative method is establishing concurrent measures of metabolic rates or body temperature with  $T_{sk}$  to extrapolate a threshold (Willis 2007), which may better quantify the effect of extrinsic and intrinsic variables on torpor patterns.

#### **4.5 Conservation Implications**

My study demonstrated that individual female *Myotis lucifugus* may employ different thermoregulatory strategies depending on intrinsic factors (e.g., body condition and reproductive condition) and extrinsic factors (e.g., weather). The high amount of torpor use among females in spring suggests that thermoregulatory strategies are likely pertinent for the survival and reproduction of this species in regions with cool climates. Climate change, disease, and roost availability may affect torpor use and have implications for the population growth and persistence of insectivorous heterothermic species (Frick et al. 2010b, Jonasson and Willis 2011, Francl et al. 2012, English et al. 2018). It will be important to understand the causes of inter-individual variation in torpor use as individuals with a higher degree of phenotypic flexibility may be more successful at persisting through environmental variations (Vuarin et al. 2013), such as those caused by climate change (Nussey et al. 2007, Charmantier et al. 2008), or diseases affecting

thermoregulation, such as white-nose syndrome (Jonasson and Willis 2011, Norquay and Willis 2014). Reproductive timing and rates may be influenced by variation in environmental variables (Racey and Swift 1981, Grindal et al. 1992, Lewis 1993). Years with extreme weather conditions may decrease insect abundance (Ransome and McOwat 1994, Rodenhouse et al. 2009, Frick et al. 2010*b*, Hallmann et al. 2017, English et al. 2018) and have been associated with lower reproductive rates and later reproductive timing in temperate bat species (Racey and Swift 1981, Grindal et al. 1992, Lewis 1993). This is likely due to increased thermoregulatory costs and a reduction in food availability, which may lead females to increase their use of torpor or abandon reproduction due to energy shortages (Grindal et al. 1992, Lewis 1993).

White-nose syndrome may negatively affect reproductive success by disrupting the thermoregulatory strategies used among pregnant females during cold spring weather (Willis et al. 2006, Frick et al. 2010*b*). Females in early spring may rely on torpor use to save energy and time parturition until it is most favourable for offspring survival (Willis et al. 2006, Frick et al. 2010*b*). If individuals in very poor body condition use less torpor, then females coming out of hibernation with low body mass due to white-nose syndrome may limit torpor use in spring (Jonasson and Willis 2011). This may result in earlier parturition dates (Francl et al. 2012) that occur before warm ambient temperatures are reached, which may not be conducive for juvenile growth and survival (Tuttle and Stevenson 1982, Willis et al. 2006). Identifying the fitness consequences of thermoregulatory strategies among reproductive females in regions without white-nose syndrome may help predict the effects of this disease on the reproductive success of bats in regions with white-nose syndrome (Frick et al. 2010*b*).

The availability of roosts with a broad thermal regime may be important to the fitness of female bats, given the various thermoregulatory strategies used among individuals and reproductive conditions in my study. Bat boxes have been suggested as a conservation tool for bats by acting as a replacement to trees and cabins (Brittingham and Williams 2000, Smith and Agnew 2002, White 2004, Flaquer et al. 2005). The females in my study used a variety of thermoregulatory patterns while roosting in bat boxes, which suggests that bat boxes may be suitable to most of the thermoregulatory needs of female *M. lucifugus* in cool, wet regions. However, there were some differences in torpor patterns between pregnant females in bat boxes and cabins (Appendix A). The greatest torpor depth and lowest  $T_{sk}$  recorded was by a pregnant female roosting in a cabin and was 29.32°C and 4.33°C, respectively, and reflects greater torpor depths than females roosting in a bat box where the greatest depth was 23.26°C and lowest  $T_{sk}$  was 14.22°C. Temperatures can vary by location within a building (Johnson and Lacki 2014) and may explain the deeper torpor bouts used by bats roosting in the cabin compared to bat boxes. Additionally, most of the adult females vacated the study site by August 15 and some post-lactating females were found roosting in trees (Appendix H). Tree roosts may facilitate deeper torpor use than anthropogenic structures and may be more suitable for the thermoregulatory response employed by postlactating females (Johnson and Lacki 2014, Rintoul and Brigham 2014, Kaupas 2016). This suggests that bat boxes may not have a broad enough thermal regime to be suitable for all thermoregulatory strategies used among female *Myotis lucifugus*. The difference in torpor use between roost types and the use of trees by some individuals in my study suggests that a variety of roost types



are important to the thermoregulatory strategies used among females bats (Lausen and Barclay 2006, Johnson and Lacki 2014).

## 5. CONCLUSION

The results of my study highlight that reproductive condition, inter-individual variation, and weather explain variation in torpor use among female *Myotis lucifugus*. The influence of reproductive condition and weather on torpor patterns have been widely studied (Audet and Fenton 1988, Hamilton and Barclay 1994, Chruszcz and Barclay 2002, Willis et al. 2006, Solick and Barclay 2007, Dzal and Brigham 2013, Johnson and Lacki 2014, Rintoul and Brigham 2014, Czenze et al. 2017), however, this study illustrates the importance of including inter-individual variation within reproductive condition as an explanatory variable when explaining thermoregulatory strategies. Inter-individual variation in torpor use may have implications for fitness and some thermoregulatory strategies may be selected over others. Therefore, further research linking individual characteristics (e.g., heritable traits and body condition) to the various thermoregulatory strategies used would be useful in understanding how populations will respond to a changing environment or disease.

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## APPENDIX A

### Roost Type and Torpor Patterns Among Pregnant Females

In addition to bat boxes, data was collected from pregnant females roosting in a cabin from 30 June to 08 July 2017. To determine if there were differences in torpor use between females roosting in the cabin and bat boxes, a multiple nominal Bayesian analysis was performed on torpor duration, depth, and the heterothermy index (HI). The prior probabilities for roost type and individual were made relatively uniform. The models were made hierarchical with bat day and individual bat as random effects nested within the roost type predictor variable. Additionally, the torpor candidate models were run with cabin data and without it to determine if the cabin data changed the outcome.

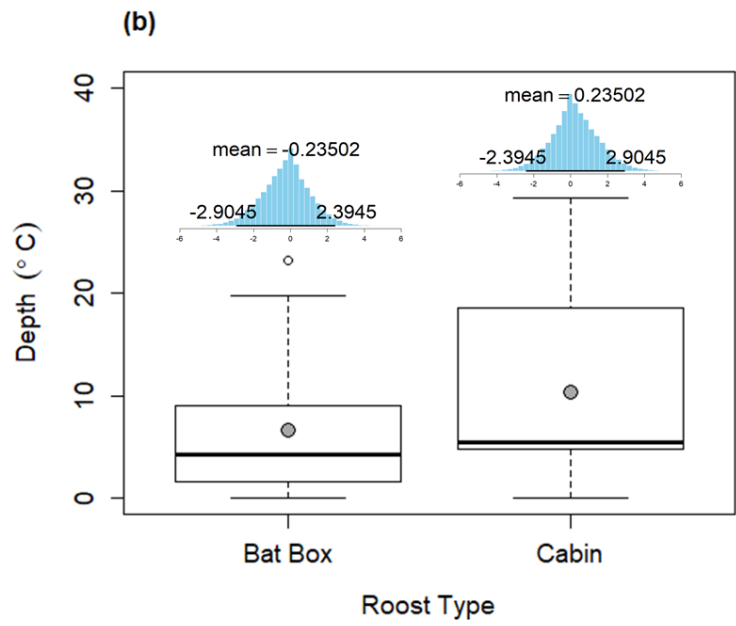
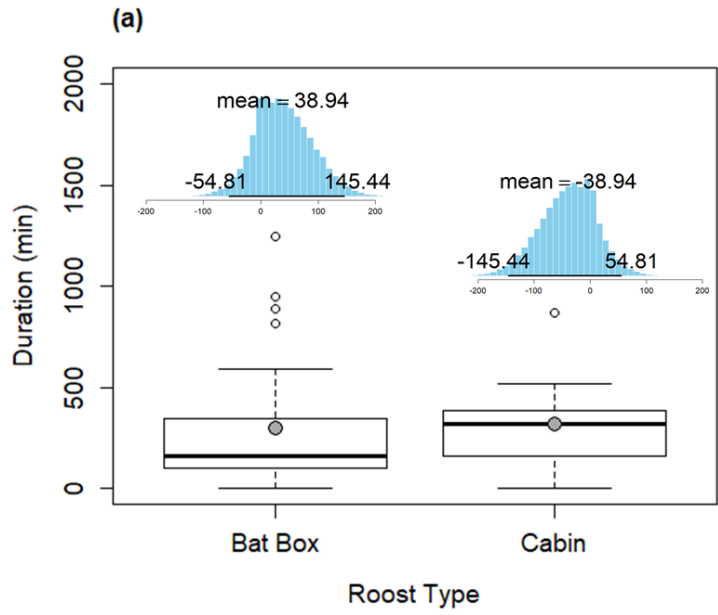
Females roosting in cabins had higher mean torpor duration, depth, and HI than females roosting in bat boxes (Table A1) (Figure A1). The greatest depth of a female roosting in the cabin was 29.32 °C below the torpor threshold and the lowest  $T_{sk}$  was 4.33 °C, whereas in bat boxes, the greatest depth was 23.26 °C and the lowest  $T_{sk}$  was 14.22 °C. For example, on the same day, females roosting in the cabin used torpor at a greater extent than females roosting in a bat box (Figure A2). Bat box had a positive effect on torpor duration while the cabin roost had a positive effect on torpor depth and HI (Figure A1). However, these effects were small and the 95% HDI of the posterior distributions of roost type for each torpor pattern overlapped zero (Figure A2), indicating uncertainty in the estimates. Despite the small effect size, removing the cabin data changed how the mean torpor depth for pregnant females compared with post-lactating females. The mean torpor depth of pregnant females from both bat boxes and the cabin ( $7.7 \pm 7.9$  °C) was

higher than post-lactating females ( $7.1 \pm 6.0$  °C). Removing the cabin data resulted in a lower mean torpor depth in pregnant females ( $6.6 \pm 7.0$  °C) compared to post-lactating females. Additionally, removing the cabin data from the torpor models changed which model explained most of the variation in torpor frequency, depth, and HI. The model that explained the variation in torpor duration did not change. Therefore, data from individuals roosting in a cabin were removed from the data set to avoid any influence roost type may have on the outcome (Lausen and Barclay 2006, Rintoul and Brigham 2014).

Temperatures within a building can vary by location (Johnson and Lacki 2014) and may result in bats using torpor differently depending on their location within a cabin. Bat boxes do not have the variety of spaces that buildings have and bats may be limited in their torpor use.

Table A1. Mean  $\pm$  SD torpor characteristics and lowest  $T_{sk}$  (skin temperature) of pregnant female *Myotis lucifugus* roosting in bat boxes and cabins in Newfoundland from 30 June to 08 July 2017. n refers to the number of individuals and N refers to the number of bat days.

Torpor Characteristic	Bat Box	n, N	Cabin	n, N
Duration (min)	298.70 $\pm$ 318.70	11, 30	320.00 $\pm$ 223.00	5, 13
Depth (°C)	6.60 $\pm$ 7.00	11, 30	10.30 $\pm$ 9.40	5, 13
HI (°C)	3.90 $\pm$ 4.10	11, 30	4.90 $\pm$ 5.30	5, 13
Lowest $T_{sk}$ (°C)	14.22	11, 30	6.00	5, 13





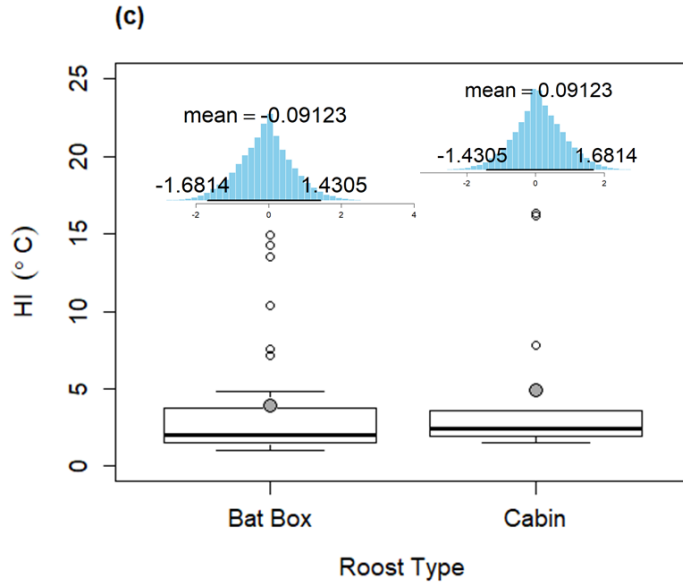


Figure A1. Torpor (a) duration, (b) depth, and (c) the heterothermy index between pregnant *Myotis lucifugus* roosting in bat boxes ( $n = 11$ ,  $N = 30$ ) and in a cabin ( $n = 5$ ,  $N = 13$ ) in Newfoundland. The top and bottom of each box show the upper and lower quartiles and the dashed vertical lines represent the maximum and minimum values. The black bars represent the median, the grey dots represent the mean, and open circles represent outliers. The posterior distributions of roost type are displayed above the boxes.  $n$  = number of individual bats,  $N$  = number of bat days.

