

TALL TIMBER: ROOST TREE SELECTION OF REPRODUCTIVE  
FEMALE SILVER-HAIRED BATS (*LASIONYCTERIS NOCTIVAGANS*)

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Shelby Joyce Bohn, candidate for the degree of Master of Science in Biology, has presented a thesis titled, ***Tall Timber: Roost Tree Selection of Reproductive Female Silver-Haired Bats (LASIONYCTERIS NOCTIVAGANS)***, in an oral examination held on August 18, 2017. The following committee members have found the thesis acceptable in form and content, and that the candidate demonstrated satisfactory knowledge of the subject material.

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## Abstract

Habitat loss is the most significant contributor to the extinction of species worldwide, and yet for many species, habitat requirements remain largely unknown. Identifying habitat is important, especially because the most cost effective strategy for conservation and management is preserving habitat before it is converted or degraded rather than trying to restore it after the fact. Identifying habitat is also important from a scientific perspective because it can help to explain some of the ecological choices made by individuals when potentially conflicting priorities exist. Habitat requirements change for many species, both seasonally and throughout their life cycles, and identifying habitat during key developmental or life history periods will provide further information about priorities of these species. North American bat species show distinct differences in the habitat they use during the summer and winter, which provides us with an opportunity to understand how the selection pressures of reproduction have shaped the habitat use of these species. Silver-haired bats (*Lasionycteris noctivagans*) are small Vespertilionids that are solitary during their regional seasonal migration, but form small groups or maternity colonies of reproductive females on the summering ground. I captured female silver-haired bats during the reproductive season in Cypress Hills Interprovincial Park, Saskatchewan, Canada and characterized the trees that they roosted in during the day to understand why they chose the roosts that they did. These bats chose trees that were near other dead trees with cavities, presumably to reduce the cost of roost switching, a behaviour commonly undertaken by tree-roosting Vespertilionids. Bats also chose trees that were in plots with higher basal area. Roost choices did not vary over the course of

the reproductive season, likely because the priorities of pregnant and lactating bats were similar. I quantified the roost characteristics chosen by silver haired bats while pregnant and lactating. The analysis suggests that the surrounding trees can also be important factors in roosting decisions. Protecting habitat critical for reproduction can be an important conservation step, but understanding why it is critical can yield even more clues for managing both natural resources and bats species.

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## **Dedication**

To my Mom, who lanced her finger so that I could look at red blood cells under my first home microscope – the first of many times that you directly or indirectly encouraged me as a developing scientist. Thank you for making the phrase “strong independent woman” both a running joke, and something to aspire to.

To my Dad, who first showed me how to be brave in the natural world around me, starting with the three acres behind our house. I’m sorry about that time I made you walk 20 km when you came to help me with fieldwork, but thank you for always doing the literal and figurative walking.

Lastly, thanks to Mark Brigham and the wonderful, brilliant members of his lab. Thank you Mark, for supervising and encouraging science in a way that doesn’t sacrifice wonder and humour, but rather emphasizes it. Thank you to current and former Brigham-ites, for sharing an office with me, encouraging me, challenging me, and for making me proud to be a part of this family.

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# **Chapter 1 – Paving Paradise: The importance of identifying and conserving habitat before it's gone**

## **1.1 Background**

Habitat is both fundamental to our understanding of the natural world, and a vaguely defined concept. Broadly speaking, “habitat” refers to spatial occurrences or environmental requirements of a species, population, or individual. Habitat can be as broad as the geographic range of a species occurring from Northern Canada all the way to Mexico, or as precise as a single tree branch (Young et al. 2005; Klug et al. 2012) depending on the scale that we consider, all of which have important conservation implications (Hall et al. 1997). Habitat can also include a temporal scale (Hall et al. 1997) to reflect anything from gradual range shifts over decades, seasonal migration (Downes et al. 1986; Jonasson & Guglielmo 2016), or daily movements. Preserving critical habitat is one of the most important strategies for species conservation and management (Fahrig 2001; Hodgson et al. 2011), but due to this inherent ambiguity, identifying critical habitat can be challenging. Critical habitat under the Canadian Species at Risk Act (SARA) refers to habitat that is specifically required for species recovery (Environment and Climate Change Canada 2016), which can include both high quality habitat and habitat that is necessary for specific key windows in an animal’s lifecycle.

Preserving natural habitat before it is converted or altered is the most cost effective way to conserve wildlife (Hodgson et al. 2011) and as human disturbance continues to alter the landscape, any habitat that remains unchanged may become increasingly important (Ball 2002). According to simulation modelling by Fahrig (2001),

when the amount of available habitat is reduced below a certain threshold, it can lead to steep, sudden population declines, which means that it is important to identify habitat while populations are still stable. Identifying key areas to preserve is not only cost effective but it allows for development to proceed in a sustainable manner.

Many species of bat in North America rely on trees as habitat at some point over their lifespan, which means that their interests intersect with those of forest managers or forestry companies. Several species including big brown bats (*Eptesicus fuscus*) use dead or dying trees (Kalcounis & Brigham 1998), which are sometimes removed by more extensive management practices, and many species roost in trees with large diameters (Kalcounis-Rüppell et al. 2005), which are sought after for lumber harvesting. My objectives were to identify roosting habitat used by female silver-haired bats while they were pregnant and lactating, a life-history stage when they roost together in small groups within trees hollows. I aimed to quantify habitat characteristics to understand female silver-haired bats' priorities for habitat during the reproductive season and determine if these priorities changed with reproductive stage.

## **Chapter 2 – Roost Selection of Female Silver-haired Bats**

### **2.1 Introduction**

Habitat is an essential requirement for all animals, and can influence factors like growth rate (Richner 1989), adult survival (Gillis et al. 2005), and reproductive success (Prindiville Gaines & Ryan 1988; Bonar et al. 2016). For example, striped mud turtle (*Kinosternon baurii*) nests located near vegetation have higher embryonic survival than nests located in open habitat, because the shallow nests that females construct are vulnerable to temperature fluctuation (Wilson 1998). Habitat can vary in quality; either

naturally (Wilson 1998; Gillis et al. 2005; Bonar et al. 2016;) or as a result of anthropogenic factors such as agriculture (Heisler et al. 2013), urban development (Richner 1989), or natural resource harvesting (Rittenhouse et al. 2008; Ludlow et al. 2015). This variation is important for all life stages, however there is likely additional selection pressure on habitat use during energetically difficult circumstances like food shortage (Whitehouse et al. 2013), winter (Korslund & Steen 2006), or climate change (Whitehouse et al. 2013, Deutsch et al. 2015). For example, unseasonably warm spring temperatures can induce Great Tits (*Parus major*) to initiate egg laying sooner in the breeding season but an early start can expose parents to unpredictable spring weather and resulting food shortages. When this happens, breeding success differs between habitats indicating that the birds in these different habitats vary in their ability to cope (Whitehouse et al. 2013). Habitat can therefore offer some kind of additional benefit, making it a valuable resource for animals experiencing energetic challenges.

