Home range, habitat selection, and annual survival of little brown bats (*Myotis lucifugus*) in central Canada

By

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Abstract:

The little brown bat (*Myotis lucifugus*) is one of several hibernating bat species in North America affected by a fungal pathogen that causes a disease known as White-nose syndrome (WNS). As a result, little brown bat populations have experienced massive declines, resulting in federal and provincial efforts to conserve the species. However, limited knowledge about space requirements and long-term survival rates may be limiting the effectiveness of management efforts. In my thesis I fill gaps in the scientific literature to provide information on which conservation efforts can use to incorporate more species-specific information and base quantitative objectives on. In my first data chapter, I determine how energetic demands associated with reproduction and WNS affect home range and habitat selection. Reproductive bats must balance high daily energetic costs to support pregnancy and milk production, requiring large home ranges. However, energy and time constraints associated with reproductive activities, such as juvenile care, may restrict the space that they can use. I tested two competing hypotheses to determine which of the two, time or energetic constraints, ultimately affect home range size during pregnancy and lactation. I used radiotelemetry to quantify night-time home ranges of reproductive female little brown bats from a WNS-positive maternity colony. Results indicated that lactating females used smaller home ranges than pregnant bats, suggesting that time constraints drive variation in space use among individuals. In my second data chapter, I estimate annual survival rates in two populations of little brown bats near the northern limit of the species' range. I used seven years (2011-2017) of mark-recapture data for 4932 individual little brown bats to test the hypothesis that demographic characteristics, such as sex and age, along with seasonal environmental factors, affect variation in annual survival of little brown bats. At both hibernacula, annual survival varied over time with both age and sex of bats but did not vary with either summer or winter climatic variables. Male survival was generally higher than female survival and young-of-the-year survival was lower than that of adults. These results indicate that demography, and not environmental conditions influence inter-annual survival rates at my study sites. The results from this chapter suggest that females and juveniles are vulnerable groups in these populations. As a general management plan, conservation efforts should target female and juvenile demographic groups for protection, likely at maternity colonies where they are found at high densities during the summer. Taken together these result fill crucial knowledge gaps and provide critical baseline information on which management efforts can be based.

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Chapter 1: General introduction

Well-designed wildlife management strategies can help protect species, communities, and ecosystems from biotic and abiotic threats, such as invasive species or climate change (Fryxell et al. 2004). The best wildlife management plans often rely on quantitative objectives as goals against which progress can be measured, and often incorporate species-specific biological considerations into the planning process (Clark et al. 2002; Fryxell et al. 2004; Tear et al. 2005). For populations of endangered species, knowledge of species-specific habitat requirements and population demographic characteristics are especially important for management planning and implementation of recovery plans (Olden 2003). However, in conservation biology, there are taxonomic and geographic biases when it comes to studying and managing endangered species (Clark and May 2002; Roberts et al. 2016). These biases often lead to gaps in knowledge for many endangered species, and basic information about space use and population trends is often lacking. For example, in many aquatic ecosystems, marine protected areas are being established to protect avian and fish biodiversity. However, many of these protected areas have proven ineffective in protecting targeted species (Agardy et al. 2011; Bouma et al. 2014). Lack of information about the space requirements for species often results in protected areas being too small or inadequate in the ecosystem diversity they contain. This is especially impactful for predatory species, which require large foraging areas, and migratory fish and bird species, which may require many types of habitats as stopover points during migration. Consequently, marine protected areas often only protect a small portion of habitat that animals may need during their life cycle (Grüss et al. 2011). The failure to incorporate of these key biological considerations has resulted in the ineffectiveness of many marine protected areas in protecting biodiversity (Agardy et al. 2011). As such, incorporating biologically relevant information into conservation planning and protected area design is critical for the successful management.

For many species, seasonality can affect vulnerability to conservation threats. In the temperate zone of North America, seasonality causes predictable fluctuations in resource abundance and energetic demand. These fluctuating energetic constraints can lead to dramatic seasonal changes in a range of behaviours, including space use and habitat selection. Consequently, habitat requirements for a species can change between seasons. For example, caribou (*Rangifer tarandus*) forage from sedges and low-lying bushes in the tundra during the summer but migrate to dense forests during the winter to take advantage of available foods, such as lichen (Gunn and Miller 1986; Thomas et al. 1996; Parker et al. 2005). Resources can be severely limited in winter foraging grounds, making caribou herds more vulnerable to adverse weather, forcing them to forage in areas where they are at greater risk of predation (Wittmer et al. 2005). Furthermore, during the summer calving season, female caribou and their newborn calves experience a period of increased vulnerability. Individual females will reduce total space used for foraging during calving to minimize predation risk, while taking advantage of peak summer productivity (Ferguson and Elkie 2004).

Unlike caribou, many species of small-bodied mammals in the temperate zones cannot migrate large distances to habitats with available resources in winter. Furthermore, small-bodied mammals cannot meet heightened energetic costs associated with thermoregulation, due to their high surface to volume ratio, at a time when food is limited. Therefore, many small temperate mammals hibernate, relying on long multiday torpor bouts during which respiratory, cardiac and metabolic rates drop dramatically and body temperature is allowed to fall (Lyman et al. 1982; Schmidt-Nielsen 1997; Geiser 2004). Depending on latitude, some species spend as much as five to eight months in hibernation (Humphries et al. 2002; Ruf and Geiser 2015). A long duration of hibernation, combined with seasonal variation in resource availability, appears to have favoured separation of reproductive investment between males and females of several species (Sandell 1990; Birkhead and Møller 1993). Separation of the male and female reproductive cycle allows each sex to uncouple copulation from pregnancy and parturition, enabling optimization of the timing of reproductive investment around seasonal conditions (Sandell 1990, Ferguson et al. 2006, Orr and Zuk 2014). The uncoupling of reproductive events and investment by both sexes enables both sexes to meet the high energetic demands of reproduction by engaging in reproductive activities during periods of peak of resource availability before and after hibernation (Birkhead and Møller 1993). However, the delay between male and female reproductive investment is likely affected by factors, such as maximum longevity, body size, and mate quality, and not just seasonal resource availability (Sandell 1990, Birkhead and Møller 1993, Orr and Zuk 2014). In small, short-lived species, such as the Richardson's ground squirrels (*Urocitellus richardsonii*) the length of the delay between male and female reproductive investment may not be as long as longer-lived species. Richardson's ground squirrel males will invest energy during the winter developing testes and emerge from hibernation earlier than females (Michener 1998). Rewarming body temperature and emerging from hibernation is necessary because low body temperatures inhibit sexual maturation and prevent spermatogenesis (Williams et al. 2014). Furthermore, by emerging earlier than females, males can establish territoriality and prepare for intraspecific competition with other males for access to females (Michener and Locklear 1990; Michener 1998). Females Richardson's ground squirrels emerge 3-4 weeks after males and invest very little energy into mating. By delaying emergence from hibernation, female ground squirrels synchronize their increases in energy demands during pregnancy and lactation with seasonal increases in plant productivity, allowing them to maintain constant body mass throughout lactation (Michener 1998).

Similar to ground squirrels, hibernating bat species have evolved temporal separation of reproductive investment, however the delay between male and female reproductive investment is drastically longer. Furthermore, the timing of hibernation emergence for males and females is the opposite of that for ground squirrels. Male bats make the bulk of their reproductive investment before entering hibernations, while females delay reproductive investment until emerging from hibernation in the spring (Racey 1979). For example, male little brown bats (*Myotis lucifugus*) invest energy into reproduction during fall, developing sperm and chasing females for copulation (Thomas et al. 1979; Birkhead and Møller 1993; Speakman 2008). Females invest relatively little energy in reproduction during the fall, and store sperm over the winter (Wimsatt 1945). Reproductive females then emerge from hibernation earlier than males during spring and congregate together to form maternity colonies. Females remain in these aggregations throughout pregnancy and lactation, taking advantage of social thermoregulation to reduce metabolic costs (Kerth 2008). Males will emerge significantly later than females and disperse after emerging from hibernation, because they are not limited by the energy and time demands of reproduction during the spring and summer.

Foraging Theory and Constraints on Space Use

Seasonality can have a large impact on energetic demands of species, especially during reproduction. These seasonal changes in energetic demands can translate into seasonal changes in habitat requirements and area necessary for survival. Energetic costs and other constraints can structure the home range that an individual animal uses for daily activities, such as foraging (Burt 1943; Powell and Mitchell 2012). These costs can be particularly impactful for females in many species, because females experience higher energetic demands during reproduction than males and often contribute more time and energy into parental care than males (Powell et al. 1997; Mitchell and Powell 2007). These seasonal increases in energetic demands may force females to increase home range sizes and forage over larger areas, or forage more efficiently within their home range (Mitchell and Powell 2012). Other costs and constraints, such as travel time, parental care, and predation risk can also significantly impact how animals select foraging habitat (Mitchell and Powell 2004). Consequently, animals must make decisions while foraging to optimize their energy yield, while minimizing costs (Pyke 1984). Mitchell and Powell (2012) built on traditional optimal foraging theory and outline two alternative strategies that animals may use to balance opportunity costs and optimize their foraging. In the first foraging strategy, animals may be forced to maximize energy intake, foraging over a larger area and visiting patches with high quality food items. Animals employing this foraging strategy maximize total energy intake, but also experience increased travel costs and predation risk associated with longer foraging time (Krebs and Davies 1997; Stephens et al. 2007). High energetic demands may also require that animals be more selective about the habitat they forage in, and they may choose more distant resource-rich patches, with fewer competing conspecifics, over closer patches. Alternatively, some individuals may be forced to adopt a foraging strategy that minimizes foraging time and total space use to meet their minimum energetic demands for survival (Ydenberg and Krebs 1987). If individuals are constrained by non-foraging activities, such as territory defense, predator avoidance, or parental care, maximizing total energy intake may not be possible. Black bears (*Ursus americanus*) for instance, minimize home range size to the area producing enough food to meet daily energetic demands, because costs of intraspecific competition and territory defense constrain the amount of space available (Mitchell and Powell 2004; Mitchell and Powell 2012). These non-energetic constraints are particularly important for central place foragers, which return to a nest or roost located centrally within their home range. Central place foragers may need to bring food items back to a central location for processing before consumption, in which case the time to travel and process food items may represent a considerable constraint on home range size (Ydenberg 2007).