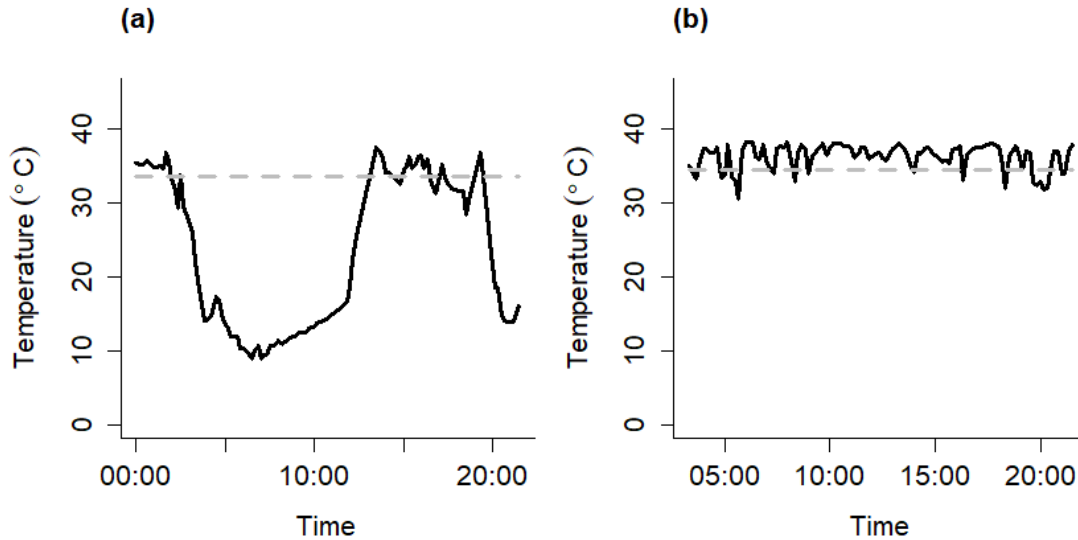


Figure A2. Skin temperature patterns of pregnant *Myotis lucifugus* roosting in a (a) cabin and (b) bat box on July 02, 2017 on the Avalon Peninsula in Newfoundland.

## APPENDIX B

### Examples of Thermoregulatory Patterns Among Individuals, Reproductive Conditions, and Days

Torpor patterns varied among individuals in the same reproductive condition and on the same day. For example, two pregnant females used two different thermoregulatory patterns on the same day (Figure B1). One individual had long and deep drops in skin temperature ( $T_{sk}$ ), while the other maintained  $T_{sk}$  at normothermia. Additionally, the recaptured individual had different thermoregulatory patterns during pregnancy and

lactation on days where mean ambient temperature was similar (16.3 and 15.7 °C) (Figure B2). During pregnancy, this individual exhibited deeper, and longer drops in  $T_{sk}$  compared to lactation.

Torpor patterns for individuals varied across days, and this variation may be due to differences in weather. For example, the same pregnant individual used different torpor patterns on two different days (Figure B3). The individual had a greater mean torpor duration and depth on the day with higher maximum wind speeds and more precipitation (550 min; 18.2 °C) compared to the day with lower wind speeds and precipitation (250 min; 1.2 °C). The average ambient temperature was similar for both days.

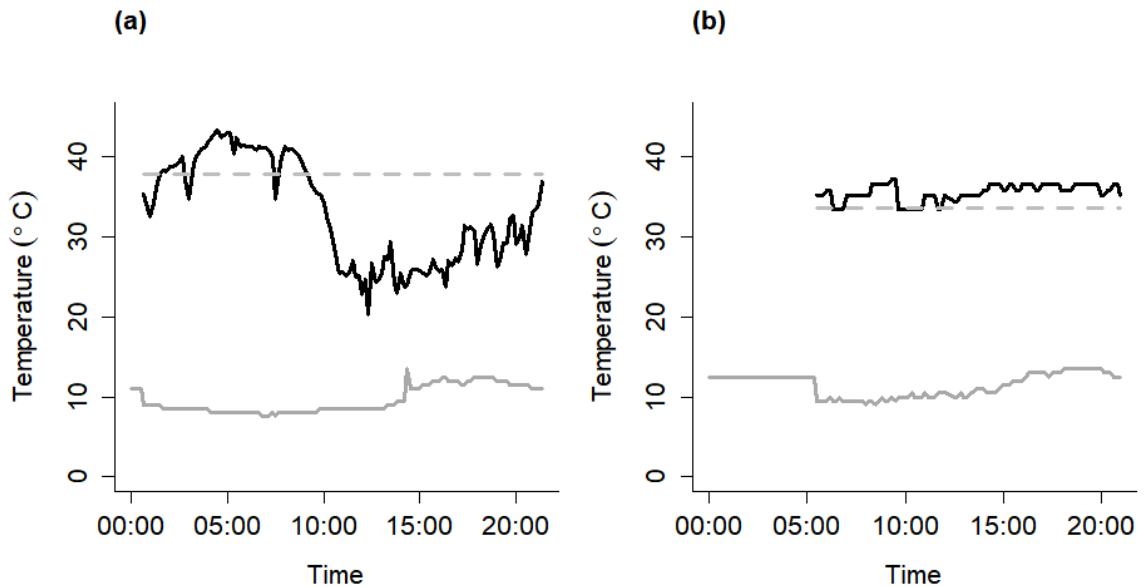


Figure B1. Two pregnant *Myotis lucifugus*, individual (a) #23 and (b) #24 on 05 July 2017. Individual #23 weighed 8.91 g at capture and #24 weighed 10.22 g. The black line represents skin temperature (°C), the dashed grey line represents the torpor onset threshold (°C), and the solid grey line represents roost temperature (°C).

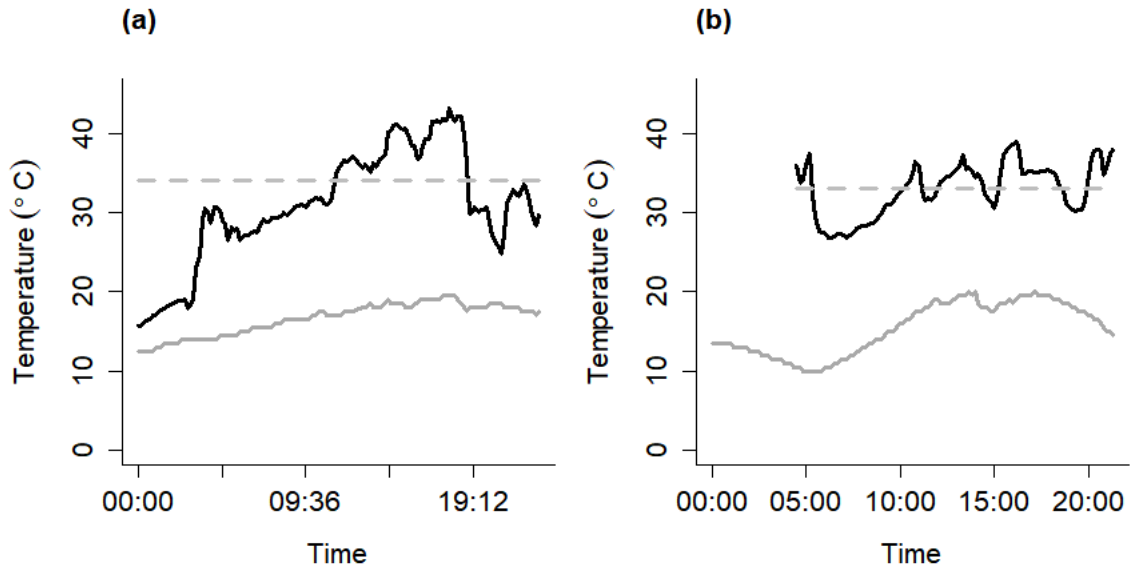


Figure B2. The same individual female *Myotis lucifugus* during (a) pregnancy and during (b) lactation on 08 July 2017 and 23 July 2017, respectively. On 08 July 2017, the average ambient temperature was 16.3 °C, the maximum wind speed was 40 km/hr, and there was 3 mm of precipitation. On 23 July 2017, the average ambient temperature was 15.7 °C, the maximum wind speed was 50 km/hr, and there was no precipitation. The black line represents skin temperature (°C), the dashed grey line represents the torpor onset threshold (°C), and the grey line represents roost temperature (°C).

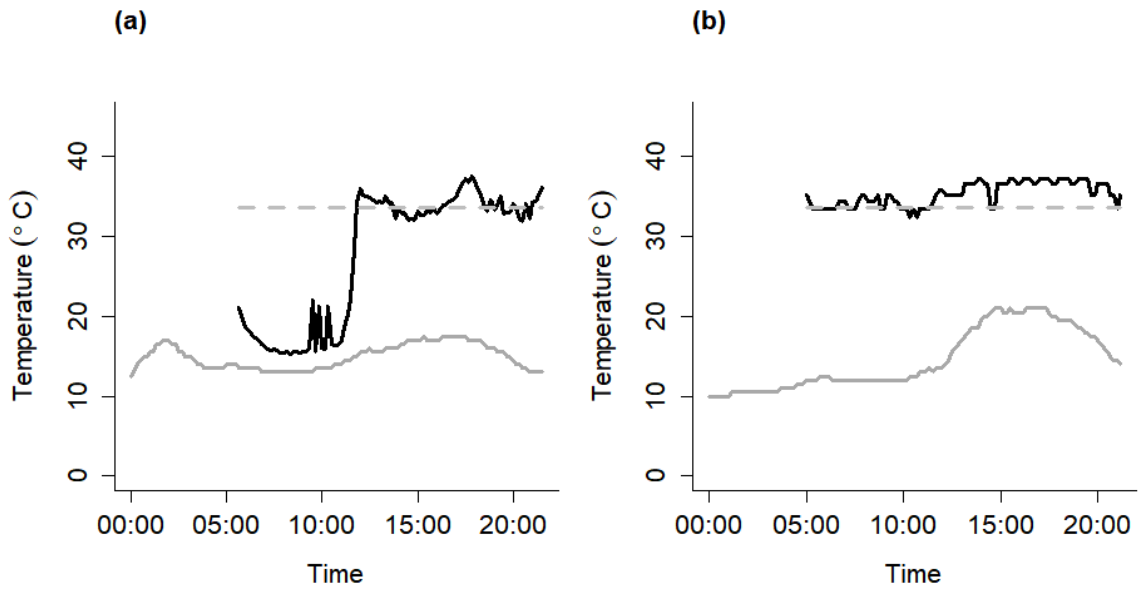


Figure B3. A pregnant *Myotis lucifugus* on (a) 03 July 2017 and (b) 04 July 2017. The average ambient temperature, maximum wind speed, and precipitation was 15.2 °C, 57 km/hr, and 0.6mm on 03 July 2017 and 14.9 °C, 48 km/hr, and 0.3 mm on 04 July 2017. The black line represents skin temperature (°C), the dashed grey line represents the torpor onset threshold (°C), and the solid grey line represents roost temperature (°C).

## APPENDIX C

### Weather and Torpor Patterns Between 2016 and 2017

The mean daily ambient temperature, relative humidity, maximum wind speed, and precipitation did not differ between 2016 and 2017 at Salmonier Nature Park and St. John's Newfoundland (Table C1). There was some variation among dates within a year, however, the peak in mean daily ambient temperature occurred on July 15 for both years (Figure C1). The posterior distributions of year overlapped zero, suggesting little effect of year (Figure C2).