The reproductive season provides energetic challenges as well, especially for species that give birth to altricial young and provide parental care. For mammalian species, parental care is provided primarily in the form of female lactation (reviewed in Gittleman & Thompson 1988), which is the most energetically expensive phase of reproduction (Kurta et al. 1989). To successfully raise offspring, mothers must provide for the needs of their young while also offsetting this cost. One strategy used by some pregnant and lactating mammals is to use torpor, which is physiologically similar to hibernation. Torpor entails a decrease in metabolic rate by lowering the thermoregulatory set point, and a subsequent lowering of body temperature, but only for hours or days instead of seasonal hibernation, which can occur for weeks at a time (Wang & Wolowyk

1988; Geiser 2004). Torpor is an effective energy reduction strategy and is commonly used when endotherms are faced with other kinds of challenging ecological conditions like poor weather (Willis et al. 2006a), or decreased prey availability (Wang & Wolowyk 1988). Some mammals employ daily torpor during the reproductive season (Chruszcz & Barclay, 2002; Rintoul & Brigham, 2014), but often less than non-reproductive individuals (Geiser & Masters 1994; Dzal & Brigham 2013), since it might delay fetal or newborn development (Racey & Swift 1981; but see Willis et al. 2006a) and subsequently extend the need for parental investment.

Insectivorous bats in North America are interesting in this respect because the balance between energy savings and rate of offspring development is often emphasized. Female bats must raise their young during a relatively short reproductive season and as nocturnal animals, provide parental care and forage for insects during a short nightly active period. Mothers must provide enough care to allow their pup or pups to grow to adult size and learn to fly, echolocate, and forage prior to undertaking either a fall migration or storing enough fat to survive hibernation for the winter (Kunz 1982; Kurta & Baker, 1990). Torpor offers potential savings that some pregnant or lactating bats take advantage of (Chruszcz & Barclay 2002; Willis et al. 2006a), but it is impractical to be the sole strategy for balancing energy budgets (Kurta et al. 1989), and these bats likely need to use additional strategies for saving or acquiring energy.

Bats may incur energetic savings as a result of the roost or roosts that they select (Kunz & Lumsden 2003). Roosts also likely provide important sites for protection from predators (Lewis 1995) and poor weather (Patriquin et al. 2016). Roosts may also reduce energetic costs associated with commuting to and from foraging areas or water sources

(Lewis 1995), and they have been predicted to provide internal environments that are stable and within a favourable temperature range (Kunz & Lumsden 2003). Bats that are able to find roosts with characteristics that allow them to save energy can instead invest in parental care rather than predator avoidance, maintaining homeostasis, or other costly concerns.

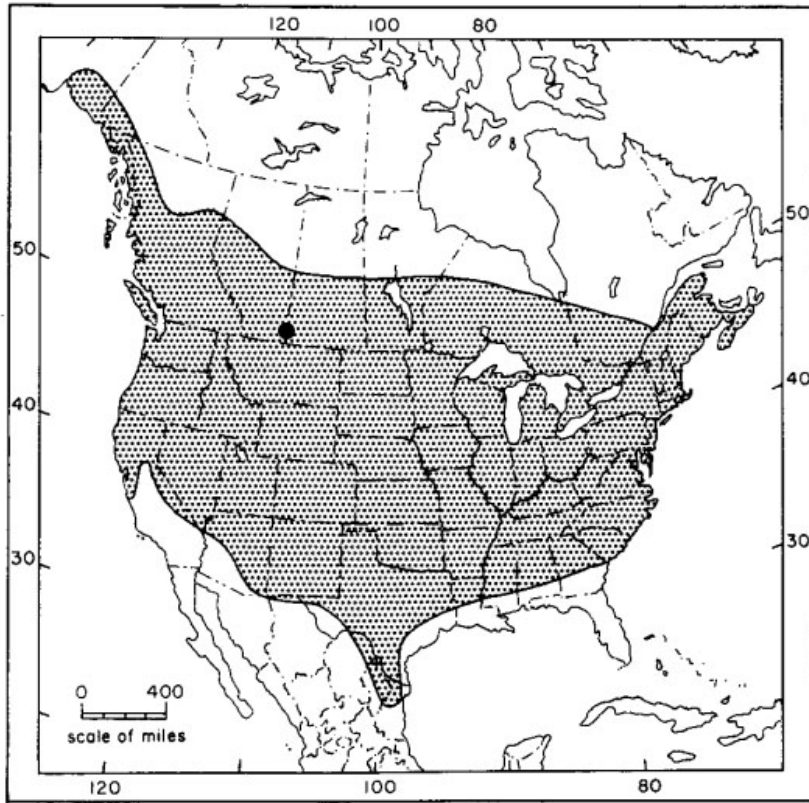
Considerable attention over the past two decades has been focused on roost selection by bats, particularly North American tree-roosting species (Brigham et al. 1997; Betts 1998; Chruszcz & Barclay 2002; Kalcounis-Ruppell et al. 2005; Willis & Brigham 2005; Willis et al. 2006b; Clement & Castleberry 2013; Womack et al. 2013). However, roosting behaviour and selection criteria differ between species (Willis et al. 2006a, 2006b; Clement & Castleberry 2013), sex (Mattson et al. 1996; Betts 1998), location (Brigham 1991; Patriquin et al. 2016), and reproductive state (Mattson et al. 1996; Chruszcz & Barclay, 2002; Patriquin et al. 2016). For example, big brown bat (*Eptesicus fuscus*) maternity colonies in British Columbia, Canada, primarily used cavities in hollow trees, with each cavity used by more than 100 bats on average. Meanwhile maternity colonies of the same species in Ontario, Canada were primarily in structures built by humans and comprised of less than 40 bats on average, illustrating the variation that can occur within species that have extensive ranges (Brigham 1991).

Most of what we know about silver-haired bat roost selection is for non-reproductive individuals (Campbell et al. 1996), at migratory stopover sites (Barclay et al. 1988; McGuire et al. 2012), or mild regions within their range (Campbell et al. 1996; Betts 1998; Vonhof & Betts 2010). Thus management decisions for these bats in

temperate areas or during the reproductive season should take into account the habitat preferences bats facing different circumstances may have.