Identifying the foraging strategy that animals use and the constraints that limit home range size is important for explaining how animals use their environment. Understanding how animals respond to seasonal energetic demands by optimizing their foraging strategies can be critical for identifying the amount of space that animals need for survival. For endangered species, identifying these space and habitat requirements can be used to designate critical habitat for protection and recovery of the species.

Quantifying Vital Rates of Free-ranging Wildlife

While understanding space use and home range of individuals is important for identifying important habitats, long term monitoring of population trends is also crucial for conservation. Long-term monitoring programs can also provide useful information that benefits both wildlife and people. Wildlife monitoring programs can help track the spread of invasive species and the changes to ecosystem health that they cause. For instance, the Eurasian zebra mussel (*Dreissena polymorpha*) is a freshwater invasive species that outcompetes native North American freshwater mussels (Order Unionoida). Long-term monitoring of zebra mussel revealed that high reproductive and growth rates enabled them to push out native mussel species, drastically altering ecosystem health (Barbiero and Tuchman 2004; Lucy 2006; Smeltzer et al. 2012). Ongoing monitoring of this species in lake ecosystems is essential to the protection of freshwater ecosystems and the fish that people rely on. Long-term population monitoring also has a critical role in the surveillance of wildlife diseases (Childs et al. 2007). These monitoring programs can provide information about incidence rates of diseases and patterns of disease spread, enabling preventative measures to minimize the spread of zoonotic wildlife diseases from animals to humans (Deem et al. 2001).

Rabies is often a focal point of wildlife monitoring programs, due to the risk of transmission to both people and domesticated animals. Monitoring rabies in wild populations of urban adapted species, such as skunks (*Mephitis mephitis*) and raccoons (*Procyon lotor*) have quantified the spread of the disease in urban centres and identified localized areas of risk (Greenwood et al. 1997; Childs et al. 2007; Weissinger et al. 2009). Consequently, large national- and international-scale monitoring programs are critical from a public health and wildlife health perspective.

Monitoring programs are also essential for tracking the success of endangered species recovery plans and management efforts (Block et al. 2001). Long-term monitoring programs can allow estimation of vital rates (e.g., survival, mortality) in wildlife populations, and are important for understanding population dynamics (Lebreton et al. 1993). Endangered species monitoring programs allow managers to track population trends, detect changes in demographics, and compare survival rates from different populations. Long-term monitoring has been an essential component in the management of species threatened by habitat loss. For instance, because of habitat loss, the threatened Greater Prairie-Chicken (*Tympanuchus cupido*) was reduced to a single population with very few individuals (Westemeier et al. 1998). Ongoing monitoring, active translocation and population supplementation have allowed managers to intervene in time to increase population genetic diversity, preventing inbreeding depression and extirpation of the population. Long-term population monitoring is also a critical component in adaptive conservation management (Schreiber et al. 2004). Long-term monitoring can be used to identify historic trends and compare effectiveness of different recovery strategies (Runge 2011). Thus, establishment and maintenance of long-term monitoring programs is important for endangered species conservation because it can inform decision making, detect changes in populations trends and enable continual improvement of species management plans (Beissinger and Westphal 1998; Morris and Doak 2002; Chirakkal and Gerber 2010).

Bats (Order Chiroptera) are one taxon facing a range of conservation threats but long-term monitoring programs for bats are often difficult because most species are cryptic with high mobility (O'Shea et al. 2003). Despite this difficulty, establishment of monitoring programs for bat species is important, because bats provide diverse ecosystem services, pollinating plants, as well as providing economic benefits by consuming insect pests (Boyles et al. 2011). Successful programs, with a diverse range of objectives, have been implemented for a few populations of a select few bat species around the world (O'Shea et al. 2003; Meyer et al. 2010; Ingersoll et al. 2013). For instance, monitoring has been used to estimate vital rates and population dynamics of bat communities to identify responses to timber harvesting in Australia (Law et al. 2018). Monitoring programs have also been essential in tracking the demographic trends in populations of endangered bat species, including little brown bat, tri-colored bat (*Perimyotis subflavus*), Indiana myotis (*Myotis sodalis*), and northern myotis (*Myotis septentrionalis*) in the eastern U.S. (Ingersoll et al. 2013). Furthermore, monitoring data have also been used in predictive modeling to estimate the impacts of climate change, habitat loss, and wildlife disease to predict future population trends (Frick et al. 2010; Meyer et al. 2010; Hayes and Adams 2017).

Typical methods of long-term monitoring programs rely on permanent or semi-permanent marks to identify recaptured individuals over time for capture-mark-recapture analysis (Lebreton et al. 1992). Traditionally, capture-mark-recapture involves physically banding or tagging individuals at an initial encounter, with resampling of the population in the future, recapturing some proportion of previously marked individuals. However, capture and recapture can be stressful for animals, which can potentially affect behaviour and survival of individuals (Knox et al. 2013). Because of this, passive redetection methods are becoming increasingly common as a method of monitoring bat species (Gibbons and Andrews 2004). One method of passive detection involves subcutaneous injection of a passive integrated transponder (PIT tag). Each PIT tag has a unique code that can be detected by a remote antenna/datalogger when animals come within range. PIT tags are permanent and are particularly effective for monitoring hibernating bat species, because large aggregations of individuals often show high site-fidelity to hibernacula where a permanent reader and antenna can be placed (Norquay et al. 2013). Furthermore, bats can be marked in large numbers at fall swarms, allowing for relatively large sample sizes and more reliable estimate of population-specific vital rates, compared to conventional mark-recapture methods (Ellison et al. 2007). These passive redetection methods alleviate some of the difficulties in the monitoring of bat species, making long-term monitoring more effective and feasible to implement in conservation programs.

White-nose Syndrome

Establishment of long-term monitoring programs for populations of bat species in North America is becoming increasingly urgent. Hibernating bat species in North America are being threatened by a cold-loving fungal pathogen, *Pseudogymnoascus destructans*, which causes a disease known as white-nose syndrome (WNS) in affected bats (Blehert et al. 2009; Gargas et al. 2009). WNS causes damage to exposed skin, particularly of the wings, disrupting normal physiological activity during hibernation (Warnecke 2013). This, in turn causes individuals to increase the frequency of their energetically expensive arousals throughout hibernation (Cryan et al. 2010; Warnecke et al. 2012; 2013; Verant et al. 2014). Frequent arousals result in excess energy expenditure and premature depletion of fat reserves, leading to emaciation and mortality (Reeder et al. 2012). Ultimately, WNS-associated mortality has led to drastic population declines in hibernating bat species across North America (Frick et al. 2010, Thogmartin et al. 2013, Pettit and O'Keefe 2017). In addition to causing mortality during winter, WNS may also have far-reaching carryover effects, affecting the minority of bats that survive hibernation with the disease and emerge in spring (Davy et al. 2017). The fungus is not thought to cause direct impacts on bats during the active season because it can only grow at low temperature (Verant et al. 2012) but surviving individuals emerge from hibernation with extensive wing damage and severely depleted fat reserves and may need to invest what little energy reserves they have left into tissue recovery. This is particularly impactful for female bats which typically use fat reserves stored the previous fall as 'capital' to invest in early spring reproduction. Without adequate fat stores females may not be able to maintain pregnancy (Jonasson and Willis 2011). Consequently, carryover effects of WNS may affect reproduction and recovery potential in affected populations. In particular, increased energetic demands associated with healing and reduced energy stores may require bats to change their foraging behaviour and increase the space they need to forage (Harestad and Bunnel 1979).

Due to the far-reaching impacts of WNS on bat populations across North America, three hibernating bat species have been listed as endangered in Canada (COSEWIC 2013), and one species has been listed as threatened in the U.S. (U.S. Fish and Wildlife Service 2016). With the ongoing spread of WNS and the official listing of these hibernating bat species, there is a necessity to conduct further research to fill knowledge gaps in our basic understanding about these endangered species. Estimating vulnerability of healthy populations and the effectiveness of management efforts on affected populations contribute to the successfulness of future conservation efforts. Furthermore, understanding how WNS may affect vital rates in populations of the species can allow a targeted approach to management.