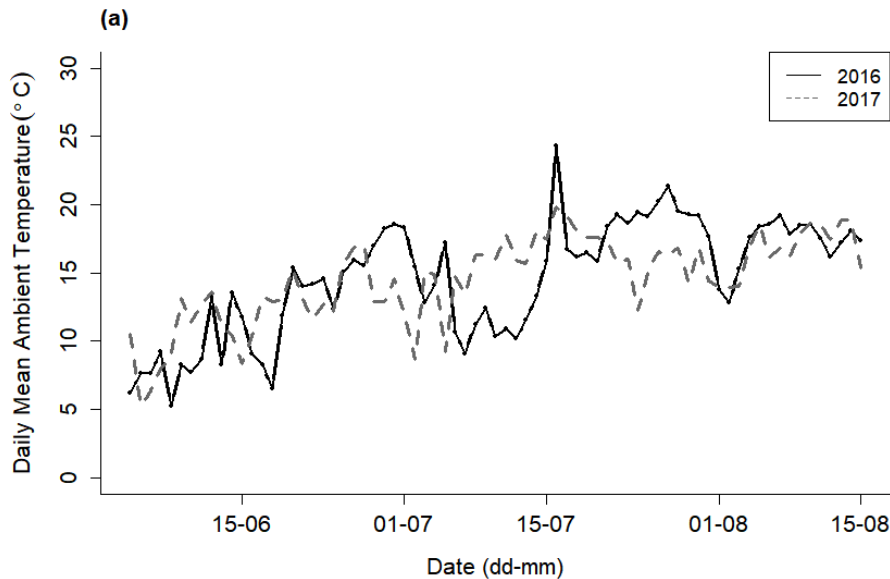
There were some differences in torpor duration for not-obviously pregnant females and torpor depth and the heterothermy index for post-lactating females between 2016 and 2017 (Table C2). However, the posterior distributions of year overlapped zero, indicating that year had little effect on torpor patterns (Figure C3). Additionally, the sample size for 2016 was much smaller than 2017.

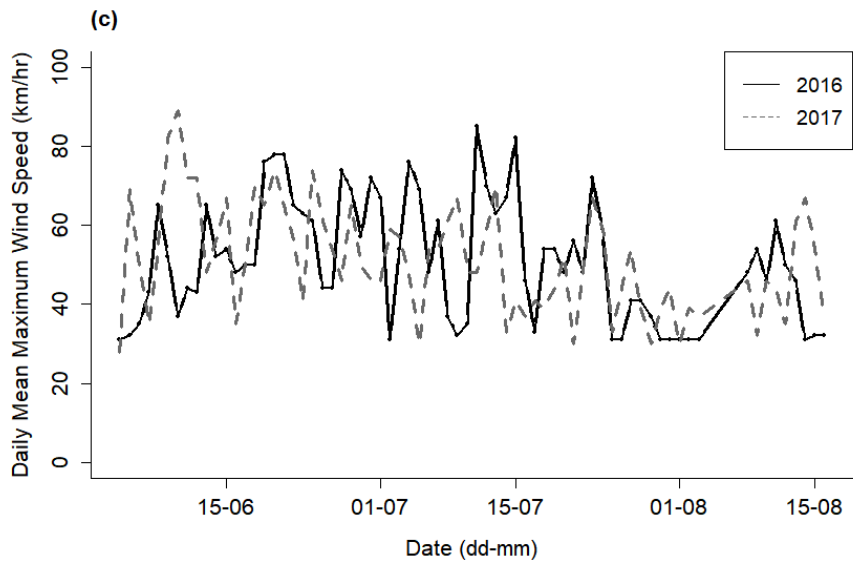
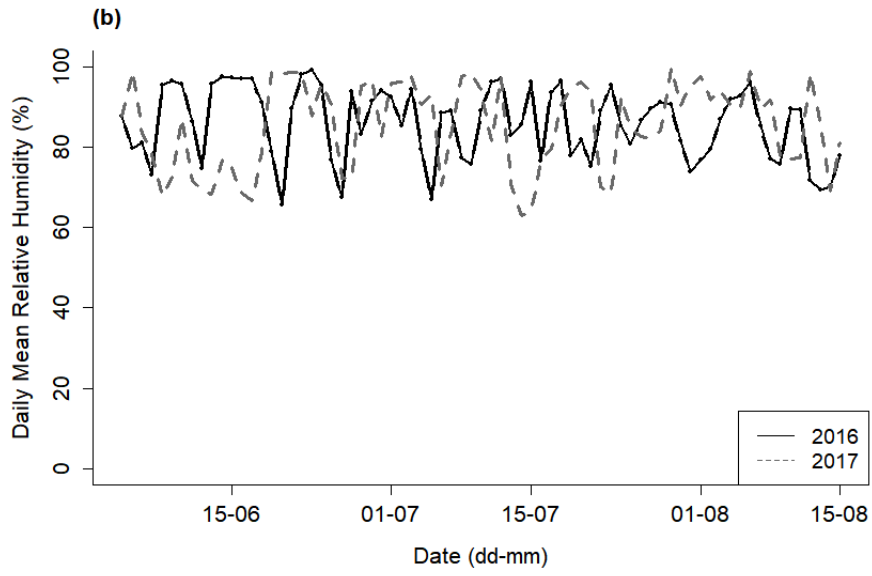
Table C1. Mean  $\pm$  SD weather variables from 2 June to 16 August, 2016 and 2017. Temperature and humidity were recorded using iButtons at Salmonier Nature Park, Newfoundland. Wind speed and precipitation data were taken from Environment Canada's weather station in St. John's, Newfoundland. n refers to the number of days.

Weather Variable	2016	n	2017	n
Mean ambient temperature ( $^{\circ}$ C)	14.6 $\pm$ 4.2	73	14.6 $\pm$ 3.2	73
Relative humidity (%)	85.9 $\pm$ 9.1	73	85.4 $\pm$ 10.8	73
Maximum wind speed (km/hr)	51.2 $\pm$ 15.5	74	51.1 $\pm$ 14.0	70
Precipitation (mm)	3.7 $\pm$ 9.8	72	3.7 $\pm$ 7.9	70

Table C2. Mean  $\pm$  SD torpor characteristics of lactating, post-lactating, and not-obviously pregnant *Myotis lucifugus* in Newfoundland in 2016 and 2017. n refers to the number of individuals and N refers to the number of bat days.

2016						
Torpor Characteristic	Not-Obviously Pregnant	n, N	Lactating	n, N	Post-Lactating	n, N
Duration (min)	572.00 $\pm$ 207.17	2, 5	248.75 $\pm$ 159.95	3, 8	310.00 $\pm$ 167.03	3, 3
Depth ( $^{\circ}$ C)	9.63 $\pm$ 5.05	2, 5	4.92 $\pm$ 4.42	3, 8	10.93 $\pm$ 1.10	3, 3
HI ( $^{\circ}$ C)	5.66 $\pm$ 3.48	2, 5	2.69 $\pm$ 0.94	3, 8	6.29 $\pm$ 2.09	3, 3
2017						
Torpor Characteristic	Not-Obviously Pregnant	n, N	Lactating	n, N	Post-Lactating	n, N
Duration (min)	891.76 $\pm$ 402.31	2, 17	242.29 $\pm$ 200.47	8, 34	328.24 $\pm$ 311.72	5, 34
Depth ( $^{\circ}$ C)	8.34 $\pm$ 5.90	2, 17	4.09 $\pm$ 3.91	8, 34	6.76 $\pm$ 6.18	5, 34
HI ( $^{\circ}$ C)	5.82 $\pm$ 3.16	2, 17	2.67 $\pm$ 1.65	8, 34	3.70 $\pm$ 2.84	5, 34







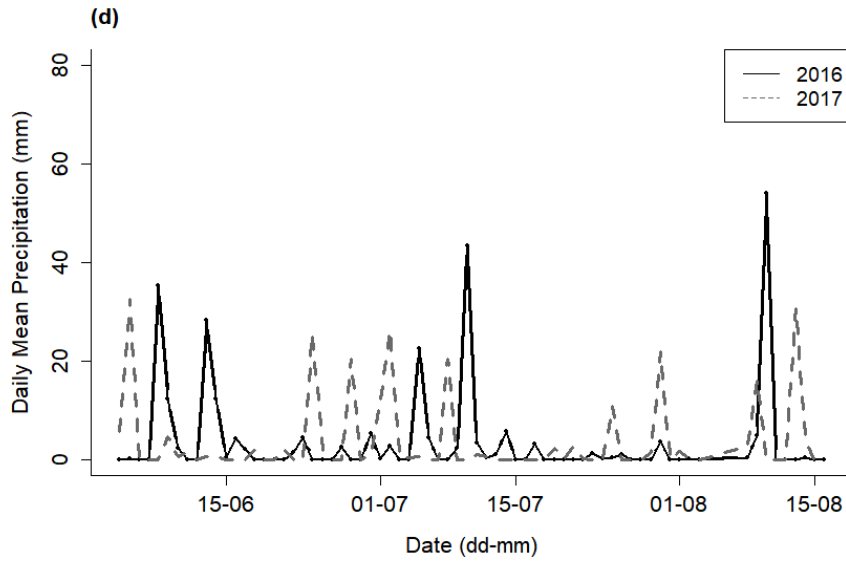


Figure C1. Daily mean ambient temperature (a), relative humidity (b), maximum wind speed (c), and precipitation (d) from June 2 to August 16, 2016 and 2017. The solid black line represents 2016 and the dashed grey line represents 2017. Temperature and humidity were recorded using iButtons at Salmonier Nature Park, Newfoundland. Wind speed and precipitation data were taken from Environment Canada’s weather station in St. John’s, Newfoundland.

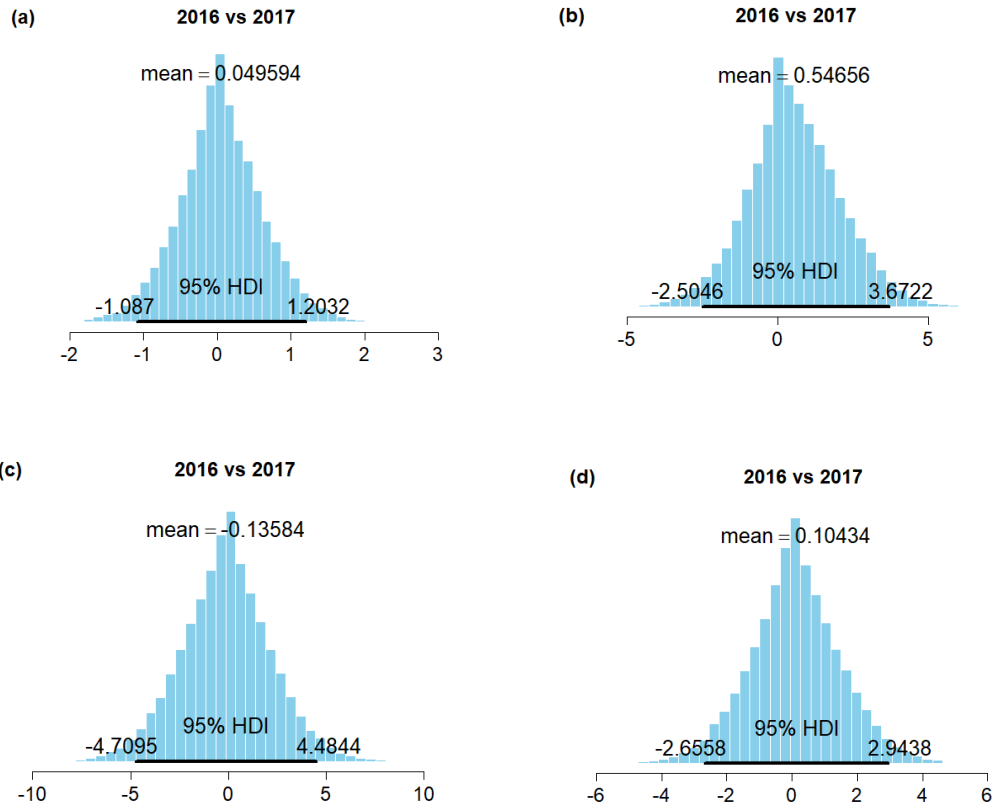


Figure C2. The posterior distributions of the differences in estimates between years for daily mean (a) ambient temperature, (b) relative humidity, (c) maximum wind speed, and (d) precipitation. Data was collected from 2 June to 16 August, 2016 and 2017. Temperature and humidity were recorded using iButtons at Salmonier Nature Park, Newfoundland. Wind speed and precipitation data were taken from Environment Canada's weather station in St. John's, Newfoundland