The Cypress Hills of Saskatchewan are near the northern extent of the silver-haired bat's summer range (Cryan, 2003, Figure 1), and this region is strongly seasonal.





**Figure 1:** Geographic range of the silver-haired bat (*Lasionycteris noctivagans*), the black circle represents Cypress Hills Interprovincial Park, SK. Modified from Kunz, 1982.

It is not uncommon even in mid-summer for overnight temperatures to fall below freezing, which should further increase the cost of foraging and the selection pressure to find suitable daytime roosts. There is also some uncertainty around whether silver-haired bats found in more southern parts of their range actually migrate at all (Cryan 2003). The conditions in some parts of the range may be mild enough throughout the year that residents in the Pacific Northwest and Southern United States are able to hibernate (Cryan 2003) and even forage opportunistically during the winter (Falxa 2007). The pronounced differences in prey availability and temperatures between seasons in the Cypress Hills lead to the assumption that summer residents have migrated there from other parts of their range. Females in this region likely face pressure to rear their offspring rapidly so that they can successfully migrate in the fall.

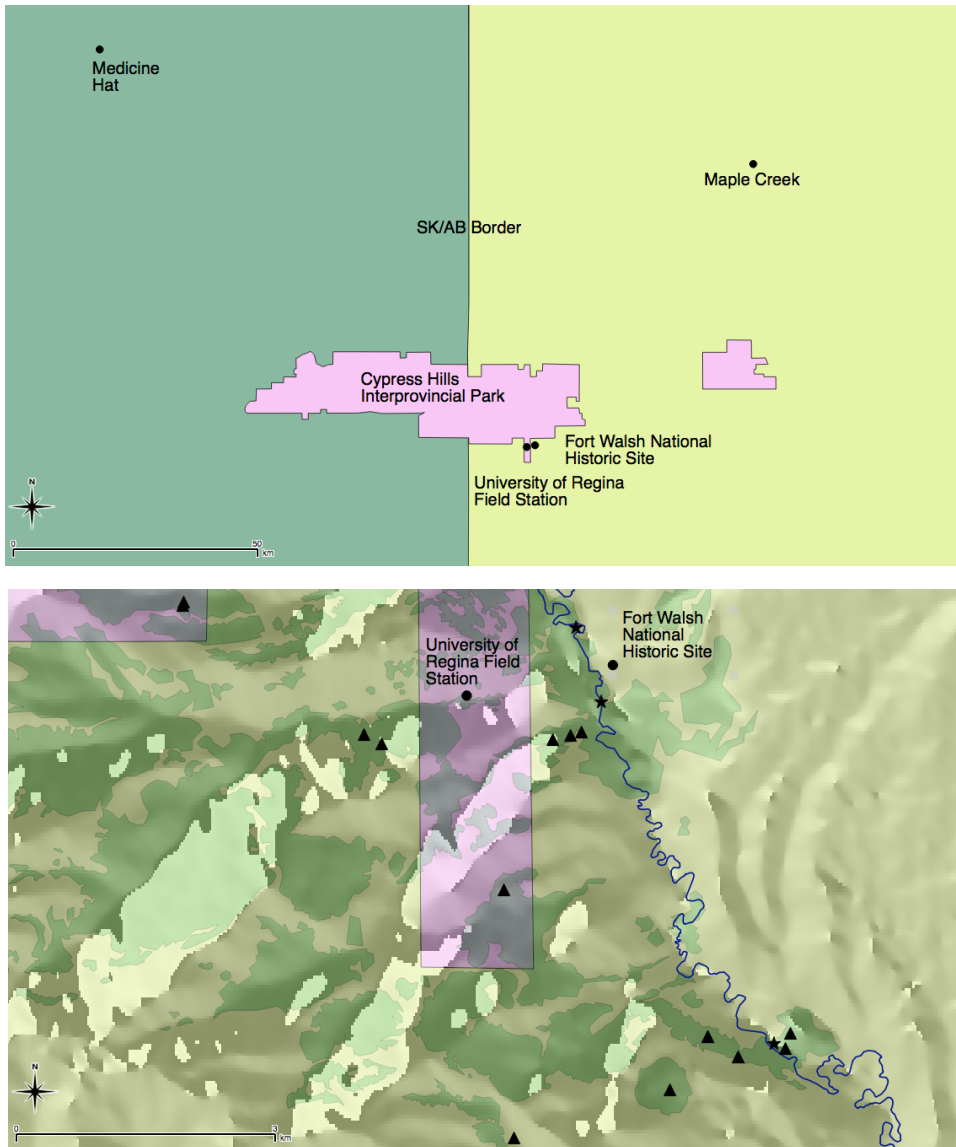
I tested two hypotheses regarding roost selection of reproductive silver-haired bats near Cypress Hills Interprovincial Park, Saskatchewan. First, I expected that these bats would choose roosts both at the tree and surrounding forest scale that offered benefits that could contribute to successful reproduction, such as increased protection from predators, access to other suitable roosts nearby, access to sunlight for warmer roosts, or roost and forest structure that would help newly volant pups to fly more easily. Second, that the selection of roost attributes would change throughout the reproductive season, as energetic demands on the mothers also changed.

## 2.2 Methods

### 2.2.1 Study Site and Species

Silver-haired bats are small (8-15 g) insectivorous bats (Family: Vespertilionidae) found throughout most of North America as far north as Alaska, through most of Southern Canada and the Central United States, and extending south into Mexico (Figure 1). They are generally considered migratory (Barclay et al. 1988, Cryan et al. 2003), although the specific route and distance of their migration remains poorly understood (Baerwald et al. 2014). Silver-haired bats are solitary while they migrate (Barclay et al. 1988), but once they arrive on the summer breeding ground form small maternity colonies in hollow trees composed of fewer than 60 bats (Campbell et al. 1996; Betts 1998; this study).

I captured silver-haired bats while they flew over the Battle Creek in the West block of Cypress Hills Interprovincial Park, Saskatchewan and surrounding private land (49° 57' N, 109° 89' W; hereafter Cypress Hills; Figure 2) between May and August 2015 and 2016. Willis et al. (2003) and Sauchyn (1993) describe Cypress Hills in detail, but briefly, this area is characterised by a mosaic of native short grass prairie punctuated by old growth forest on steep, undulating hills. Forests near Cypress Hills are mainly dominated by trembling aspen (*Populus tremuloides*), white spruce (*Picea glauca*) in wetter areas, and lodgepole pine (*Pinus contorta*) on drier slopes.