Study species

The little brown bat is a hibernating insectivorous bat species whose geographic range extends from Alaska to Mexico and is one of the species most severely impacted by WNS (Fenton and Barclay 1980; Frick et al. 2010, Petitt and O'Keefe 2017). Like many hibernating bat species, the little brown bat has separation of reproductive investment, and because of this males and females have distinctly different seasonal behaviours. During the fall, male and female little brown bats form large assemblages at the entrances of hibernacula, a behaviour known as swarming (Fenton 1969; Fenton and Barclay 1980; Schowalter 1980). Up to and during this period, reproductive males invest heavily into spermatogenesis (Gustafson 1979) and bats engage in promiscuous mating, where males chase females and both males and females mate with multiple individuals (Thomas et al. 1979). Some mating also occurs during hibernation, and males may mate with torpid females, but spermatogenesis and most mating occurs during the swarming period before individuals enter hibernation.

After emerging from hibernation in early spring females will begin to invest both time and energy into reproduction. During pregnancy at maternity colonies females typically experience high energetic demands of reproduction at a time when food is scarce and ambient temperature may be cold. Therefore, pregnant females must balance periods of normothermy which maximizes fetal growth, and torpor use to minimize energy expenditure (Dzal and Brigham 2013). Energetic demands of reproduction increase even further during lactation because milk-production is energetically expensive (Kurta et al. 1989). During lactation, females must allocate their nightly activity between foraging to meet energy costs of lactation and time-consuming parental care. Consequently, during the reproductive season female bats are heavily constrained both energetically and temporally, making foraging efficiency and energy management essential for survival of both the mother and newborn juvenile (Kunz et al. 1998).

The broad objective of my thesis is to provide information about the influence of energetic and time constraints on space use, habitat selection, and annual survival of little brown bats to fill crucial knowledge gaps important for management of this endangered species. For Chapter 2, I used radiotelemetry to quantify space use and habitat selection during pregnancy and lactation to test two competing hypotheses regarding whether energetic or temporal constraints primarily limit the amount space and types of habitats required for foraging and survival. I also compared my home range data to estimates of home range sizes required by pregnant and lactating bats collected for a colony of bats studied at a similar latitude before invasion by WNS. Specifically, I tested the hypothesis that energetic constraints imposed by WNS lead to a carryover effect of WNS on space use. For Chapter 3, I used a long-term monitoring dataset for PIT-tagged little brown bats at two hibernacula to determine how demographic and environmental factors influence annual and regional variation in apparent survival of little brown bats. Little information is available about how seasonal changes in energetic demands associated with reproductive investment during pregnancy and lactation might translate into changes in space use and habitat requirements. Furthermore, in both healthy and WNS-affected populations the extent to which temporal sex-based separation of reproductive investment affects survival rates of males and females is unclear. Understanding how these sex differences affect space use and survival in this endangered species is important to determining vulnerability of population demographic groups to infection by WNS and habitat loss. Therefore, my thesis should provide useful information important for management of endangered bats in the face of WNS.

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Chapter 2

Home range size and space use by pregnant and lactating little brown bats (*Myotis lucifigus*) following invasion of white-nose syndrome

Abstract:

Energetic and time constraints can affect home ranges of animals with individuals forced to increase home range size when foraging efficiency is low and energy demand is high or reduce home range size if constrained by the time required for non-foraging activities (e.g., defending a territory, competing for mates, or provisioning offspring). For female bats, time constraints may vary by reproductive stage because lactating females must visit roosts frequently throughout the night to nurse pups. Reproductive status influences energy demand for bats, with especially high costs during lactation relative to pregnancy, which could also influence foraging habitat selection and home range. White-nose syndrome (WNS), a disease that affects hibernating bats, has negative consequences for energy balance in winter and may have carryover effects into spring and summer, potentially influencing energy and home range. I used radiotelemetry to quantify night-time home ranges of reproductive female little brown bats (*Myotis lucifugus*) to test predictions of two hypotheses. The 'time constraints hypothesis' predicts that home range size should decline during lactation compared to pregnancy, but nightly visits to roosts should increase as females return to nurse pups throughout the night. Alternatively, the 'energetic constraints hypothesis' predicts that, if energetics exert a stronger influence than time limitation, frequency of visits to the maternity roost should remain stable between pregnancy and lactation, whereas home range should be negatively correlated with ambient temperature (T_a), which predicts thermoregulatory costs and food availability. Finally, I tested the hypothesis that WNS results in a seasonal carryover effect on home range and space

use, predicting that bats recovering from WNS have larger home ranges than pre-WNS bats because of the need to spend more time and cover more area to balance their energy budgets. I outfitted bats from a WNS-positive colony in northwestern Ontario, Canada with radiotransmitters during pregnancy (n = 7 individuals, N = 34 bat nights) and lactation (n = 12 individuals, N = 69 bat nights) and used telemetry to quantify home range size. Consistent with the time constraints hypotheses, home ranges were smaller during lactation compared to pregnancy and lactating bats made more roost visits than pregnant bats. However, I also found support for the energetic constraints hypothesis as bats in my study used home ranges that were about 50-60 times larger than those quantified for pre-WNS little brown bats at a different site. My findings suggest that, at the local scale, time constraints drive variation in space use among individuals but that energetic constraints imposed by WNS influence variation in space use among and within populations.

Introduction:

Conservation of endangered species often involves protection of habitats critical for survival and reproduction. Identification of these critical habitats can be challenging, in part because, for many species, habitat selection and space use vary both within and among individuals (Gehrt and Fritzell 1997; Coltrane and Sinnott 2013) depending on energy requirements (Jetz et al. 2004), resource abundance (Schradin and Pillay 2006) and population density (Hoset et al. 2008). For species that live in the temperate zone, seasonality can have particularly strong effects on resource abundance and energy demand leading to potentially large differences in habitat selection within individuals throughout the year. For example, caribou (*Rangifer tarandus*) migrate between summer tundra habitats to forests during the winter to take advantage of seasonal variation in resource abundance (Gunn and Miller 1986). Seasonal space use in caribou populations also changes with reproductive condition, and herds will drastically reduce space use during the calving period in summer to take advantage of high summer food abundance and to protect juveniles (Ferguson and Elkie 2004).

Many other temperate-zone species are too small to migrate large distances to exploit seasonally available resources and have evolved to hibernate instead. In part because of the long period of hibernation, the timing of reproduction is temporally separated by sex in species such as the Richardson’s ground squirrel (*Urocitellus richardsonii*) and many temperate bats (Buchanan 1987; Birkhead and Møller 1993, Michener 1998). While most mammals show temporal separation of reproductive investment, particularly large-bodies species with long gestation periods, for small-bodied mammals, hibernation appears to prolong the delay between male and female reproductive investment (Birkhead and Møller 1993). For ground squirrels, males depend on energy reserves stored as fat before hibernation, so they can emerge earlier than females to produce sperm and defend a territory from rival males (Michener and Locklear 1990; Michener 1998). Females emerge 3-4 weeks after males and are receptive for mating within days of emergence, which synchronizes the timing of their greatest energetic demands (i.e., lactation) with peak seasonal resource abundance (Michener 1998).

Many temperate bat species exhibit similar separation in the timing of reproductive investment between sexes, although the pattern is reversed for males and females. This is especially important in the temperate zone where a long duration of hibernation necessitates separation of reproductive investment, to maximize survival of both sexes (Birkhead and Møller 1993). For example, male little brown bats (*Myotis lucifugus*) invest energy into sperm production during summer, and mate in fall and, to a more limited extent, during winter (Thomas et al. 1979; Birkhead and Møller 1993; Speakman 2008). Females, on the other hand, are capital breeders, depending on fat stored in the fall to support reproduction the following spring (Racey and Swift 1981). Females store sperm from fall and winter mating for up to 150 days post-mating (Wimsatt 1945; Fenton 1970). They then emerge from hibernation earlier than males, often when weather is still cold, and food is still unavailable, and congregate to form maternity colonies to begin gestation. Females benefit from having young as soon as possible to maximize the time for young-of-the-year (YOY) growth and fat accumulation before the next hibernation season which can be a bottleneck for YOY survival (Norquay and Willis 2014; Chapter 3). This intense pressure on females for early reproduction and rapid offspring growth could have pronounced implications for the space required for foraging and home range size during the active season.

In addition to between-sex differences in seasonal energetics, within sexes there can be pronounced differences in energy expenditure throughout the year, with implications for space use. For example, Kurta et al. (1989) used doubly-labeled water to show that daily energetic demands of free-ranging female little brown bats increased by approximately 20% during lactation relative to pregnancy. Females bats should, therefore, alter feeding behaviour and nightly activity throughout the reproductive season to meet these heightened energetic demands of lactation (Racey and Swift 1985; Rydell 1989; Feldhamer et al. 2001). There is little published research, however, on how these changes in energetic demands affect foraging behaviour and space use in little brown bats or any insect-eating bat species.