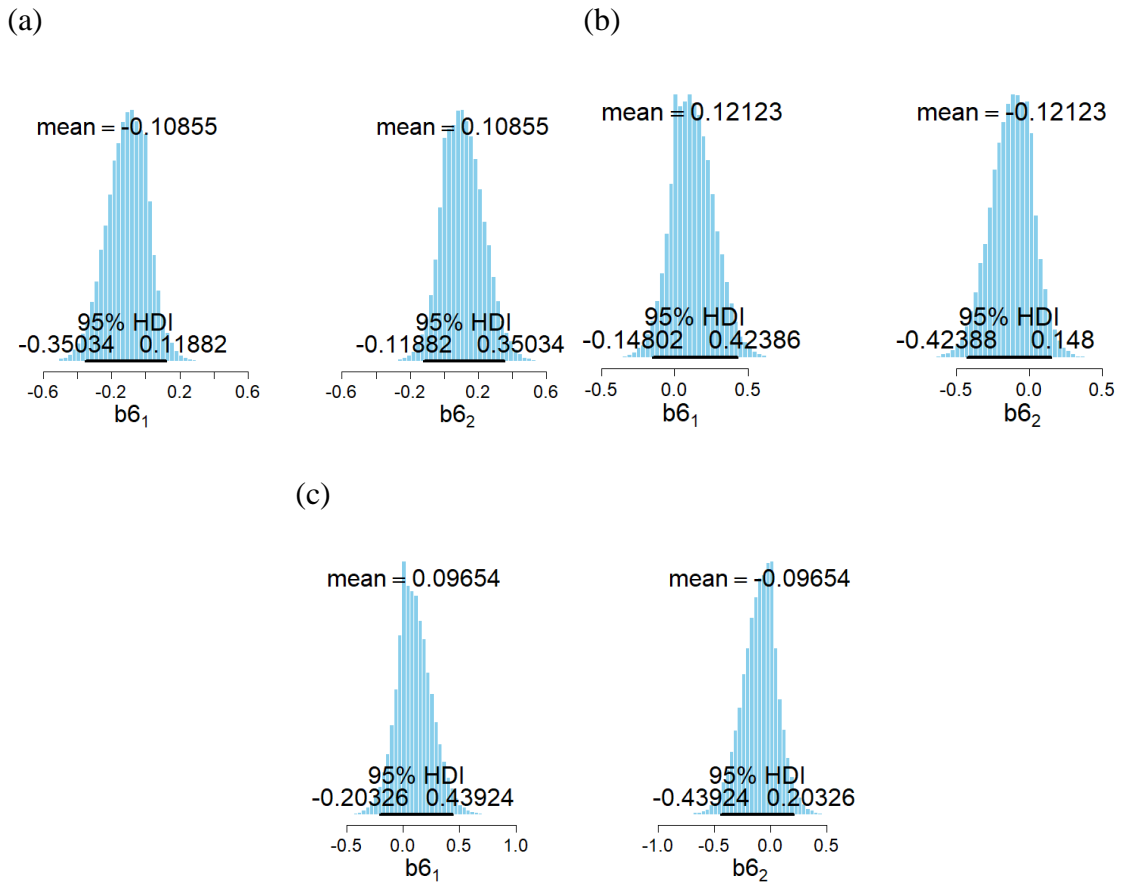


Figure C3. The posterior distributions of 2016 and 2017 for torpor (a) duration, (b) depth, and (c) the heterothermy index. Data was taken from not-obviously pregnant, lactating, and post-lactating female *Myotis lucifugus* at Salmonier Nature Park, Newfoundland between June and August, 2016 and 2017.

## **APPENDIX D**

### **Posterior Distributions for Sampling Period and Weather Conditions**

The posterior distributions of reproductive (sampling) period for each weather variable (mean and minimum ambient temperature, maximum wind speed, and precipitation) demonstrate that weather differed among sampling periods. The greatest difference in mean ambient temperature occurred between the not-obviously pregnant and lactating periods (Figure D1a). For minimum ambient temperature and maximum wind speed, the greatest difference was between the not-obviously pregnant and post-lactating periods (Figure D1b, c). The greatest difference in precipitation occurred between the pregnant and lactating periods (Figure D1d).

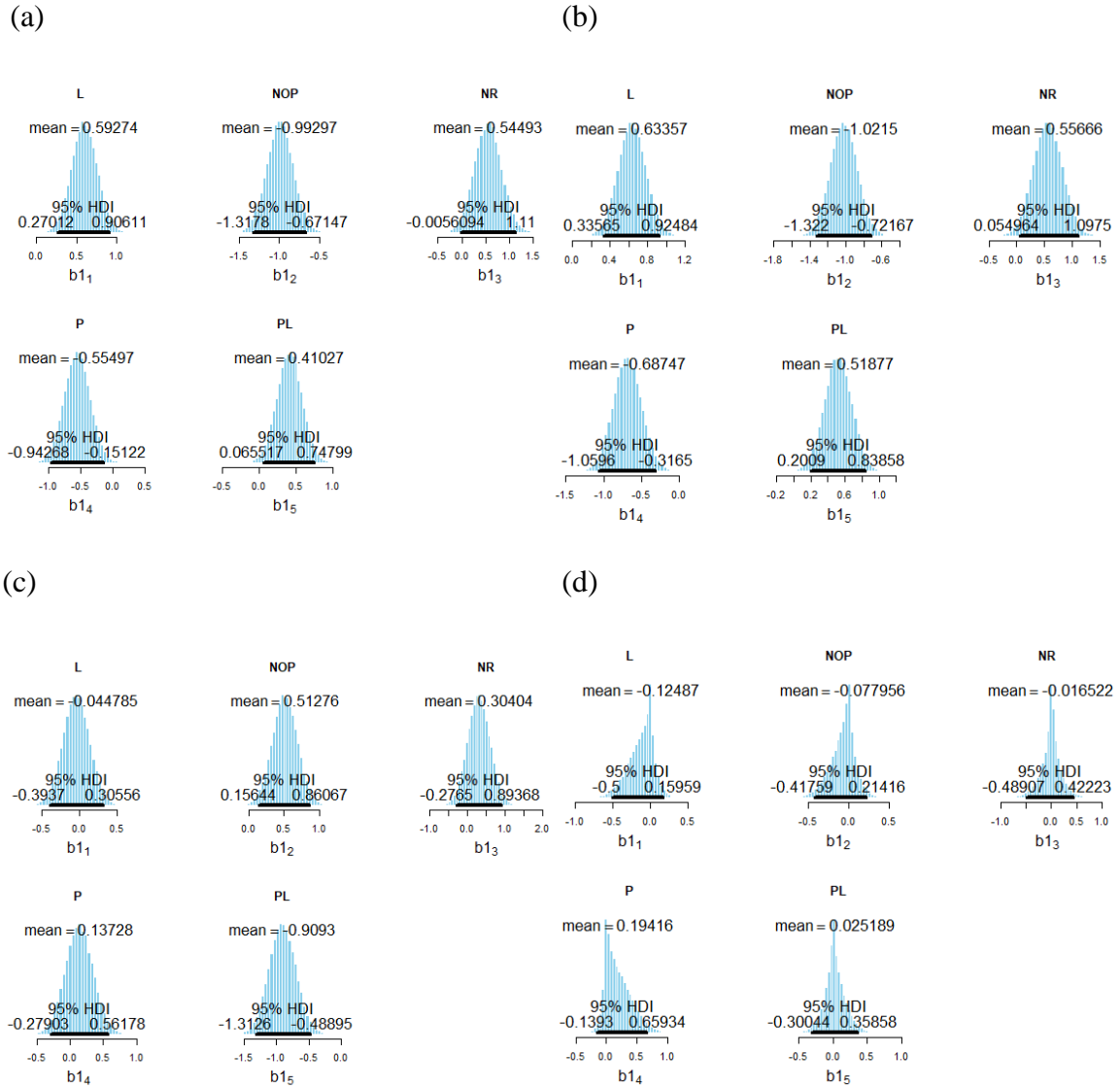


Figure D1. The posterior distributions of the estimates of the lactating, not-obviously pregnant, non-reproductive, pregnant, and post-lactating periods for (a) mean ambient temperature, (b) minimum ambient temperature, (c) maximum wind speed, and (d) precipitation. Data was collected from 2 June to 16 August, 2016 and 2017. Temperature and humidity were recorded using iButtons at Salmonier Nature Park, Newfoundland. Wind speed and precipitation data were taken from Environment Canada’s weather station in St. John’s, Newfoundland. L = lactating, NOP = not-obviously pregnant, NR = non-reproductive, P = pregnant, and PL = post-lactating.

## APPENDIX E

### Skin Temperature and Torpor Patterns Among Reproductive Conditions and In Different Weather Conditions

The most frequently used skin temperature ( $T_{sk}$ ) pattern (Table E1) and the mean torpor duration, depth, and HI (Table E2) varied among reproductive conditions. The first pattern involved maintaining  $T_{sk}$  at normothermia, pattern #2 included frequent and shallow fluctuations in  $T_{sk}$ , and pattern #3 involved moderate drops in  $T_{sk}$ . The fourth pattern was characterized by long and deep drops in  $T_{sk}$  while pattern #5 involved low  $T_{sk}$  maintained over one day, in which normothermia was never reached. The sixth pattern was characterized by  $T_{sk}$  below normothermia over multiple days. While  $T_{sk}$  patterns varied among reproductive conditions, torpor frequency (i.e., the probability of using torpor on a given day) was similar across conditions (Table E3).

Torpor frequency varied among weather conditions. When daily precipitation was greater than 4mm, all individuals in the pregnant, lactating, post-lactating, and not-obviously pregnant conditions used torpor (Figure E1c). At 15mm of rain/day, pregnant females used torpor at greater depths than lactating females (Figure E3c). For some weather variables, there were small correlations with torpor patterns, however, there was a large amount of variation around the means (Figures E2-E4). There was a small, negative correlation between minimum ambient temperature and torpor duration ( $r = -0.33$ ,  $n = 139$ ), depth ( $-0.24$ ,  $n = 139$ ), and HI ( $-0.28$ ,  $n = 139$ ). Maximum wind speed was weakly correlated with duration ( $r = 0.12$ ,  $n = 139$ ), depth ( $0.15$ ,  $n = 139$ ), and HI ( $0.18$ ,  $n = 139$ ). There was a trivial, negative relationship between precipitation and duration ( $r = -0.09$ ,  $n = 139$ ), depth ( $-0.07$ ,  $n = 139$ ), and HI ( $-0.09$ ,  $n = 139$ ).

Table E1. Number of bat days that each torpor pattern was used out of the total number of bat days (N) for each reproductive condition among female *Myotis lucifugus* roosting in bat boxes at Salmonier Nature Park, Newfoundland from June to August 2016 and 2017.

Pattern	Reproductive Condition				
	Not-Obviously Pregnant (N=22)	Non-Reproductive (N=7)	Pregnant (N=30)	Lactating (N=43)	Post-Lactating (N=37)
1	0	4	7	19	5
2	1	2	16	10	10
3	2	0	2	12	14
4	14	1	6	2	7
5	3	0	0	0	1
6	2	0	0	0	0

Table E2. Mean  $\pm$ SD torpor duration, depth, and heterothermy index (HI) of female *Myotis lucifugus* in different reproductive stages. Data was taken from individuals roosting in bat boxes at Salmonier Nature Park, Newfoundland from June-August 2016 and 2017. n refers to the number of individuals and N refers to the number of bat days.