**Figure 2:** (Top) Cypress Hills Interprovincial Park (shown in pink) is in Southwest Saskatchewan and Southeast Alberta. (Bottom) Silver-haired bat (*Lasionycteris noctivagans*) roosts (▲) were located near the southern-most extent of the west block of Cypress Hills Interprovincial Park in Saskatchewan (shown in pink). Bats were captured using mist nets (★) along the Battle Creek (in blue). Open grassland is represented in beige and tree cover is shown in green.

### **2.2.2 Capture and Morphometrics**

All procedures were approved by the University of Regina President's Committee on Animal Care (AUP #15-04, Appendix A) in accordance with the Canadian Council on Animal Care and the American Society of Mammalogists (Sikes et al. 2016). Procedures were conducted under a Saskatchewan Ministry of Environment academic research permit. Individual bats were captured using mist nets (Ecotone, Gdynia, Poland; Avinet, Freeville, NY) set over the Battle Creek and other possible flyways. Captured bats were temporarily kept in cloth bags until I recorded age (based on the ossification of the third metacarpal epiphysis; Anthony 1988), sex, mass, forearm length, and reproductive status (based on gentle palpation of the abdomen and presence of bare patches around the nipples). I uniquely marked individuals with a passive integrated transponder tag (PIT-tags; Trovan Ltd. ID 100-01, Douglas, UK) injected subcutaneously between the shoulder blades and then fitted each bat with a radio transmitter (Holohil Systems Ltd. Carp, ON, Canada) attached with latex-based surgical glue (Osto-Bond, Montreal Ostomy, Vaudreuil, QC, Canada). The PIT tag and radio-tag collectively represented less than 5% of an individual's body mass (Aldridge & Brigham 1988). After PIT-tagging and fitting with a radio-transmitter, I gave bats water and ~ 10 mealworms (*Tenebrio spp.*) to account for lost foraging opportunities and released bats <4 km from the point of capture (see Holland et al. 2006).

### **2.2.3 Roost Characteristics**

I tracked individuals to their day roost, using a handheld receiver (R-1000; Communication Specialists, Orange, CA) and 3- or 5- element yagi antennas (AF Antronics, Inc., Urbana, IL). I continued to track bats to their roosts until I could no

longer locate the signal or I confirmed the tag had fallen off either by finding the tag, or by finding a stationary radio signal during good foraging conditions. Once I located a roost, I recorded the diameter at breast height (DBH), tree species, tree height (using a clinometer; Suunto, Vanataa, Finland), and the extent of decay using a version of British Columbia's Wildlife Tree Classification System modified to include deciduous trees (Table 1; Vonhof & Barclay 1996).

**Table 1:** Decay classification for deciduous or coniferous trees, modified from the British Columbia Wildlife Tree Classification System used in Vonhof & Barclay 1996

Decay Class	Characteristics
1	Live and healthy. No decay or obvious damage present
2	Live and mostly healthy. Some damage present (e.g. broken top, cracks, hollows, external fungal growth)
3	Recently dead. Some leaves or needles still present. Heartwood is hard.
4	Dead. All leaves or needles are missing; top may be broken, loose bark, missing less than half of branches, hard heartwood and spongy sapwood.
5	Dead. Most branches and bark are missing, broken top, heartwood is spongy and sapwood is soft
6	Dead. No branches or bark, broken at mid trunk
7	Stub > 3 m tall
8	Stub < 3 m tall
9	Downed

I used a wedge prism to establish variable radius plots around roost trees and comparison plots around random trees (Carrol et al. 1999). I recorded understory density using a Robel pole and made measurements 10 m away from the focal tree in each of the cardinal directions. Similarly, I measured percent canopy cover using a densiometer 2 m away from the focal tree in each of the cardinal directions. I also calculated distance to the nearest tree of equal height (Mattson et al. 1996; Willis et al. 2006b), and the distance to the nearest tree of any height in these plots. For the purposes of this thesis, I defined tree as any woody vegetation that the prism determined to be in our plot. I considered forest canopy height to be the mean tree height of all trees in a given plot, and calculated the difference between focal (both roost and comparison) trees and mean canopy height. I also recorded the number of cavities on focal and plot trees as well as the direction that focal cavities faced (corrected for true North).

Random comparison plots are commonly used in this type of study to assess differences between chosen habitat and available habitat (Betts 1998; Willis & Brigham 2005). Generally researchers randomly select coordinates to situate random comparison plots to make the comparison (Betts 1998) but due to the patchwork of forest and grassland in the Cypress Hills, this method would likely yield comparisons that are not biologically meaningful. I modified the method outlined in Willis & Brigham (2005) for finding random comparable habitat. I selected a random direction and walked 50 m from the roost tree, and used the available tree nearest to this point as the comparison tree. I considered a tree available if it had loose, sloughing bark or at least one crack or cavity that a bat could potentially use as a roost.



#### **2.2.4 Statistical Analyses**

I conducted all statistical analyses in R (version 3.1.1 GUI 1.65, R Development Core Team, 2014), and all results are reported as mean  $\pm$  SD unless stated otherwise. I compared unmatched occupied roost trees and surrounding plots of forest with random comparison trees and plots using Generalized Linear Mixed Models (GLMMs) with binomial distributions and logit link functions (Bolker et al. 2009). This analysis is not possible with missing values, so I removed 4 trees from the subsequent analysis. To understand the effect of characteristics of both the focal tree and surrounding plot on whether or not a tree was occupied, I used five different models (Table 2 & 3). Each model represented a specific benefit that that particular habitat could offer to reproductive females, including predator avoidance, access to sunlight for favourable microclimate, forest clutter that might influence naïve pup flight, roost structural stability, and availability of alternative roost options nearby (see Table 4). I included the day I found each roost (recorded as the number of days after May 1<sup>st</sup>, to account for any changes in reproductive status between when I captured bats and when I found them at a roost) and year as fixed effects and individual bat ID as a random effect in all five models. I used likelihood ratio tests to determine model significance.