Little brown bat populations are currently threatened throughout North America due to the spread of an infectious cold-tolerant fungal pathogen, *Pseudogymnoascus destructans* (Pd) which causes a disease known as white-nose syndrome (WNS) (Blehert et al. 2009; Gargas et al. 2009; Lorch et al. 2011; Warnecke et al. 2012). In the decade since its discovery, WNS has caused enormous population declines killing millions of little brown bats across eastern North America and has led to the species being listed as endangered in Canada (COSEWIC 2013). WNS affects hibernating bats by disrupting torpor bouts, periods of reduced physiological activity, causing frequent arousal and rewarming (Reeder et al. 2012). Arousing during hibernation is normal, but increased frequency of arousals due to WNS drastically increases energy consumption throughout the winter, leading to premature depletion of fat stores (Warnecke 2013; Verant et al. 2014). Surviving bats emerge from hibernation with extensive wing damage and severely reduced fat stores. These physiological impacts may result in seasonal carry-over effects which could impact foraging efficiency and long-term fecundity and survival for WNS-affected survivors (Jonasson and Willis 2011; Davy et al. 2017). This may be particularly impactful for female bats, which already face high energetic demands associated with reproduction, immediately after hibernation. These high energetic demands could lead surviving females to increase space use for foraging as they attempt to maintain energy balance (Harestad and Bunnel 1979).

To date only one study has quantified space use in free-ranging little brown bats. Henry et al. (2002) followed individual, female little brown bats from a maternity colony on Grosse-Île, a 200-ha island in the St. Lawrence river near Quebec City (Lat. 47.03, Long. -70.67). Despite similar habitat across the island, bats used only a fraction of the available space and home ranges of pregnant bats averaged approximately 30 ha declining by 42% to 17.6 ha during lactation. Pregnant bats foraged over a larger area around the roost and traveled farther from the roost during foraging trips. This study suggests that populations of healthy, pre-WNS, female little brown bats in this region require approximately 30 ha of foraging habitat around their roost to support survival and reproduction during the reproductive season. However, no study has examined habitat requirements and space use following the invasion of WNS.

I used radiotelemetry to quantify night-time home ranges of reproductive female little brown bats in an area which had recently experienced declines from WNS. I tested predictions of two alternative hypotheses. What I term the ‘time constraints hypothesis’ predicts that home range size should decline during lactation compared to pregnancy, but that the frequency and duration of nightly visits to roosts should increase as females return to nurse pups throughout the night. The time-constraints hypothesis also predicts that lactating bats will be more selective about foraging habitat than pregnant bats, so they can meet energetic demands during a shorter overall foraging time, leaving more time for YOY care. Alternatively, the ‘energetic constraints hypothesis’ predicts that, if energetics exert a stronger influence than time limitation, frequency and duration of visits to the maternity roost should remain stable between pregnancy and lactation, whereas home range should be negatively correlated with ambient temperature (T_a), which affects thermoregulatory costs and food availability. Finally, I tested the hypothesis that WNS results in a seasonal carryover effect on home range and space use because of the energetic constraints imposed by reduced foraging efficiency and costs of healing tissues damage for bats recovering from WNS in spring. This hypothesis predicts that WNS survivors should have larger home ranges than pre-WNS individuals because they need to spend more time, and cover more area, to balance their energy budgets. This hypothesis also predicts a positive relationship between tissue damage from WNS and the mean number of nightly roost visits, because severe wing damage should reduce foraging efficiency and increase healing costs.

Materials and methods:

I conducted fieldwork from June to July 2017 in the Laclu area of Kenora district, northwestern Ontario (Lat. 49.786, Long. -94.692, Figure 2.1). The area is in the boreal shield ecozone and vegetation consisted of variably-dense mixed-wood forests with patches of wetland and herbaceous grasslands. The area includes many lakes in a rural, semi-developed landscape with paved roads and numerous residential and vacation homes along the shoreline. Many of these buildings are used by female little brown bats as maternity sites, where females form colonies to give birth and nurse YOY. This site was selected primarily because of the abundance of known little brown bats maternity roosts and because WNS was detected at an abandoned mine hibernaculum during the preceding winter approximately 55 km from the study area, well within the distance traveled by this species between winter and summer (Norquay et al. 2013). Temperature and weather measurements for the site were obtained from the closest Environment Canada Weather station located at the Kenora airport, approximately 20 km away. Average summer night-time low temperature during my study was 15.6 °C (min = 8.4 °C, max = 25.1 °C), which is similar to the average night-time low temperatures for the pre-WNS little brown bat colony in Grosse Île during Henry et al.'s (2002) study (17.7 °C; min 8.4 °C, max 26.5 °C).

All methods were approved under University of Winnipeg Animal Care Protocol AE04639 and Ontario Ministry of Natural Resources and Forestry Scientific Collectors Permit 1086222. Pregnant bats were caught on 1 June 2017, using a harp trap placed outside one maternity roost in a vacation home near the shoreline of Sandy Lake. Lactating bats were captured on 14 July 2017 from another building roost 150 meters away using a triple-high mist net (Kunz et al. 1988). Although the bats were captured from two different buildings, some of the bats captured during pregnancy were tracked to the second building, suggesting that these individuals were all members of the same colony. Dates for capture events were chosen based on records from a long-term mark-recapture database established using permanent tags (Gibbons and Andrews 2004). Relative age of individuals (adult vs YOY) was determined based on degree of fusion of the metacarpal epiphyses (Kunz and Anthony 1982). Pregnancy was determined by gentle palpation of the abdomen to detect a developing fetus and lactation was determined based on bare patches in the fur around the nipples (Racey 1988). I also measured body mass for all individuals using an electronic balance (FP 1000, Fuzion Diablo, Barcelona, Spain) and measured forearm length with digital calipers 100-300-8 EZ Cal, iGaging Precision Instruments, San Clemente, CA, USA. I followed Reichard and Kunz (2009) to quantify WNS-associated wing damage with scores of 0 = no scarring, discoloration, or scar tissue, 1 = < 50% of wing tissue covered in scarring and discoloration and 2 = > 50% of the wing tissue covered with scars and discoloration.

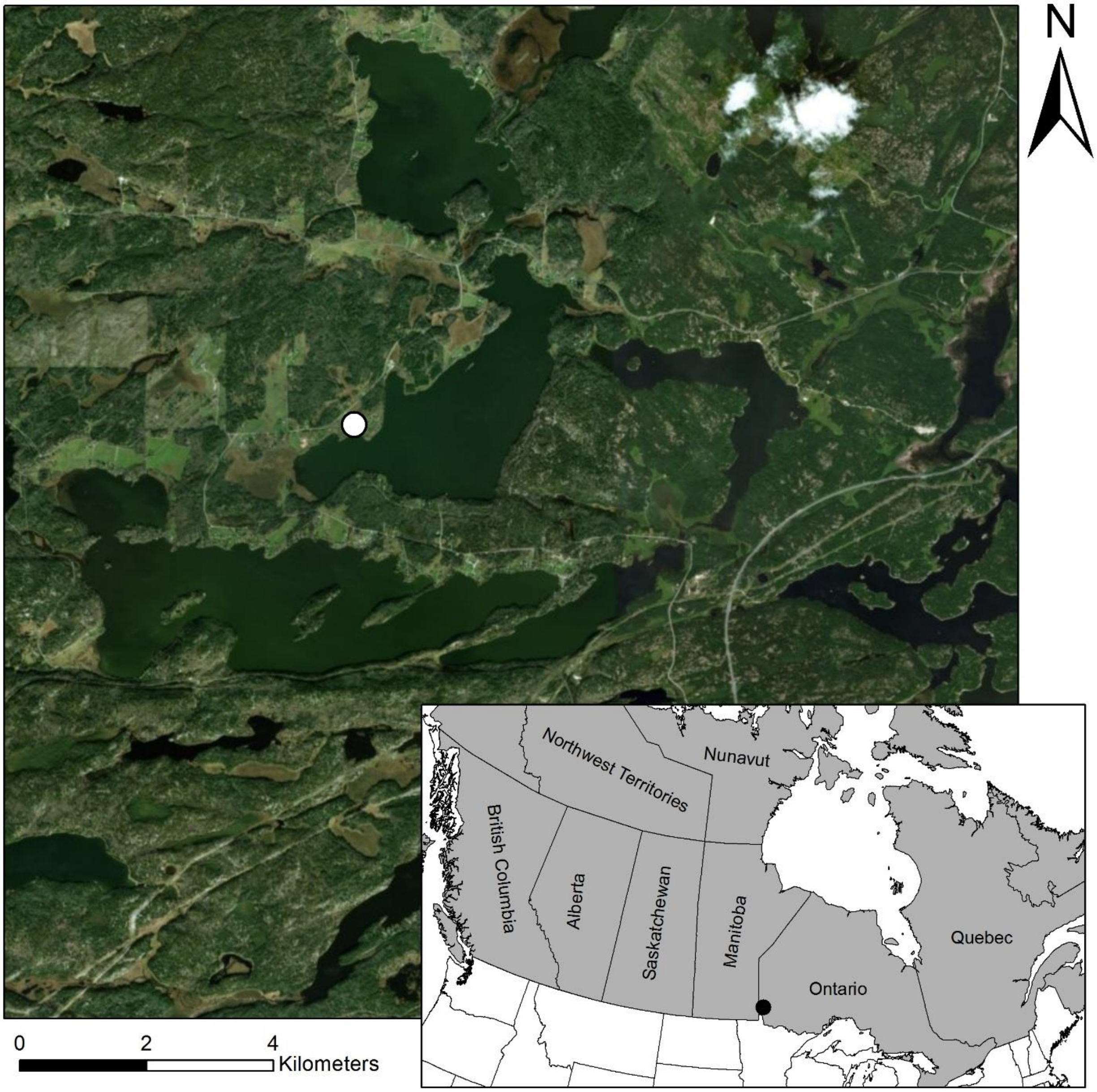

Figure 2.1: Aerial photo of Laclu region in Kenora county, Ontario, Canada, showing the location of the maternity colony (white circle), and the relative location of the study area in North America (inset map).