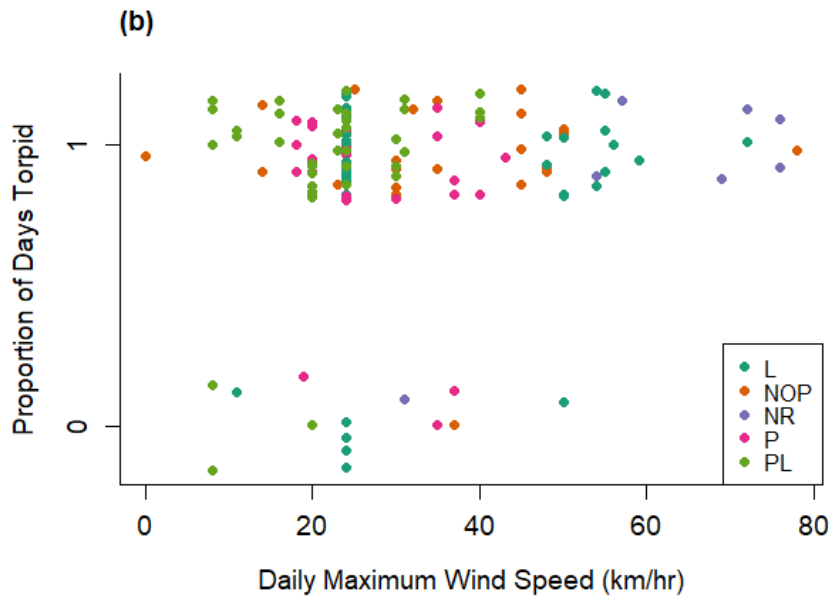
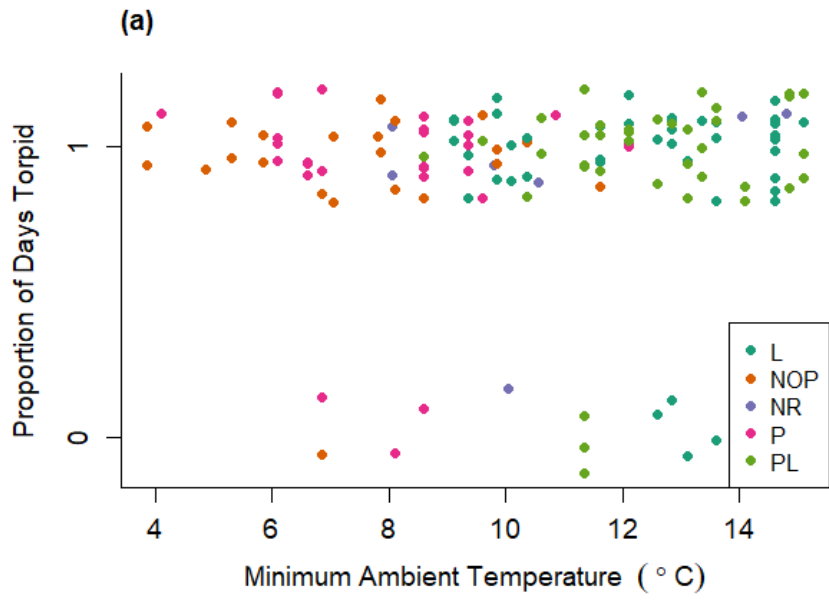
$T_{sk}$  = skin temperature.

Reproductive Condition	Torpor Characteristic				
	n, N	Duration (min)	Depth ( $^{\circ}$ C)	HI ( $^{\circ}$ C)	Lowest $T_{sk}$ ( $^{\circ}$ C)
Pregnant	11, 30	298.67 $\pm$ 318.66	6.61 $\pm$ 6.98	3.92 $\pm$ 4.09	14.22
Lactating	11, 43	243.50 $\pm$ 191.84	4.24 $\pm$ 3.97	2.68 $\pm$ 1.54	18.88
Post-Lactating	8, 37	326.76 $\pm$ 301.07	7.09 $\pm$ 6.04	3.91 $\pm$ 2.85	12.25
Non-Reproductive	2, 7	251.43 $\pm$ 247.08	4.37 $\pm$ 5.07	3.70 $\pm$ 4.89	16.00
Not-Obviously Pregnant	4, 22	819.10 $\pm$ 387.69	8.63 $\pm$ 5.63	5.78 $\pm$ 3.14	6.00

Table E3. The frequency of torpor use, measured as the number of bat days torpor was used out of the total number of bat days sampled for female *Myotis lucifugus* in different reproductive stages. Data was taken from females roosting in bat boxes in Newfoundland from June-August, 2016 and 2017. n refers to the number of individuals and N refers to the number of bat days.

Reproductive Condition	n, N	Number of days torpor used	Total number of bat days	Frequency (%)
Pregnant	11, 30	27	30	90.0
Lactating	11, 43	37	43	86.0
Post-Lactating	8, 37	34	37	91.9
Non-Reproductive	2, 7	6	7	85.7
Not-Obviously Pregnant	4, 22	21	22	95.5





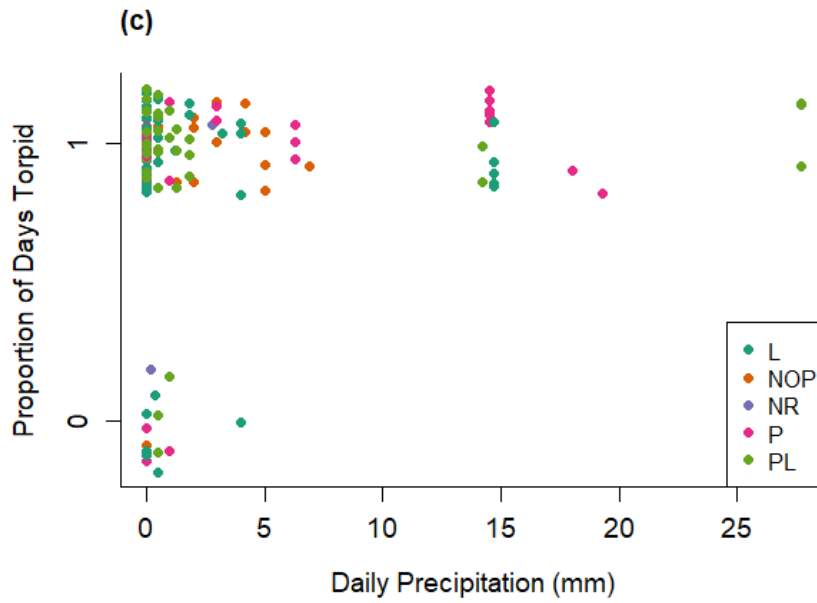
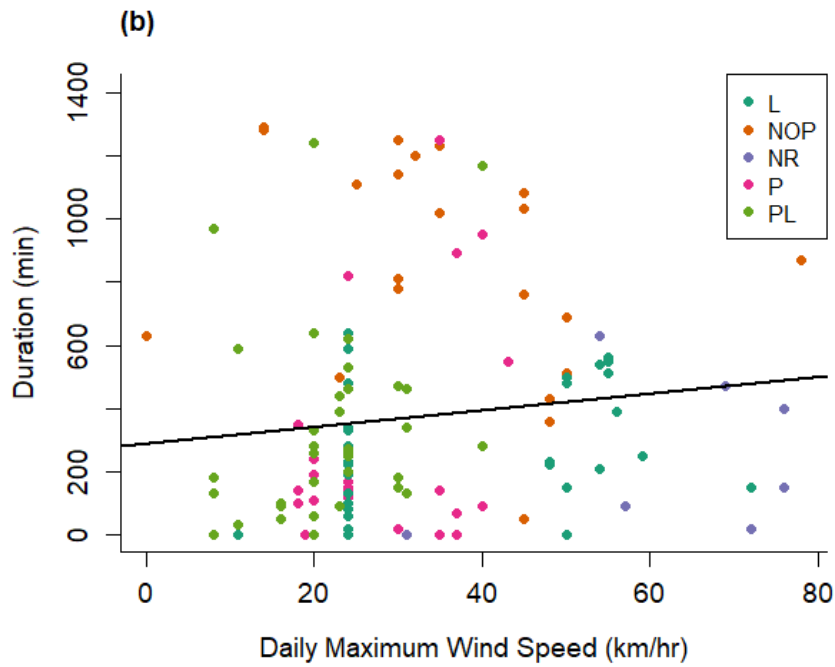
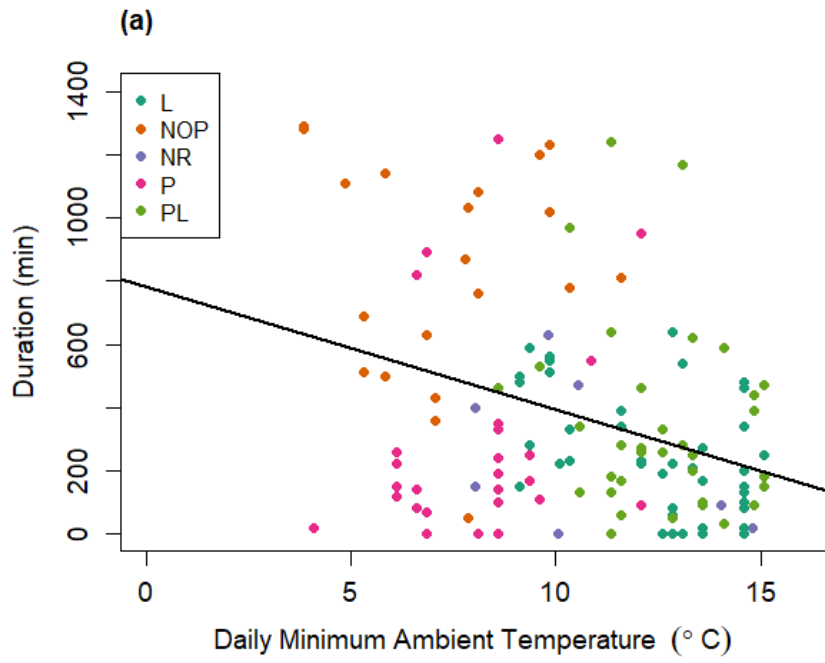


Figure E1. Proportion of days torpid (1=torpid, 0=not torpid) and mean daily (a) minimum ambient temperature, (b) maximum wind speed, and (c) precipitation in female *Myotis lucifugus* in Newfoundland from June to August 2016 and 2017. The posterior distributions of each weather variable are displayed adjacent to the plots. The data points have been jittered along the y axis to reduce over-plotting. L = lactating, NOP = not-obviously pregnant, NR = non-reproductive, P = pregnant, and PL = post-lactating.



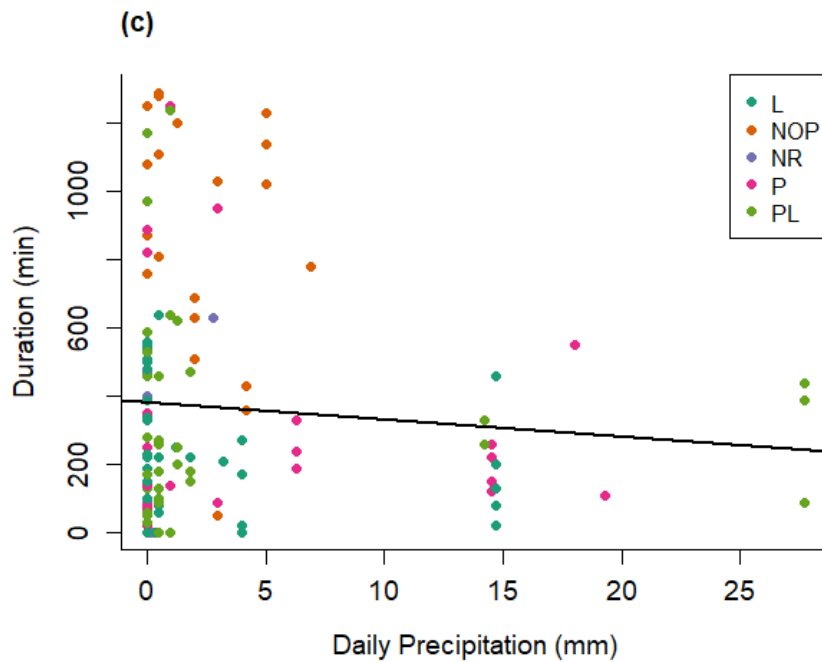
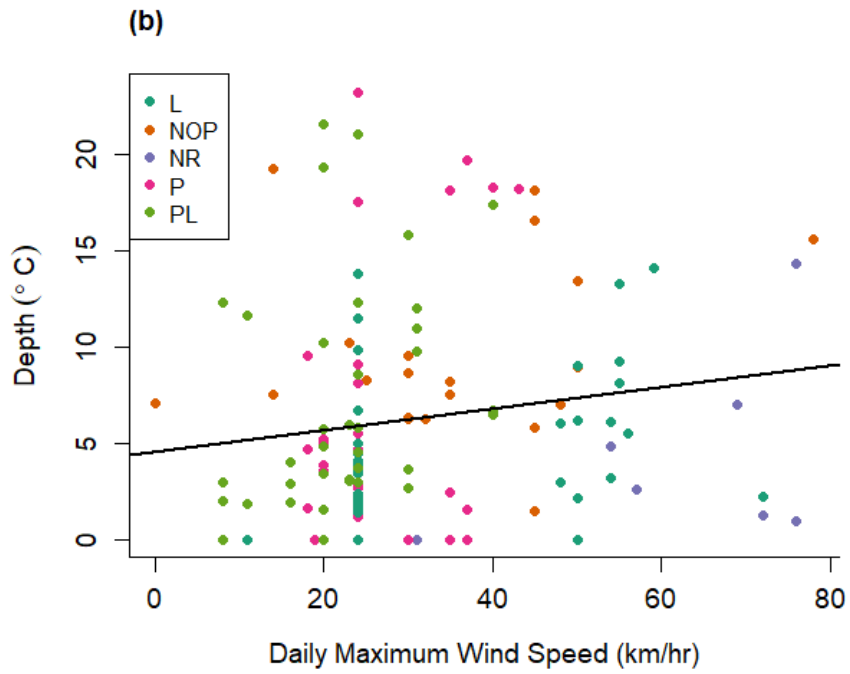
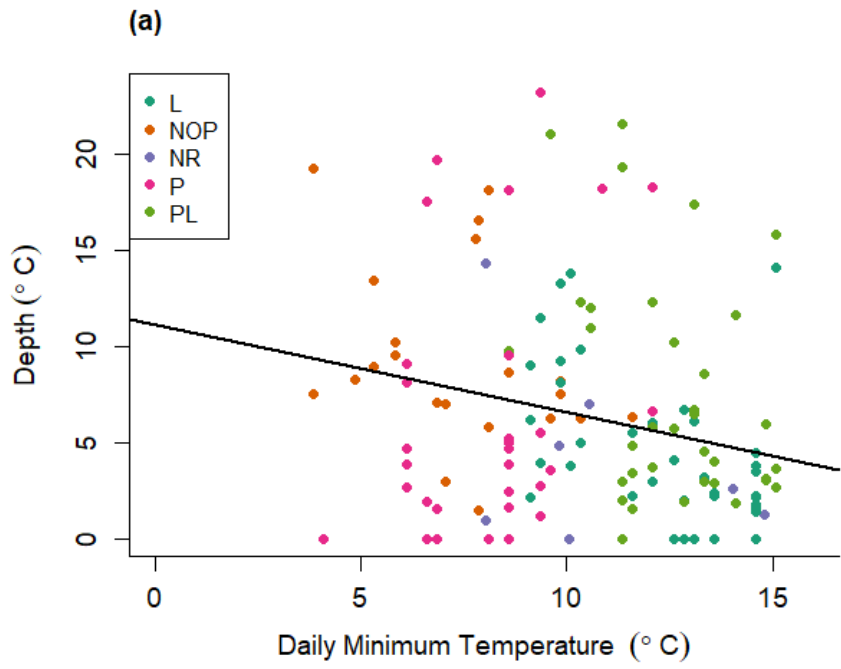