### 2.3 Results

I tagged 18 adult female silver haired bats (5 pregnant, 9 lactating, and 4 that were not visibly reproductive), and tracked nine of these bats over (2 pregnant, 4 lactating, and 2 not visibly reproductive)  $10.3 \pm 4.5$  days each to  $1.9 \pm 0.8$  trees each ( $N = 17$  trees; Figure 2). When I confirmed presence of adult females at their roosts using exit counts, roosting group size was  $5.7 \pm 4.0$  bats (Range = 1 – 8,  $n = 3$ ). Occupied roost trees were 70.6% (12/17) trembling aspen and 29.4% (5/17) balsam poplar with plots composed of 51% white spruce, 31.7% trembling aspen, 16% balsam poplar, and 1.2% other species including lodgepole pine and white willow (*Salix glauca*). Occupied trees were  $16.6 \pm 6.2$  m tall, in a decay class of  $3.3 \pm 1.7$ , and had a mean DBH of  $34.4 \pm 9.5$  cm. Random comparison trees were 68.8% trembling aspen, 25% balsam poplar, and 0.1% white spruce with plots composed of 56.3% white spruce, 31.7% trembling aspen, 9.6% balsam poplar, and 2.4% other species including white willow and saskatoon (*Amelanchier alnifolia*). Random comparison trees were  $11.8 \pm 5.7$  m tall, in a decay class of  $4.2 \pm 1.9$ , and had a mean DBH of  $33.6 \pm 16.4$  cm.

The model that best predicted occupied roost trees included variables indicative of available habitat nearby ( $p = 0.01$ ; Tables 2 & 4). Bats selected roost trees within plots that were less decayed ( $p = 0.05$ ; Figure 3; Table 4) but with a non-significant trend for more nearby cavities ( $p = 0.08$ ; Figure 4; Table 4). There was a non-significant trend for bats to select roost trees within plots with a higher basal area ( $p = 0.05$ ; Figure 5; Table 4). Neither the number of days after May 1<sup>st</sup> (as a general proxy for reproductive status) nor year had an effect on roost tree characteristics (Table 4).

**Table 2:** Definitions of characteristics used as fixed effects in explanatory candidate models used to explain roost tree selection in reproductive female silver haired bats (*Lasionycteris noctivagans*)

Variable	Definition
Basal Area	The area (m <sup>2</sup> /ha) that is occupied if all of the trees in a forest were hypothetically cross-sectioned and measured.
Canopy cover	Percentage of sky overhead that is blocked by vegetation
Cavities	Number of cavities present on focal and plot trees
Days after May 1st	The day the tree was located, measured in days after May 1st
DBH	Tree diameter at breast height (cm)
Decay class of focal tree	Decay class of focal tree (see Table 1)
Decay class of plot	Average decay class of all trees in each plot (see Table 1)
Direction of cavity	Cardinal direction (North, East, South, West) that each cavity faced
Height above canopy	Difference between mean height of all trees in a plot and focal tree height (m)
Height of focal tree	Measured from the base to the tallest point of the focal tree (m)
Neareast tree as tall or taller	Distance (m) from the base of the focal tree to the base of the nearest tree of at least the same height
Nearest tree of any height	Distance (m) from the base of the focal tree to the base of the nearest tree of any height
Understory visibility	Number of sections visible on the Robel pole averaged across the four cardinal directions (see Methods)
Year	Year of study (either 2015 or 2016)

**Table 3:** Explanatory generalized linear mixed models with negative binomial distributions and logit links. Each model represents a potential benefit to bats that roosts could offer. Options refer to other available habitat nearby, predator reflects variables that reduce possible predation, pups includes structural variables that make flight easier for naïve pups learning to fly, sun includes variables that could potentially allow more sun to reach the roost, and stability includes variables that may improve structural stability. Null is intercept only. See Table 4 for fixed effects.

Model	Likelihood Ratio p-value	Log-likelihood	Deviance	<i>df</i>
Options	0.01	-13.4	26.7	5
Predator	0.053	-13.1	26.1	8
Pups	0.12	-14.4	28.8	8
Sun	0.64	-16.8	33.5	10
Stability	0.44	-17.8	35.6	6
Null	1	-20.8	41.5	0

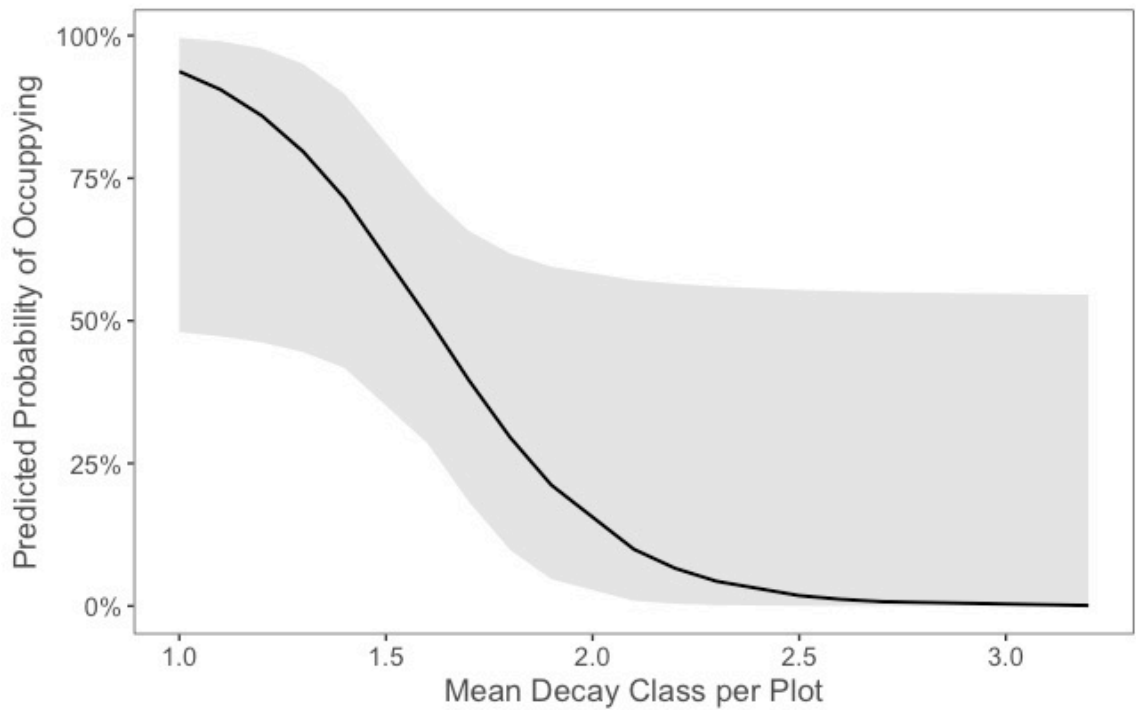
**Table 4:** Estimates of fixed effects from five competing generalized linear mixed models used to predict habitat use fit using Laplace’s approximation and the ‘lme4’ package in R