I outfitted pregnant and lactating bats with temperature sensitive radio transmitters (Model LB-2NT, 0.35g; Holohil Systems Inc., Carp, Ontario, Canada). Transmitters were attached by trimming a small patch of fur on the dorsum between the scapulae and then gluing transmitters in place using a non-toxic latex-based surgical adhesive (Osto-bond, Montreal Ostomy, Vaudreuil, Quebec, Canada). Bats were held for approximately two minutes until glue dried and were then released. Bats were not tracked on the night of release, because handling may have altered normal foraging behaviour, but they were tracked on all subsequent nights until either the transmitter battery died, or I determined that the transmitter had fallen off. I considered a tag to have fallen off if the signal did not move after more than 24-hours of good weather (i.e. dry with $T_a > 10$ °C). Individuals were tracked for a range of 2-10 days after capture.

I triangulated positions of individuals throughout the night based on transmitter signal detections by three teams of two observers each. Each team was equipped with a handheld telemetry radio receiver (R1000, Communications specialist Inc., California, USA) attached to a 5-element Yagi antenna (Wildlife Materials International Inc., Illinois, USA) mounted on a 5-meter long telescoping pole. Teams were stationed at locations across the approximately 80 km^2 study area designed to maximize signal coverage of an area centred on the maternity roost. At 10-minute intervals throughout the night, observers used the null-to-null method to triangulate positions for each bat. When using the null-to-null method an observer first approximates the direction of the strongest signal and then identifies null directions on either side of that signal at which the signal is no longer detectable. The final recorded direction of the bat is then determined by bisecting the angle between the null directions (Amelon et al. 1988). I chose this method because the strongest signal direction could only be determined using auditory cues to an accuracy of 2-3 degrees. Once the signal direction for a given bat was recorded by each team, teams coordinated by walkie talkie and then switched to the next transmitter to ensure that signal detections were synchronized. A 10-minute sampling interval was selected to minimize temporal autocorrelation between readings. Based on published flight speeds for little brown bats of approximately 20 km/h (Gould 1955; Hayward and Davis 1964), individuals should have been able to travel across a significant portion of my sampling area within 10-minutes.

I recorded the number of visits back to the maternity roost throughout the night, using a stationary datalogging telemetry receiver (SRX-600, Lotek Wireless Inc, Newmarket, Ontario, Canada) positioned at the maternity colony. This receiver was programmed to cycle through my list of frequencies every 10 minutes. When a frequency was detected, the datalogging receiver recorded the time and intensity of the signal. I was then able to determine when each bat was in the roost based on the magnitude of, and variation in, signal intensity. When bats were present in the roost, signals were maximal and stable, while absence from the roost were indicated by either a gap in recorded signals or drastically reduced and fluctuating signal strength (Figure 2.2).

All analyses were conducted in R (version 3.5.0, R Core Team 2018). I used the ‘sigloc’ package (Berg 2015) to convert intersections of recorded compass bearings at each sampling time into position fixes as Universal Transverse Mercator (UTM) coordinates. I then used these position fixes to estimate home range size for each individual bat using fixed kernel density estimation (KDE) (Worton 1989). KDEs were selected over other methods of home range estimation, such as the minimum convex polygon (MCP) method, because KDE takes into consideration the relative frequency distribution of animal locations, minimizing bias to extreme points in the final home range estimate (Burgman and Fox 2003; Börger et al. 2006).

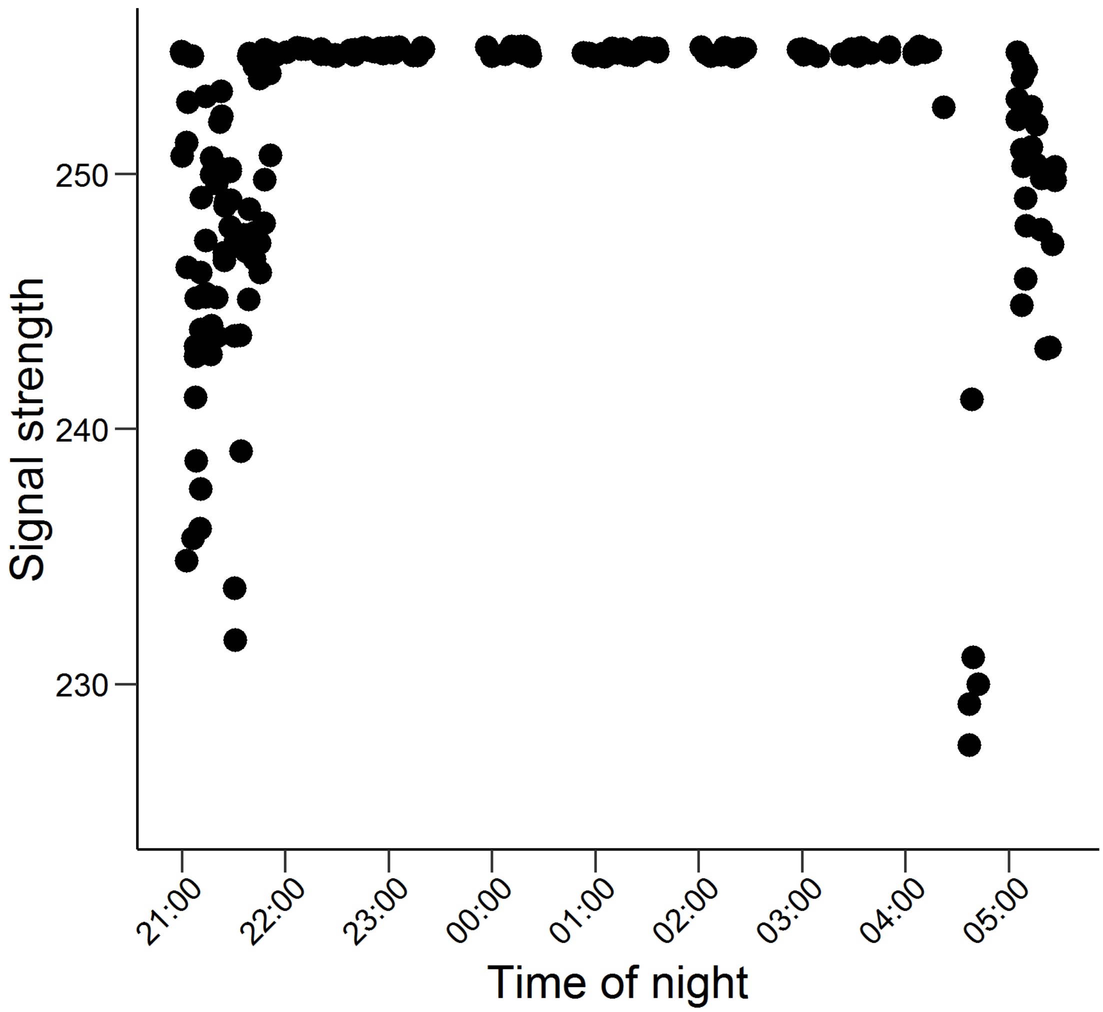

Figure 2.2: Representative time course for one individual over one night obtained from a datalogging telemetry receiver stationed at a maternity colony of little brown bat. Signal strength (range 0-255) and signal variability were used to indicate presence/absence of each bat in the roost.

Kernel density estimation requires specification of two important components: the shape of kernels and a smoothing parameter (Wand and Jones 1995). I fit each position fix with a Gaussian kernel, which converts point locations into probabilistic distributions centered around an observed location (Silverman 2018). I used the *ad hoc* method to select the most appropriate smoothing parameter (Kie 2013) because other methods, such as reference (h_{ref}) and least squares cross validation (h_{lscv}), can overestimate or underestimate final home range size, respectively (Kie et al. 2010; Kie 2013). I used reference and least squares cross validation to define upper and lower boundaries of the smoothing parameter for each bat and then determined an *ad hoc* smoothing parameter ($h_{ad\ hoc}$) within those bounds such that $h_{lscv} < h_{ad\ hoc} < h_{ref}$. I reduced h_{ref} in 10% increments until the polygon estimate for home range of a given individual fractured into two or more polygons.

I followed Laver and Kelly (2008) to assess whether my data met sampling effort and site fidelity assumptions of kernel density estimation using the using the ‘rhr’ package in R (Signer and Balkenhol 2015). Sampling effort was assessed using estimation of home range size area-curves for each bat. A home range area curve plots the number of relocations for each individual against an estimate of home range size with increasing sample size. When an increase in the number of relocations does not increase home range size it can be assumed that sampling effort was adequate to estimate home range size for that individual (Haines et al. 2006). I followed Seaman et al. (1999) and excluded bats from my analysis for which I did not record at least 30 position fixes. I tested for site fidelity by comparing the area used by each individual against the area that it could have used if its movements occurred at random (Spencer et al. 1990). This was done by generating the mean squared distance (MSD) from random permutations and comparing MSD values to the real distribution of redetection locations. My data satisfied kernel estimation assumptions, so I calculated kernel densities using the ‘adehabitatHR’ package (Calenge 2015) using 90% isopleths as final estimates for each individual’s home range (Börger et al. 2006).