Figure E2. The effects of the mean daily (a) minimum ambient temperature ( $y = -33.24x + 8.48$ ,  $R^2 = 0.0861$ ), (b) maximum wind speed ( $y = 2.38x + 1.87$ ,  $R^2 = 0.0107$ ), and (c) precipitation ( $y = -3.36x + 4.66$ ,  $R^2 = 0.0034$ ) on torpor duration in female *Myotis lucifugus* in Newfoundland from June to August 2016 and 2017. The posterior distributions of each weather variable are displayed adjacent to the plots. L = lactating, NOP = not-obviously pregnant, NR = non-reproductive, P = pregnant, and PL = post-lactating.



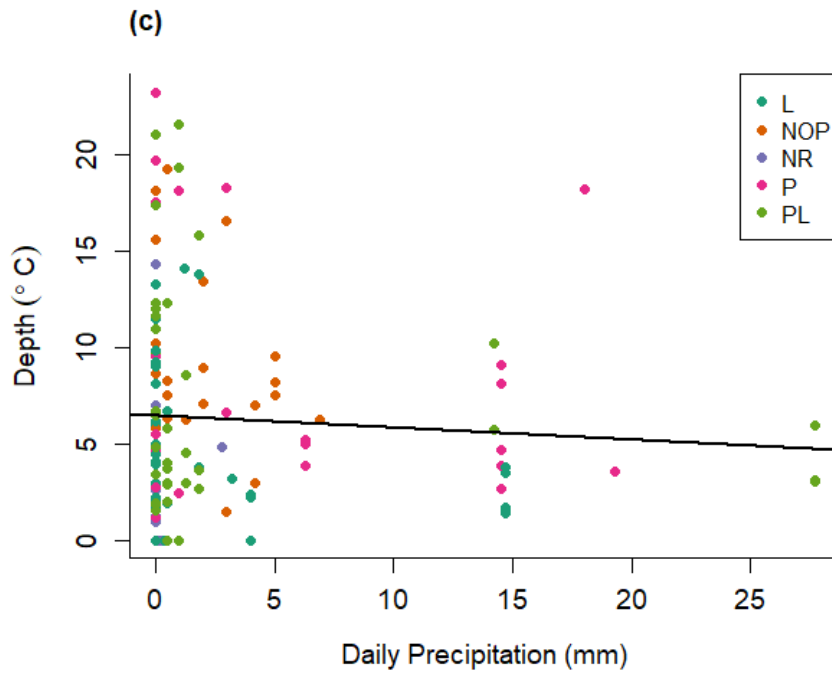
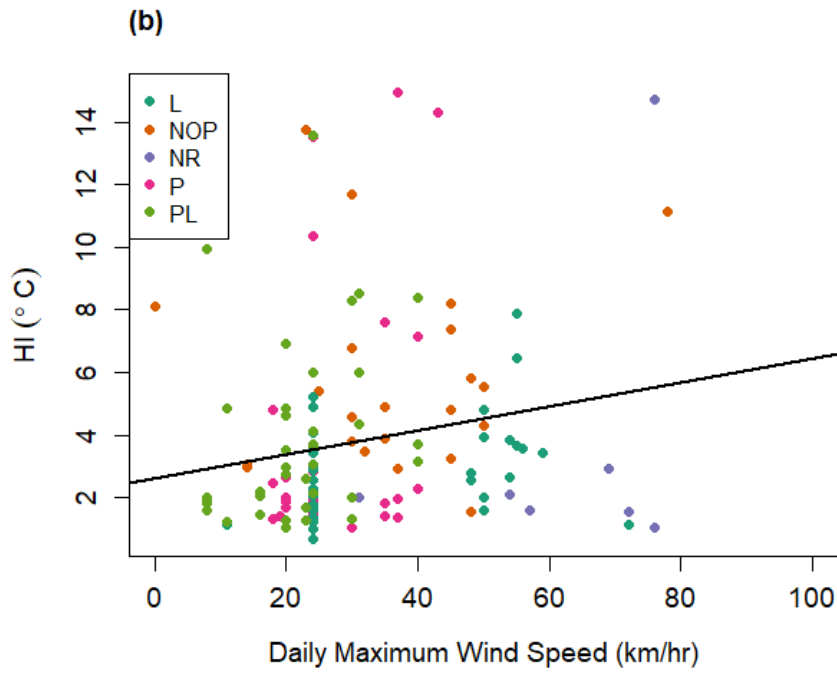
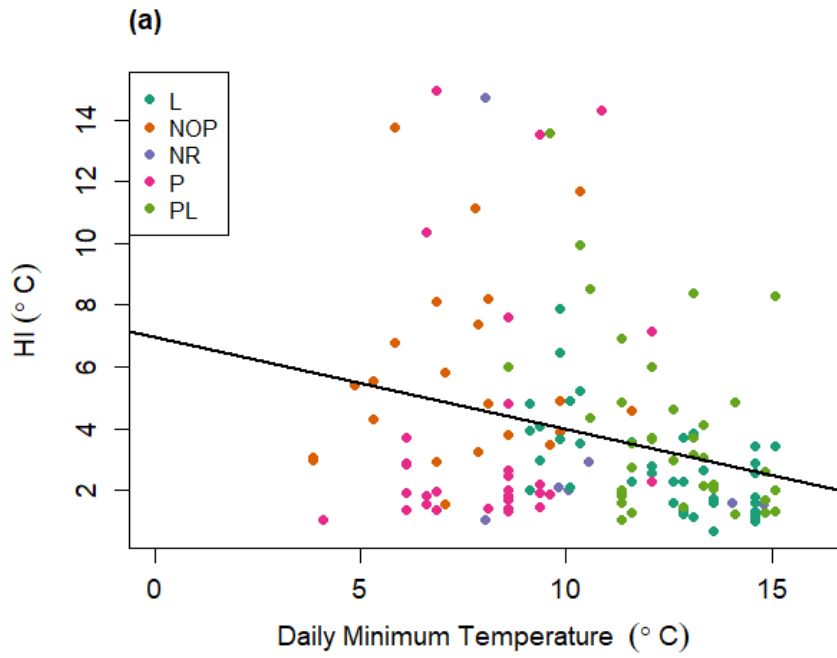


Figure E3. The effects of the mean daily (a) minimum temperature ( $y=-0.55x+0.16$ ,  $R^2=0.0732$ ,  $p<0.001$ ), (b) maximum wind speed ( $y=0.05x+0.03$ ,  $R^2=0.0142$ ,  $p=0.14$ ), and (c) precipitation ( $y=-0.03x+0.08$ ,  $R^2=0.0008$ ,  $p=0.73$ ) on torpor depth in female *Myotis lucifugus* in Newfoundland from June to August 2016 and 2017. The posterior distributions of each weather variable are displayed adjacent to the plots. L = lactating, NOP = not-obviously pregnant, NR = non-reproductive, P = pregnant, and PL = post-lactating.



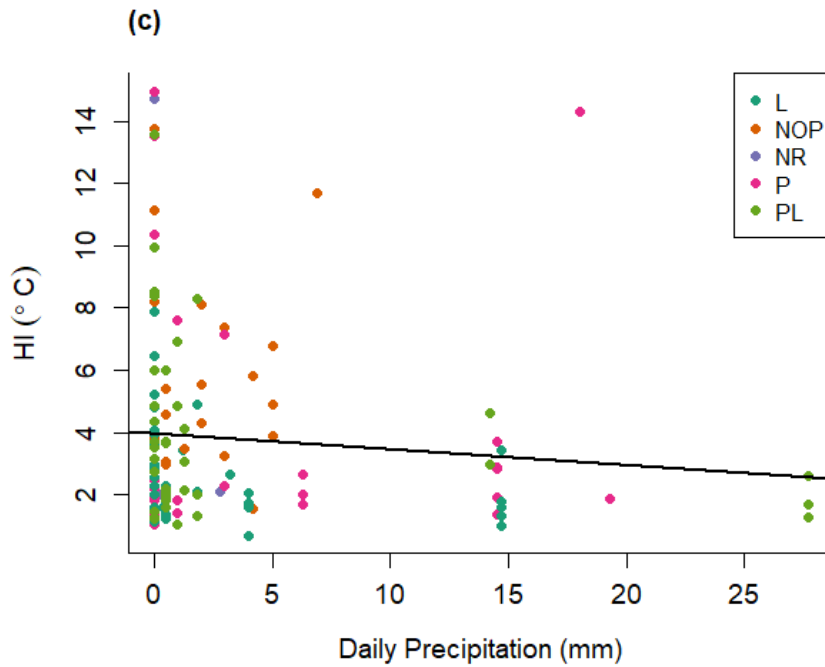


Figure E4. The effects of the mean daily (a) minimum temperature ( $y=-0.32x+0.09$ ,  $R^2=0.0788$ ,  $p<0.001$ ), (b) maximum wind speed ( $y=0.04x+0.02$ ,  $R^2=0.0260$ ,  $p=0.05$ ), and (c) precipitation ( $y=-0.03x+0.05$ ,  $R^2=0.0019$ ,  $p=0.59$ ) on the heterothermy index for torpor use in female *Myotis lucifugus* in Newfoundland from June to August 2016 and 2017. The posterior distributions of each weather variable of a multiple mixed regression are displayed adjacent to the plots. L = lactating, NOP = not-obviously pregnant, NR = non-reproductive, P = pregnant, and PL = post-lactating.