Model	Fixed effect	Estimate ± S.E.	z-value	p-value	Random effect	Variance ± S.D.
<b>Options</b>						
	Intercept	0.71 ± 3.66	0.19	0.85		
	Cavities	13.39 ± 7.62	1.76	0.08		
	Basal Area	0.17 ± 0.09	1.93	0.05		
	Decay Class of Plot	-4.46 ± 2.28	-1.95	0.05		
	Days after May 1st	-0.01 ± 0.04	-0.16	0.87		
	Year	1.64 ± 1.38	1.19	0.23		
					Bat ID	5.59 e-17 ± 7.47 e-9
<b>Predator</b>						
	Intercept	-9.35 ± 4.78	-1.96	0.05		
	Nearest Tree of Any Height	-1.35 ± 1.01	-1.33	0.18		
	Height Above Canopy	0.17 ± 0.09	1.85	0.06		
	Cavities	11.21 ± 7.33	1.53	0.12		
	Basal Area	0.08 ± 0.08	0.94	0.35		
	Canopy Cover	0.07 ± 0.06	1.29	0.20		
	Understory Visibility	0.77 ± 0.54	1.44	0.15		
	Days after May 1st	0.07 ± 0.056	1.30	0.19		
	Year	1.07 ± 1.30	0.82	0.41		
					Bat ID	0 ± 0

Pups			
Intercept	-6.76 ± 4.08	-1.66	0.10
Nearest Tree of Any Height	-0.61 ± 0.58	-1.05	0.29
Nearest Tree As Tall Or Taller	0.16 ± 0.28	0.58	0.56
Understory Visibility	0.46 ± 0.51	0.92	0.36
Basal Area	0.13 ± 0.08	1.62	0.11
Canopy Cover Height	0.05 ± 0.06	0.98	0.33
Above Canopy	0.11 ± 0.08	1.38	0.17
Days after May 1st	0.02 ± 0.04	0.55	0.59
Year	0.65 ± 1.18	0.55	0.58
			Bat ID 1.39 e-16 ± 1.18 e-8

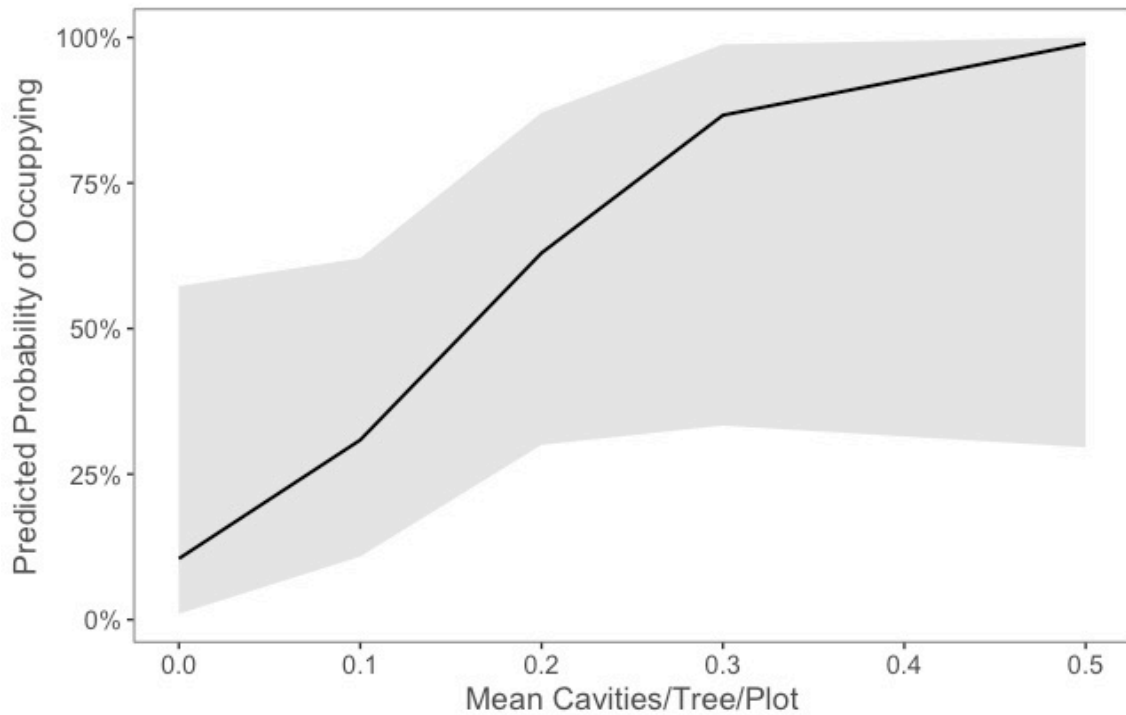
Sun			
Intercept	-3.97 ± 3.88	-1.02	0.31
Cavities	0.06 ± 0.12	0.50	0.62
Direction of Cavity - East	3.65 ± 2.46	1.48	0.14
Direction of Cavity - North	0.63 ± 1.43	0.44	0.66
Direction of Cavity - South	1.47 ± 1.50	0.98	0.33
Direction of Cavity - West	1.26 ± 1.77	0.71	0.48
Height Above Canopy	0.10 ± 0.08	1.18	0.24
DBH	-0.04 ± 0.06	-0.61	0.55

Canopy Cover	$0.05 \pm 0.05$	0.86	0.39	
Days after May 1st	$0.03 \pm 0.06$	0.50	0.62	
Year	$1.88 \pm 1.47$	1.28	0.20	
				Bat ID $4.48 \text{ e-}17$ $\pm 6.69 \text{ e-}9$
<hr/>				
Stability				
<hr/>				
Intercept	$-3.72 \pm 3.40$	-1.09	0.27	
Focal Tree Height	$0.15 \pm 0.10$	1.53	0.13	
Cavities	$0.08 \pm 0.10$	0.81	0.42	
Decay Class of Focal Tree	$0.01 \pm 0.032$	0.04	0.97	
DBH	$-0.00 \pm 0.04$	-0.06	0.96	
Days after May 1st	$0.02 \pm 0.04$	0.42	0.68	
Year	$0.58 \pm 1.01$	0.57	0.57	
				Bat ID $0 \pm 0$
<hr/>				