To estimate the types of habitat used by little brown bats during pregnancy and lactation, I used Arcmap 10.5.1 to superimpose the estimated home ranges for each individual onto a land cover map of the area. Land cover data were obtained from the Canadian Land Cover database in vector format based on Landsat images with 15 m resolution (Natural Resources Canada 2015). Habitat types were classified into categories based on composition (Table 2.1). Differences in habitat selection preferences between pregnant and lactating bats were identified using eigenanalysis of selection ratios (White and Garrott 1990; Calenge and Dufour 2006). This analysis partitions variability of the eigenvalues along axes which represent each factor (hence factorial axes), in this case for individuals and habitat type. Individual habitat preferences are expressed by differences in the magnitude and direction of the eigenvector along factorial axes (Calenge and Dufour 2006). This method enables identification of group-based habitat selection if individual eigenvectors cluster together along the factorial axes. If all individuals select the same habitat types, then most variation in habitat selection is explained by variation on the 1st factorial axis. Variability in selection between individuals is indicated by the distribution of variation across both the first and second factorial axes (Calenge and Dufour 2006). Variation on the first factorial axis suggests differences in selection for the same habitat types between individuals, while variation on the second factorial axis reveals different selection strategies across animals or groups. In the case of my analysis, if differences in habitat selection between pregnant and lactating bats exist, individual variation along both factorial axes would be apparent as distinct clusters for pregnant and lactating bats. This method also allows comparison of the proportion of habitat types used by individuals against the total proportion of habitat types available to all individuals in the study. Comparing individual habitat use against total available habitat provides an estimate of habitat selection ratio (w_i) for each individual, which identifies individual preferences for specific habitat types over others (Manly et al. 2002). I calculated w_i for each habitat type using the ‘adehabitatHS’ package in R (Calenge 2006). I tested the significance of habitat selection using a chi-square goodness-of-fit test to determine if individuals were using habitat types in proportion to the availability of those habitat types on the landscape (White and Garrott 1990, Manly et al. 2002). If values of w_i are equal to 1, it suggests that animals are not selecting or avoiding a given habitat type and that they are using that habitat in proportion to its availability. Accordingly, values of w_i >1 suggest positive selection for a given habitat, while values <1 suggest avoidance of a given habitat type.

I used parametric t-tests and non-parametric Mann-Whitney U tests, where appropriate (e.g. non-normal distribution, heterogenous variance), to compare home range sizes, and the frequency and duration of visits to the maternity roost each night, between reproductive classes. I used ordinary least squares regression models to quantify effects of T_a on home range size and estimate the relationship between wing tissue damage and the number of nightly roost visits. I assessed significance at the 0.05 level and results are reported as the mean ± 1 standard deviation.

Table 2.1: Description of habitat types used in habitat selection analysis for female little brown bats.

Habitat type	Description
Developed	Land with modification for human occupation. Includes road surfaces buildings and garden/lawn spaces.
Water	Lakes, reservoirs, rivers, streams
Sparse forest	Forest with approximately 10-25 % crown closure.
Dense forest	Forest with greater than 60 % crown closure.
Rock	Non-vegetated exposed rock surface.
Shrub	Woody vegetation of relatively low height (generally ±2 meters).
Wetland	Land with water table near/at soil surface, including fens, bogs, marshes.

Results:

I captured and attached radiotransmitters to 12 pregnant bats on 1 June 2017 and 16 lactating bats on 14 July 2017. Both pregnant and lactating bats showed evidence of wing scarring caused by recent infection with *P. destructans* with scores of pregnant bats (1.0 ± 0.31) trending higher than those of lactating bats (0.53 ± 0.14, Table 2-2), although the difference was non-significant (t = 1.55, df = 18, p = 0.07). Transmitters remained attached for 2-12 days, allowing me to collect 103 total bat-nights of home range data.

The observed MSD from the centre of activity used by each individual was less than the MSD estimate based on permutations of random movements, indicating that the movements of individuals in this study were clustered near an activity centre (i.e., the maternity roost) and that both pregnant and lactating bats showed site fidelity to the maternity colony. The bootstrapped asymptotes of the home range-area curve, which compares the estimated area of home range against an increasing number of sampled points, indicated that the number of relocations for each individual was adequate to accurately estimate home range size. This suggests that the sampling effort (number of relocations) for pregnant and lactating individuals was sufficient to meet assumptions of kernel density estimation (Table 2.2).

Pregnant bats had significantly larger home ranges (1675.73 ± 520.85 ha) than lactating individuals (1067.45 ± 377.68 ha; t = 3.0, df = 18, p = 0.007; Figure. 2.3) with a decline of 36% in home range size between pregnancy and lactation. Pregnant bats also had larger maximum distances from the maternity colony to the edge of their home range (3999.8 ± 1132.62 m), compared to lactating bats (2759.41 ± 919.75 m; U = 72.0, p = 0.037). There was no difference in the minimum distance from the maternity colony to the edge of the home range between pregnant (1261.9 ± 354.49 m) and lactating bats (1153.90 ± 324.69; t = 0.7, df = 18, p = 0.50;

Figure 2.4). Pregnant females made significantly fewer roost visits throughout the night (1.79 ± 1.27 visits) compared to lactating females (4.80 ± 1.09; $t = 5.5$, $df = 18$, $p < 0.001$; Figure 2.5). Pregnant females also made significantly longer foraging trips (104.48 ± 41.13 minutes) than lactating females (71.37 ± 21.06) before returning to the colony ($U = 69$, $p = 0.034$). There was no effect of average minimum nightly T_a on home range size for either pregnant ($F_{1,5} = 0.26$, $p = 0.63$, $R^2 = 0.05$) or lactating bats ($F_{1,11} = 2.42$, $p = 0.15$, $R^2 = 0.18$) (Figure 2.6). The relationship between wing damage (Reichard index) and number of roost visits was significant for pregnant bats ($F_{1,5} = 6.9$, $p = 0.047$, $R^2 = 0.58$) but was not significant for lactating individuals ($F_{1,11} = 0.01$, $p = 0.93$, $R^2 = 0.001$; Figure 2.7).

Analysis of selection ratios indicated that animals did not use the available habitat equally in their home ranges ($\chi^2 = 147.6$, $df = 114$, $p = 0.02$), suggesting habitat preferences. However, there was no clear clustering of either pregnant or lactating groups in the eigen analysis (Figure 2.9). Individual bats showed significant habitat selection ($\chi^2 = 441.5$, $df = 120$, $p < 0.001$) and preferred developed and water habitats in greater proportion than predicted by habitat availability ($\chi^2 = 293.8$, $df = 6$, $p < 0.001$; Figure 2.8).

Table 2.2. Summary of telemetry and morphometric data for pregnant and lactating little brown bats radio-tracked near Kenora, ON. The Reichard index quantifies WNS-associated wing damage at capture, ranging from 0 (no visible scarring), 1 (<50% wing tissue covered with scaring and discoloration), and 2 (>50% of wing tissue covered with scaring and discoloration) (Reichard and Kunz 2009).

Bat ID by reproductive status	# of Relocations	Body mass (g)	Reichard index	Home range size (ha)	Roost visits per night
Pregnant					
b5	50	11.4	0	2167.44	0.56
b7	58	9.7	1	2066.42	3.24
b9	37	8.5	2	1496.29	2.77
b11	56	9.9	0	2241.42	0.81
b13	56	9.3	2	774.54	3.36
b17	14*	10.6	1	1465.07	0.62
b19	48	10.2	1	1518.95	1.18
Mean ± SD	45.6±15.6	9.94±0.93		1675.73±520.85	1.79±1.27
Lactating					
b2	37	9.4	1	1087.44	5.24
b4	48	9.5	0	1241.89	6.27
b6	65	8.7	1	966.93	4.22
b8	43	9.9	0	803.42	4.07
b10	46	10.3	0	1925.64	5.08
b12	66	9.6	1	951.68	6.05
b14	70	10	1	735.12	5.47
b16	21*	9.3	1	798.92	4.90
b24	49	8.7	0	1112.69	3.38
b26	45	10.2	0	1087.16	4.26
b28	52	9.5	0	1668.98	5.88
b30	48	9.4	1	523.85	5.06
b34	68	7	1	973.18	2.45
Mean ± SD	50.6±13.9	9.34±0.86		1067.45±377.68	4.80±1.09

*Despite not having 30 relocations, these individuals met the assumptions for kernel density estimation, and were kept for further analysis.