## APPENDIX F

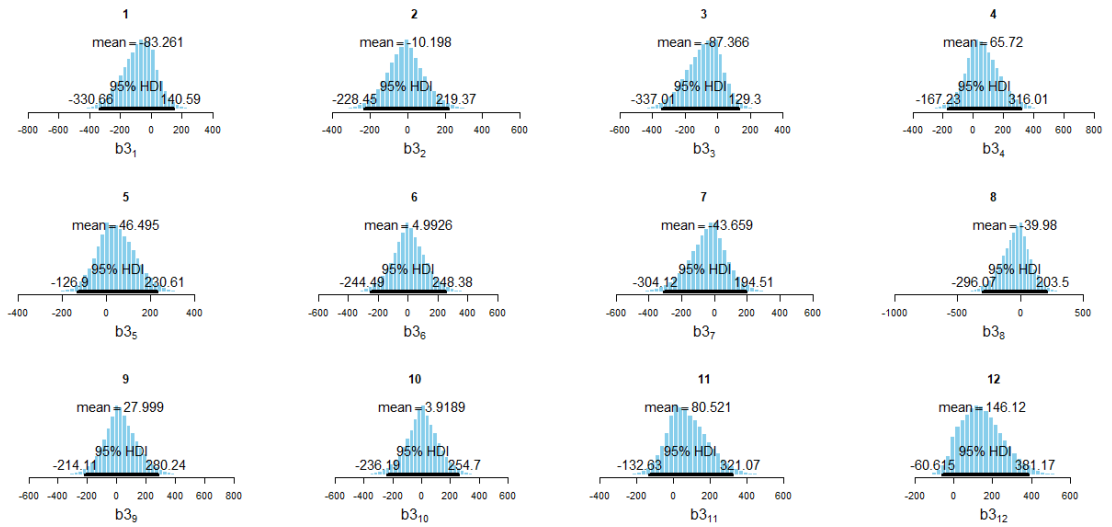
### Posterior Distributions of Other Variables in Highest Ranked Models

The 95% HDI of the posterior distributions of the highest ranked model for torpor duration (individual and reproductive condition), depth (individual, reproductive condition, and minimum ambient temperature), and heterothermy index (HI) (individual, reproductive condition, minimum ambient temperature, maximum wind speed, and precipitation) overlapped zero for most individuals, however, some individuals had strong positive and negative effects (Figure F1). For torpor duration, the individual with the most positive estimate was #17 and the most negative estimate was #13 (Figure F1a). For torpor depth and HI, the individual with the most positive estimate was #23 and the most negative estimate was #13 (Figures F1b and F1c). The posterior distributions overlap zero for torpor duration but not for torpor depth or HI, suggesting more certainty in the effect of individual on depth and HI than on duration. The body mass and forearm length for each individual was 9.27 g and 39.64 mm for #17, 8.94 g and 38.21 mm for #23, and 8.24 g and 36.95 mm for #13. All three individuals were pregnant. This suggests inter-individual variation in torpor patterns within a reproductive condition. Individuals #17 and #23 may have used torpor at a greater extent than #13 due to higher body condition, however, in pregnant females it is difficult to distinguish between fetal and body fat mass.

The 95% HDI of the posterior distributions of the highest ranked model for torpor depth did not overlap zero for minimum ambient temperature (Figures F2), indicating strong certainty in the estimate. An increase in minimum ambient temperature from 0 to 10 °C likely results in a decrease in torpor depth by 5.35 °C. The 95% HDI of the

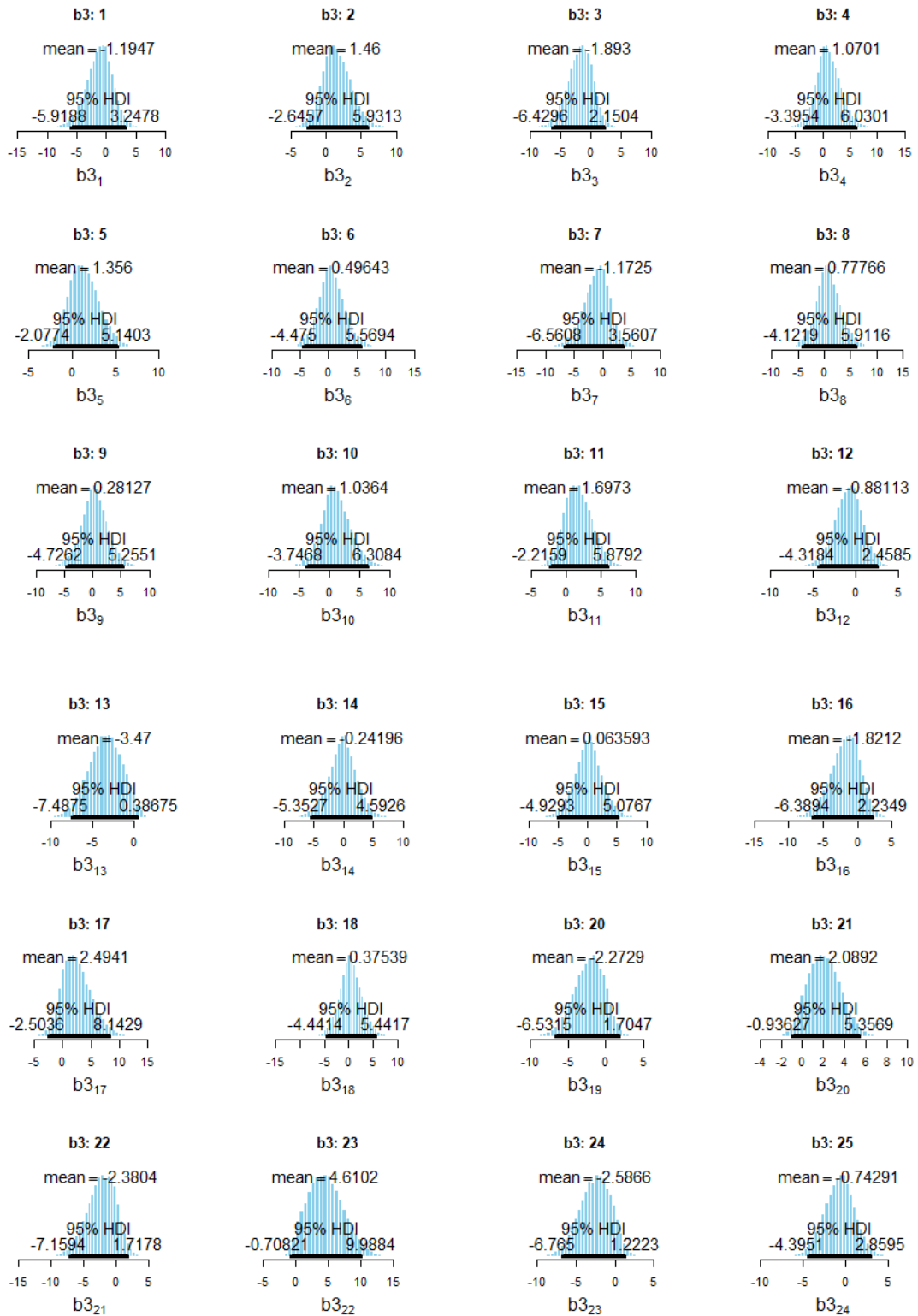
posterior distributions of the highest ranked model for HI overlapped zero for minimum ambient temperature and precipitation (Figures F3), suggesting uncertainty in the posterior estimates. The distribution of minimum ambient temperature was not centered over zero and an increase in minimum ambient temperature from 0 to 10 °C likely results in a decrease in HI by 2.3 °C. The distribution of precipitation was relatively centered over zero, suggesting no effect on HI.

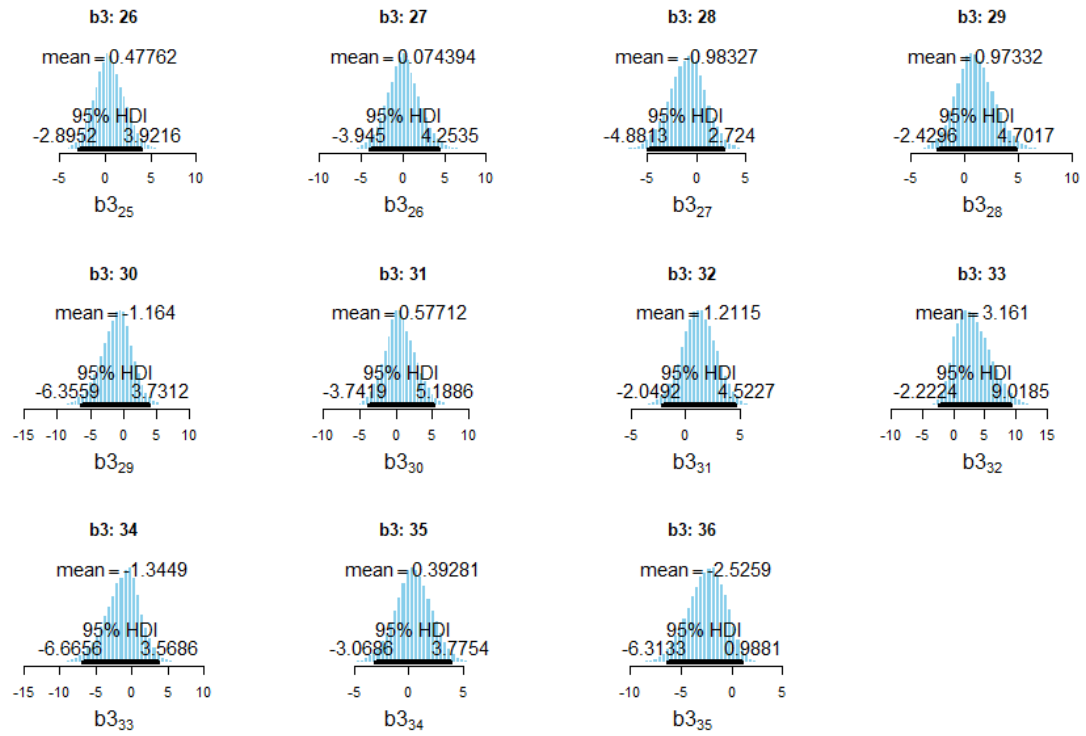
(a)



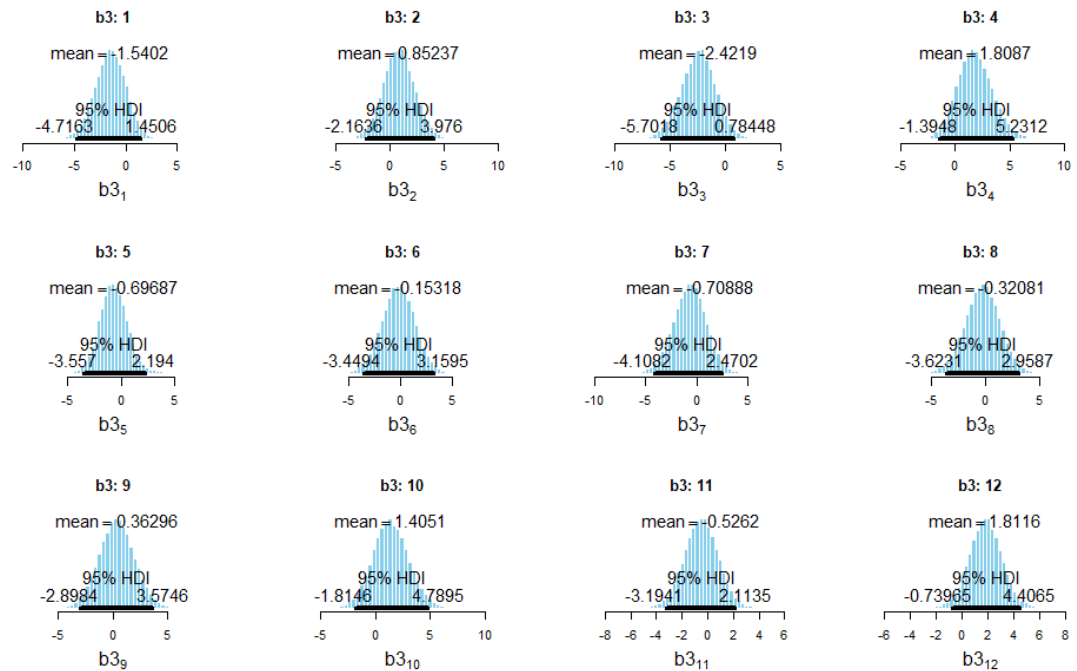


(b)





(c)