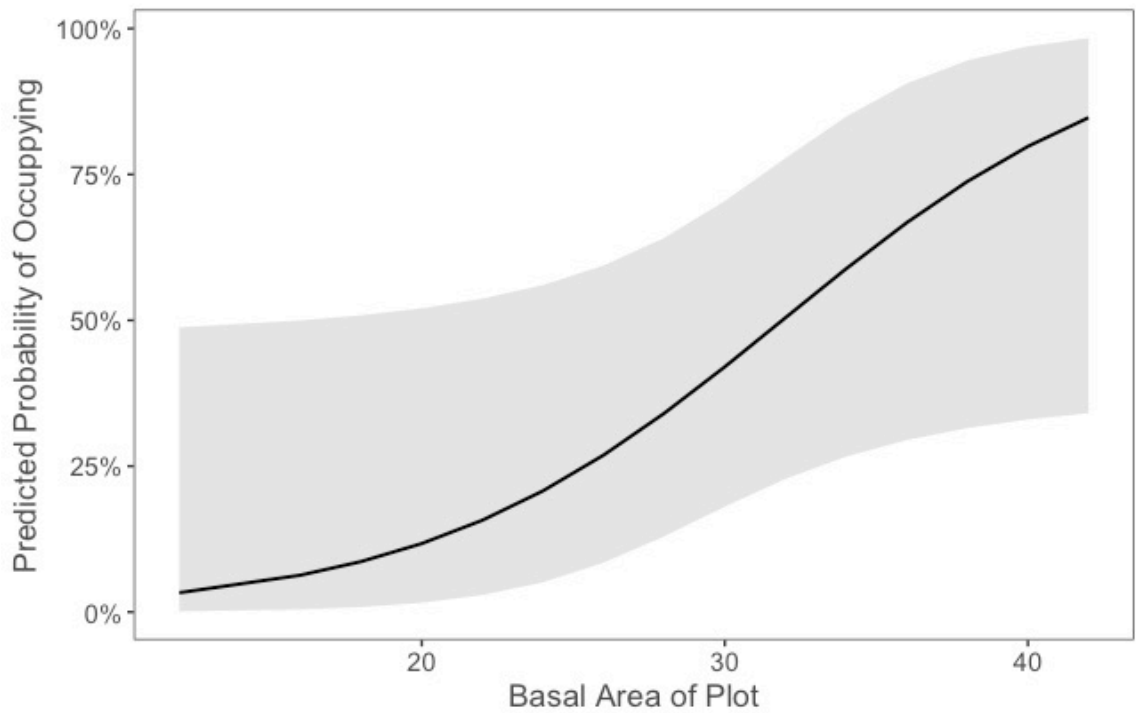


**Figure 3:** The marginal effect on the probability that female silver-haired bats (*Lasionycteris noctivagans*) occupy a specific roost tree based on the mean decay class of trees in the surrounding plot. The black line represents the prediction of the ‘options’ generalized linear mixed model with a binomial distribution and logit link function, with covariates held at their means. Grey bands represent 95% confidence intervals.





**Figure 4:** The marginal effect on the probability that female silver-haired bats (*Lasionycteris noctivagans*) occupy a specific roost tree based on the mean number of cavities per tree in the surrounding plot. The black line represents the prediction of the ‘options’ generalized linear mixed model with a binomial distribution and logit link function, with covariates held at their means. Grey bands represent 95% confidence intervals.



**Figure 5:** The marginal effect on the probability that female silver-haired bats (*Lasionycteris noctivagans*) occupy a specific roost tree based on the basal area of the surrounding plot. The black line represents the prediction of the 'options' generalized linear mixed model with a binomial distribution and logit link function, with covariates held at their means. Grey bands represent 95% confidence intervals.

## 2.4 Discussion

### 2.4.1 Roost Characteristics

I recorded and characterised roost trees used by female silver-haired bats during the reproductive season, a period that is expected to mean increased energetic challenges. Roosts were located within trembling aspen or balsam poplar trees, which are both deciduous trees within the genus *Populus*. Roost trees were mostly surrounded by white spruce and aspen forest. Consistent with my hypothesis, reproductive female silver-haired bats chose roost trees that were surrounded by additional habitat with potentially available roosts. Silver-haired bats in the Cypress Hills switched between roost trees (see results), and this has been observed elsewhere across their range (Mattson et al. 1996; Betts 1998a, 1998b). Roost switching is a common behaviour in tree-roosting Vespertilionids (Vonhof & Barclay 1996), including big brown bats in Cypress Hills (Kalcounis & Brigham 1998; Willis & Brigham 2004, Rintoul & Brigham 2014), which switch roosts even if their pups are not yet volant, bringing them to the new roost while attached at the mother's nipples (C.K.R. Willis, personal communication). If bats roost near other available habitat, mothers would have more time to forage (Vonhof & Betts 2010), and would not have to carry pups as far, making this behaviour less costly.

Roost switching has also been proposed as a predator avoidance strategy (Lewis 1995; Kalcounis & Brigham 1998), and I did observe a trend towards roost tree characteristics that I predicted would protect bats against predators (Table 4). Emerging from day roosts in the evening can be a potentially dangerous behaviour because bats are likely conspicuous to predators. Although bats in North America do not have specialized predators and therefore may not have faced the selection pressure necessary to develop precise predator avoidance strategies (Kalcounis & Brigham 1994), a high density of

potential roost trees could confuse opportunistic generalist predators by making it unclear which tree the bats are using and thus emerging from on a given night.

I predicted that female bats would choose roosts with features that would help newly volant pups reach maturity, such as reduced canopy cover and understory density. Bats did not choose roosts with these features, but it is possible that these features, which make flight more difficult for pups, also provide protection against predators. Buchler (1980) noted that little brown bats on their first flights remain near the roost, so the basal area of the plot and canopy cover above may not be the best proxies for the environment these bats were experiencing during flight.

I predicted that bats would choose roosts with access to high amounts of sunlight, which would warm roosts for pups that are not able to effectively thermoregulate. My results suggest that silver-haired bats did not choose roosts based on access to sunlight, unlike hoary bats that roost in open foliage and show a strong preference for southwest facing branches (Willis & Brigham 2005; Klug et al. 2012). Although unlike hoary bat roosts which are exposed to the elements, canopy cover and direction of roost opening may not be effective representations of actual received solar radiation (Bondo et al. In Press), and it is still unclear how these variables translate to the internal tree cavity conditions that silver-haired bats experience.

Bats did not choose roosts that were more structurally stable than other available trees. For species that use the same roosts long-term, structural stability may be an important factor (K.J. Bondo, unpublished data), but is unclear if silver-haired bats reuse maternity roosts for multiple seasons as other tree-roosting Vespertilionids do in Cypress Hills. For example, little brown bats (*Myotis lucifugus*) returned to the same area more

than 20 years later (Florko et al. 2017), and big brown bats reuse cavities within specific aspen trees for at least 10 years (Willis et al. 2003). Silver-haired bat roosting preferences are expected to be plastic while migrating through unknown habitat (McGuire et al. 2011), and if this plasticity persists during the reproductive season, it could minimize the impact of lost habitat should one roost tree be damaged, especially if there are other suitable trees nearby.