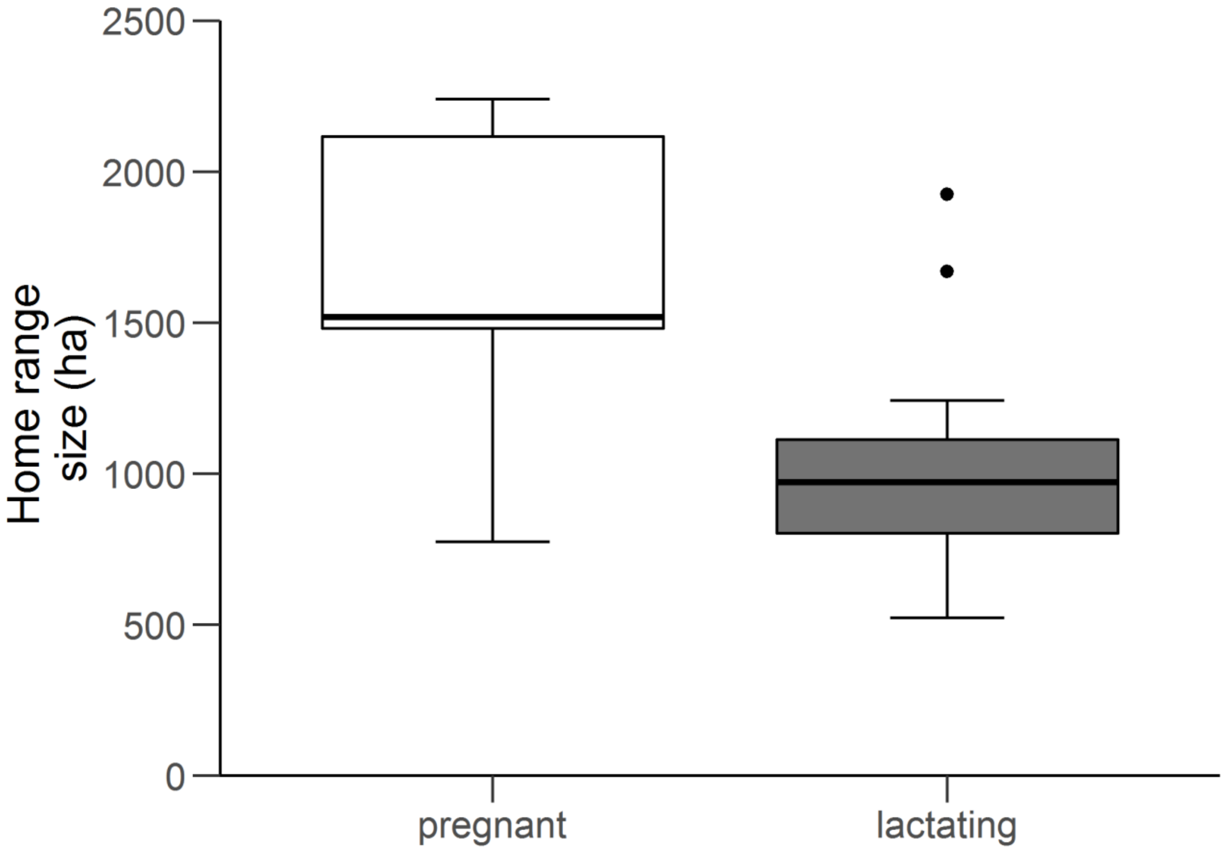

Figure 2.3: Boxplots comparing home range size of pregnant and lactating little brown bats. The black line indicates the median for each group, boxes represent the interquartile range, and whiskers represent values 1.5 times the interquartile range. Black circles represent outliers.

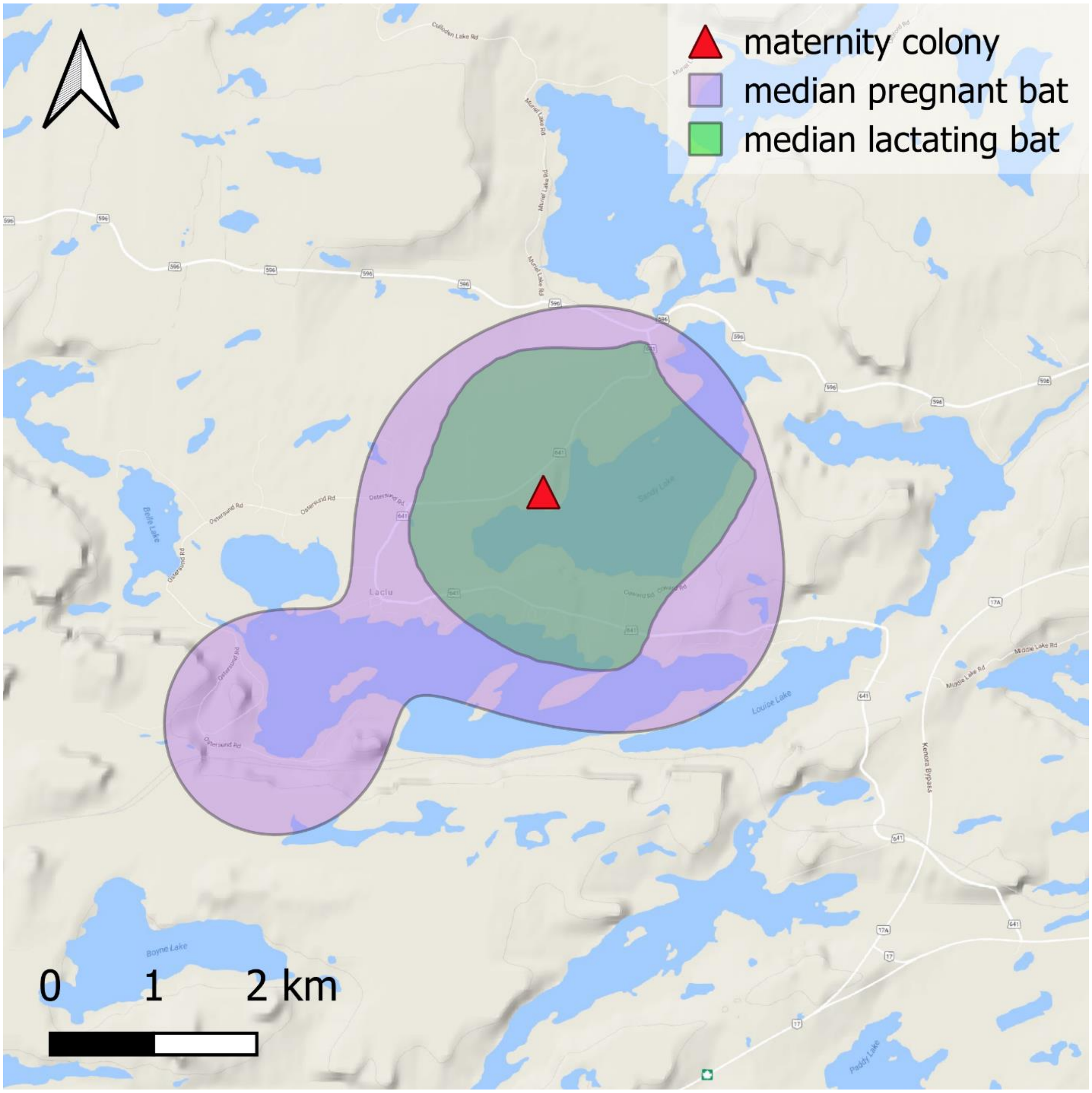

Figure 2.4: Home ranges for the individual female little brown bat with the median home range size for the pregnant (purple) and lactating (green) groups in the Laclu region of Kenora county, ON, Canada.

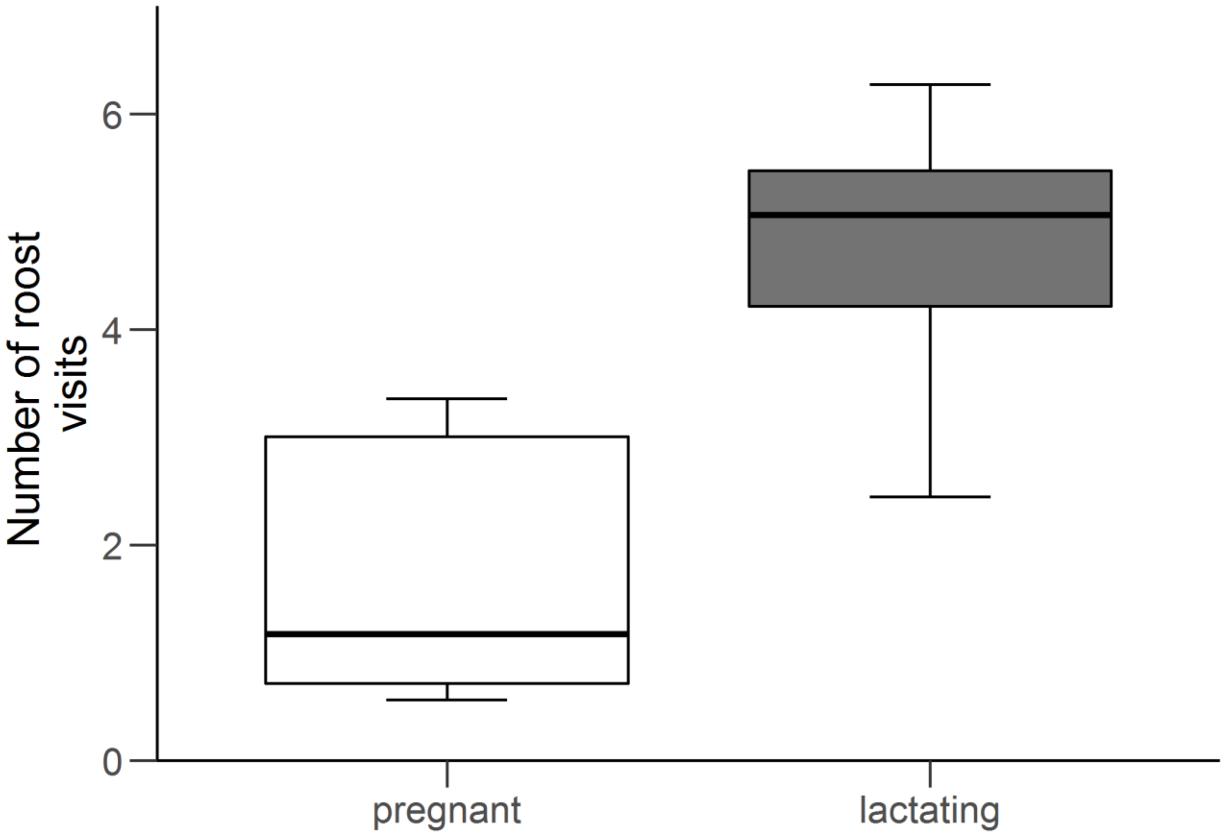

Figure 2.5: Boxplot comparing the number of nightly roost visits made by pregnant and lactating little brown bats. The black line indicates the median for each group, boxes represent the interquartile range, and whiskers represent values 1.5 times the interquartile range.