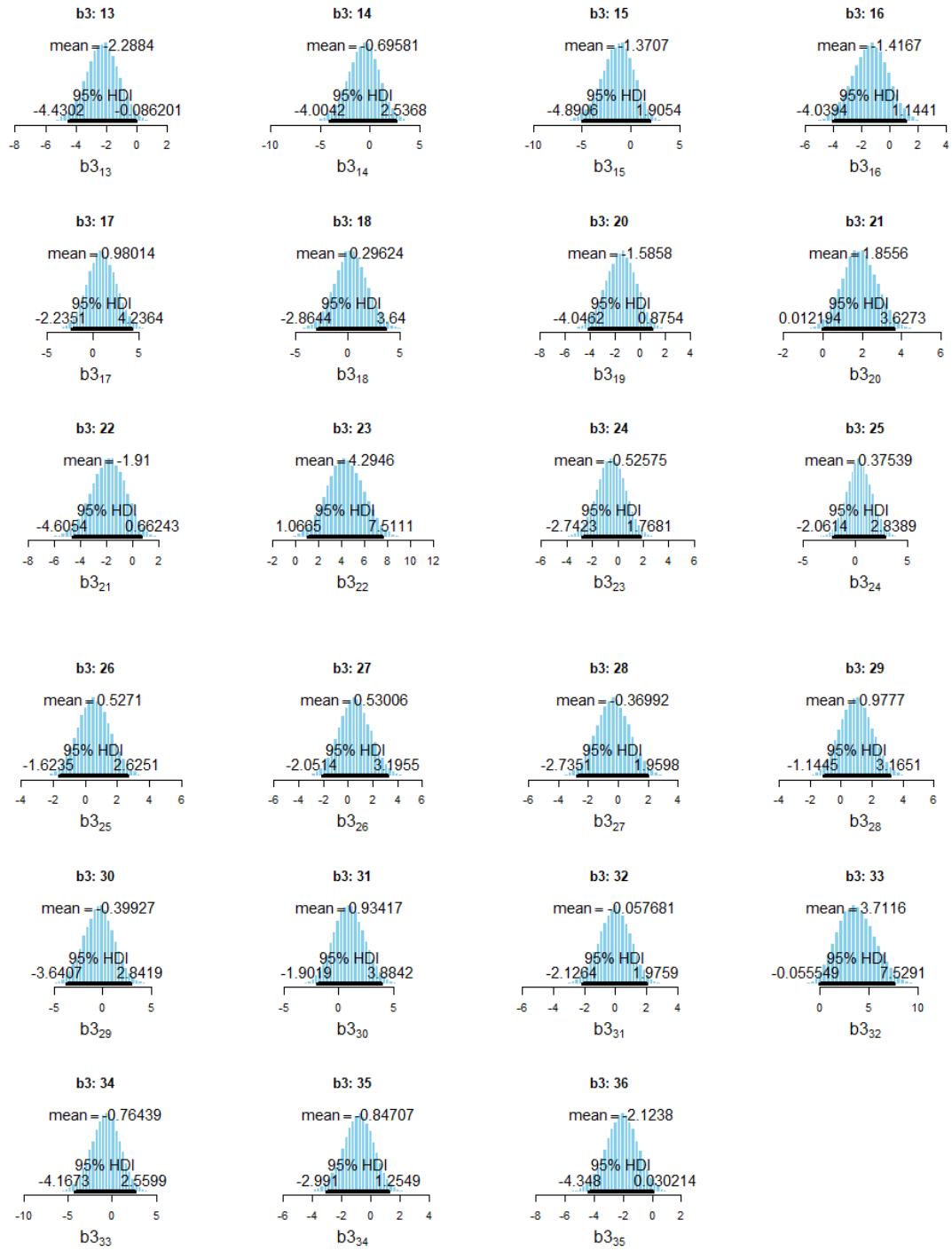


Figure F1. The posterior distributions from the highest ranked model for each individual for torpor (a) duration, (b) depth, and (c) the heterothermy index. Data was collected from female *Myotis lucifugus* in Newfoundland from June to August, 2016 and 2017.

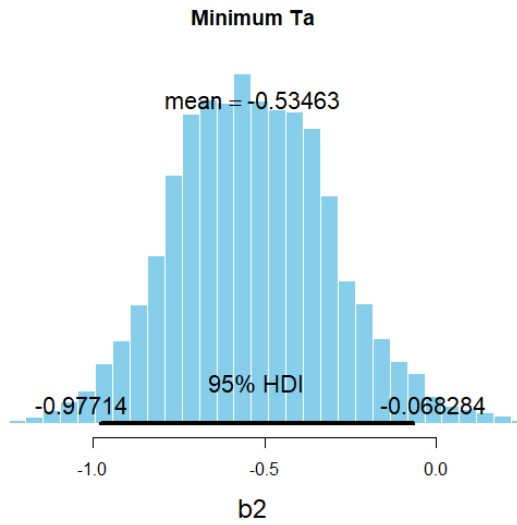


Figure F2. The posterior distribution of minimum ambient temperature for torpor depth from the highest ranked model. Data was collected from female *Myotis lucifugus* in Newfoundland from June to August, 2016 and 2017.

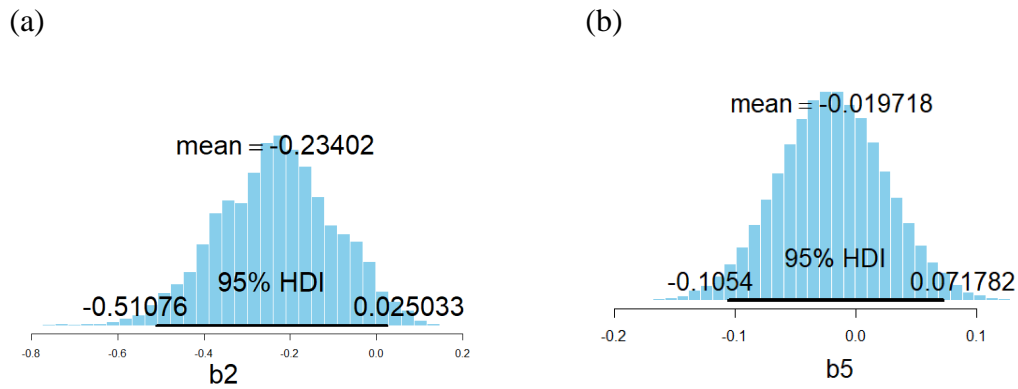


Figure F3. The posterior distributions of (a) minimum ambient temperature and (b) precipitation for the heterothermy index from the highest ranked model. Data was collected from female *Myotis lucifugus* in Newfoundland from June to August, 2016 and 2017.

## APPENDIX G

### Body Condition Index and Reproductive Condition

The body condition index (BCI) varied among individuals of different reproductive conditions with the greatest difference occurring between lactating and non-reproductive conditions (Figure G1). The posterior distributions of the lactating condition did not overlap zero, indicating a strong certainty in the estimates.

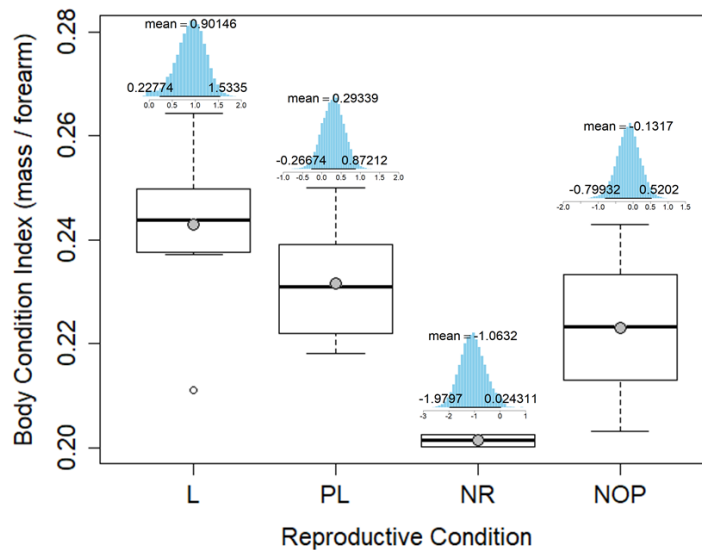


Figure G1. Body condition index (mass divided by forearm) of lactating ( $n = 10$ ), post-lactating ( $n = 8$ ), non-reproductive ( $n = 2$ ), and not-obviously pregnant ( $n = 4$ ) female *Myotis lucifugus* at Salmonier Nature Park, Newfoundland. Bats were captured from 2 June to 5 August 2016 and 2017. The top and bottom of each box show the upper and lower quartiles and the dashed vertical lines represent the maximum and minimum values. The black bars represent the median, the grey dots represent the mean, and open circles represent outliers. Above the boxes are the posterior distributions for the estimates of each reproductive condition.  $n$  = number of individual bats, L= lactating, PL = post-lactating, NR = non-reproductive, and NOP = not-obviously pregnant.



## APPENDIX H

### Roost Types Used by Female *Myotis lucifugus* on the Avalon Peninsula in Newfoundland

Female *Myotis lucifugus* captured at Salmonier Nature Park were tracked to day roosts in bat boxes, cabins, and trees (Figure H1). Pregnant, lactating, post-lactating, non-reproductive, and not-obviously pregnant females used bat boxes within Salmonier Nature Park. Nine pregnant, four lactating, and one not-obviously pregnant female were tracked to cabins. One lactating and two post-lactating females were tracked to balsam fir trees, in which two of the three trees were standing dead trees.

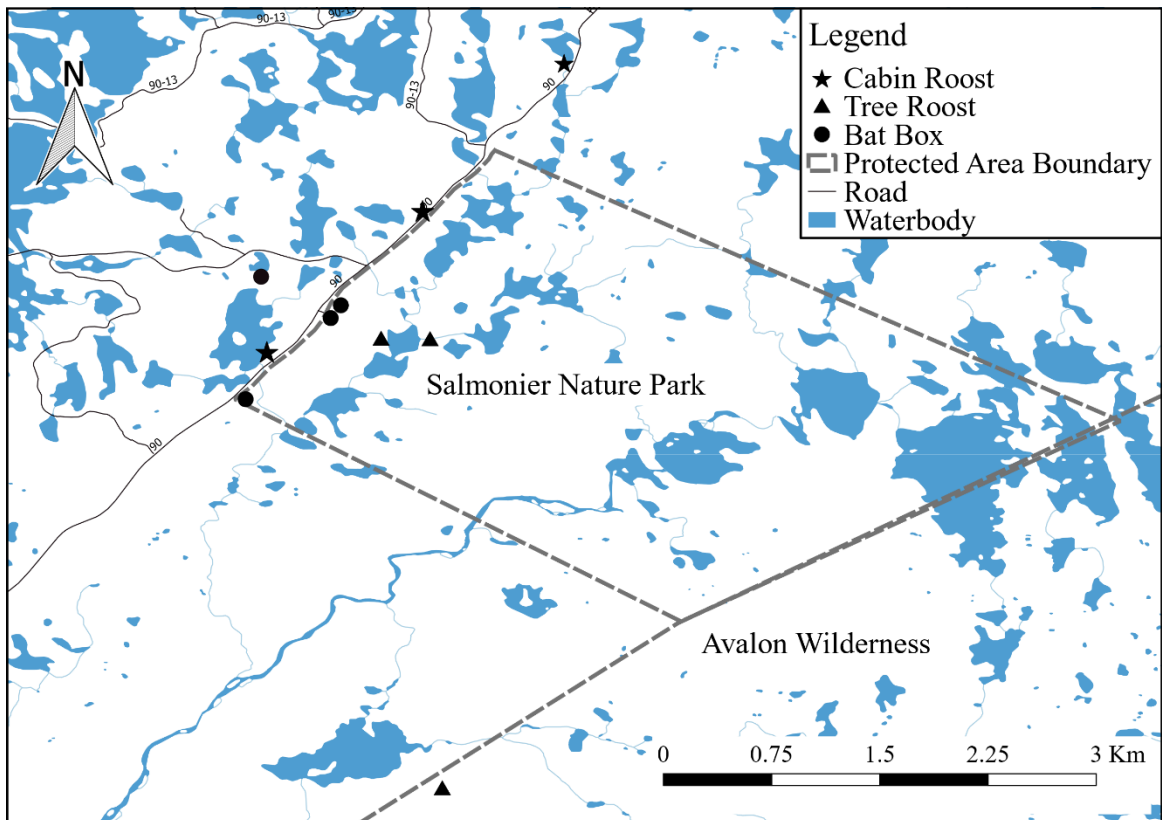


Figure H1. Roost types and locations used by female *Myotis lucifugus* on the Avalon Peninsula in Newfoundland.

## LITERATURE CITED

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