#### **2.4.2 Reproductive Status**

I found no evidence to suggest that roost preferences changed throughout the reproductive season. It is possible due to my small sample sizes for each reproductive stage, that the differences in roost choice might be indistinguishable. I did not find any roost trees used by male bats, but I would expect that those roosts would resemble roosts of non-reproductive females as males would be predicted to seek conditions that facilitate torpor use. For example, post-lactating female western long-eared bats (*Myotis evotis*) choose roosts with more stable microclimates that are more protected from the environment than pregnant and lactating females (Solick & Barclay 2006), likely reflecting a shift to prioritizing torpor use. Similarly, male big brown bats use torpor more than either reproductive or non-reproductive females, and choosing to roost outside of warm maternity colonies likely reflects this (Hamilton & Barclay 1994). The structural characteristics of roosts chosen by pregnant and lactating females may resemble each other because of similar physiological pressures of each reproductive stage and the microclimate benefits of maintaining maternity colonies as pups age.

### **2.4.3. Implications for Natural Resource Harvesting**

As human populations continue to grow worldwide, our demand for energy also increases and our past reliance on non-renewable resources is unsustainable. Renewable resources such as wind, solar, and hydro present alternatives for meeting our demand for energy in a way that is also sustainable in the longer term. However, there is no human action that does not impact the environment, and understanding and mitigating these impacts will be an important part of ensuring responsible harvesting of these resources.

Silver-haired bats are one of three species disproportionately killed by wind turbines in North America, making up approximately 18% of the >500,000 annual bat fatalities (Baerwald & Barclay 2011; Arnett & Baerwald 2013). Wind turbines present a threat to migrating bats (Arnett & Baerwald 2013; Frick et al. 2017), causing injury and death by barotrauma (i.e. internal haemorrhaging caused by pressure changes at the turbine blades) and blunt trauma (Baerwald et al. 2008). This threat may affect the population viability of the species that are most frequently killed (Frick et al. 2017). For example, population modelling based on conservative estimates of annual hoary bat fatalities caused by wind turbines and expert elicitation of probable life history variables indicate that hoary bats face a significant risk of extinction within the next 100 years (Frick et al. 2017). Frick et al. (2017) argued that these estimates are likely applicable to silver-haired bats as well, given the similarities between the species' life history traits and number of fatalities caused by wind turbines. The majority of these deaths occur between mid-August and late September (Baerwald et al. 2008), a period when summer residents begin their fall migration, leaving summering grounds. Identifying and protecting local habitat including maternity colonies on these summering grounds is

important for future mitigation strategies, especially as the demand for renewable energy sources continues to increase and policies are enacted to protect bats at wind farms.

Understanding roost priorities throughout the range of the silver-haired bat is also important because like most other species, silver-haired bats rely on forests for a part of their life history and silvicultural practices impact them (Kalcounis-Ruppell et al. 2005; Law et al. 2016). Forestry practises in North America are shifting away from even-aged management (clear cuts, etc.) to harvesting strategies that leave more natural patches, which parallel disturbances that occur in unmanaged forests (Law et al. 2016). This is helpful for maintaining forest composition, but silviculture can impact wildlife in other ways. It is important to know which structures are potential roosts for different species and when harvesting is particularly detrimental. Additional human activity near roosts during the reproductive season could be detrimental for pregnant and lactating female bats. For example, Eastern Bluebirds (*Sialias sialis*) nesting along an anthropogenic noise gradient had fewer fledglings in areas with more environmental noise (Kight et al. 2012), suggesting that human activity during specific windows could decrease reproductive success. Bat activity decreases with proximity to roadways (Berthinussen & Altringham 2011) and with increased anthropogenic noise (Bunkley et al. 2015), but it may be easier for individual bats to avoid human activity while foraging than it is for maternity colonies to relocate to structures with characteristics different than their preferred roosts.

Monitoring habitat use during sensitive or key windows of a species lifecycle can inform us about specific requirements for species survival but it can also allow for the most informed decisions around that habitat and its potential uses. This may become

increasingly important as the demand for the responsible harvesting of natural resources continues to grow, and the ecological and economic value of the remaining natural habitat increases.



## **Chapter 3 – Conclusion**

### **3.1 General Conclusions**

The energetic demand of mammalian reproduction is a constraint that motivates specific habitat preferences for many species, including bats, which show distinctly different habitat use between seasons. The roosting decisions made by silver-haired bats in the Cypress Hills of Saskatchewan are consistent with the assumptions that bats avoid additional energetic expense while raising pups. Bats roosted in trees that were near other suitable roost trees, which presumably reduces the cost of roost switching behaviour and minimizes the risk of exiting the roost nightly. When bats relocated, often their new roost remained in the same stand, possibly because of this nearby available habitat. Regardless of reproductive stage, female silver-haired bats chose roosts that were generally structurally similar to each other, in surrounding forest with comparable characteristics. Lactation is the most energetically expensive stage, but the energetic demands of pregnancy likely motivate similar preferences for cost saving habitat. Maternity colonies are composed of multiple reproductive female bats at different stages, so location of maternity colonies may be an example of compromise rather than reflecting one individual's ideal roost. The collective benefits of maternity colonies (i.e. group thermoregulation for newborn pups, even when mothers leave to forage) likely outweigh this compromise.

### **3.2 Recommendations**

Roost microclimate characteristics may be influenced by structural characteristics, but it is also possible that bats roosting in externally similar trees may be experiencing different internal thermal environments that unoccupied roosts cannot

provide. Perhaps there is even enough variation within roosts that bats with different energetic constraints and microclimate preferences are accommodated within the same roost. Using temperature dataloggers or thermal imaging cameras to understand temperature conditions within tree cavities can help us to understand the benefits that these roosts provide.

Due to roost switching behaviour by this and other bat species, conserving habitat even at the roost scale requires further understanding of this complex behaviour and likely requires the preservation of multiple trees per individual. If silver-haired bats roost with genetically related colony-mates, then conservation or loss of a maternity colony can have genetic consequences for this species. If migratory silver-haired bats show preferences for roost mates as the more sedentary big brown bats do, this could have implications for understanding the evolution of behaviours like migration and sociality.

Silver-haired bats are one of at least four species of bats found in the Cypress Hills which use trees. Considering how these bats co-occur within an existing environment can help us to expand our knowledge of interspecific resource use. If the majority of bat roosts are located near each other or in similar habitat type, it may lead to identifying an umbrella species.

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