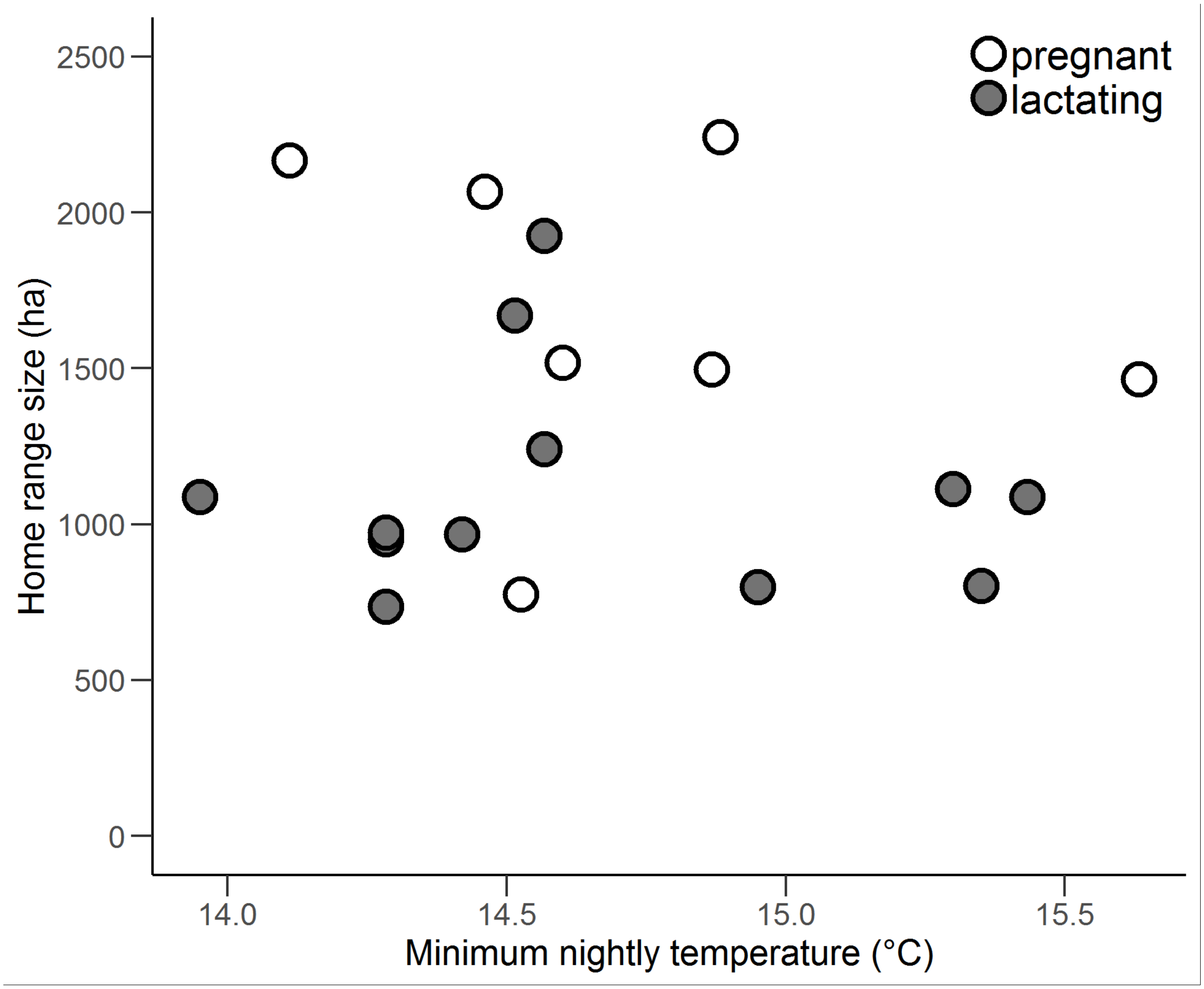

Figure 2.6: Scatterplot of the relationship between home range size and the average minimum nightly temperature for 7 pregnant (white circles) and 13 lactating (grey circles) little brown bats radiotracked near Kenora, ON.

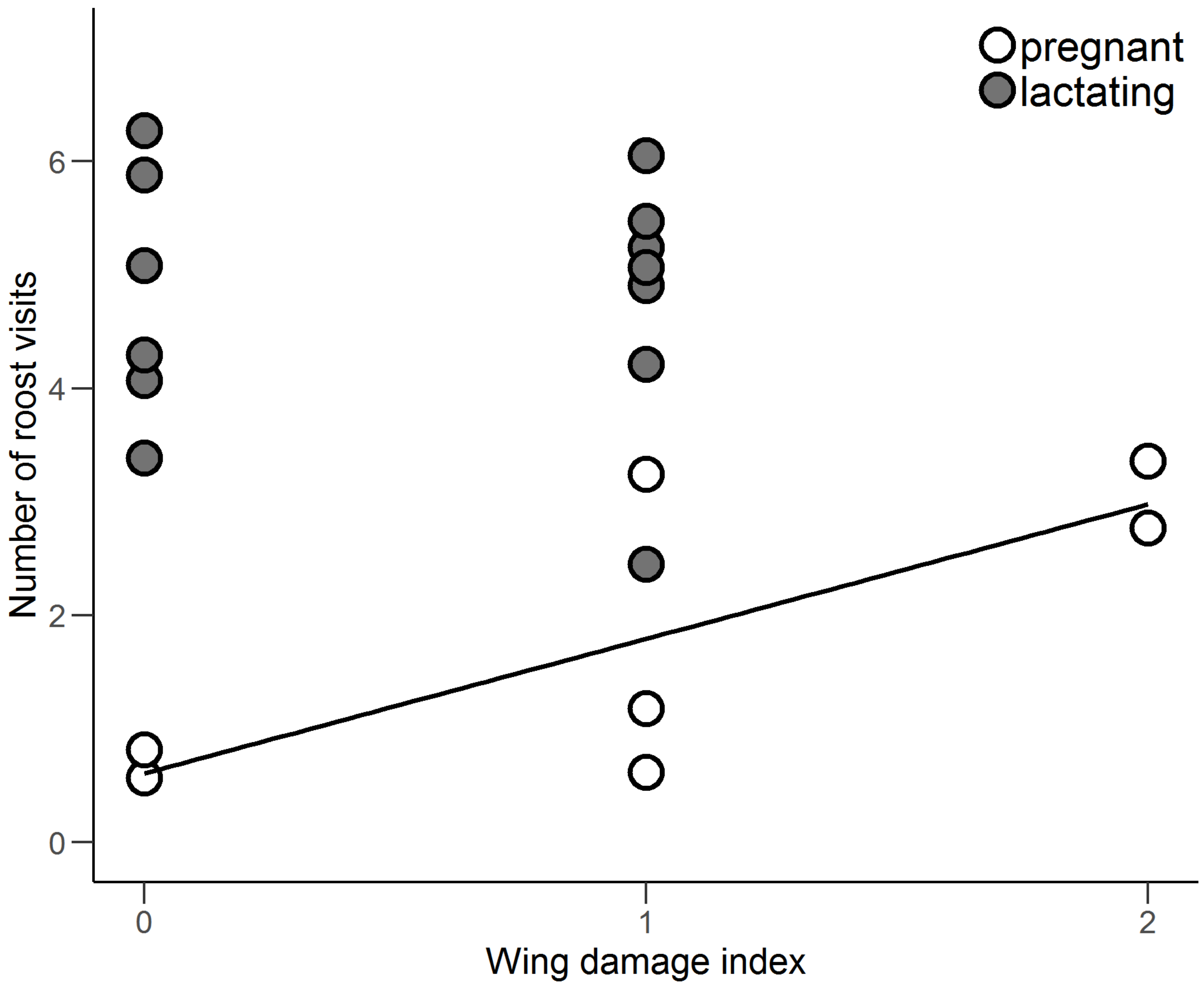

Figure 2.7: Scatterplot of the relationship between wing scarring index (Reichard index) and the average number of roost visits made by 7 pregnant (white circles) and 13 lactating (grey circles). The solid line shows the significant relationship between wing damage and the mean number of roost visits for pregnant bats.

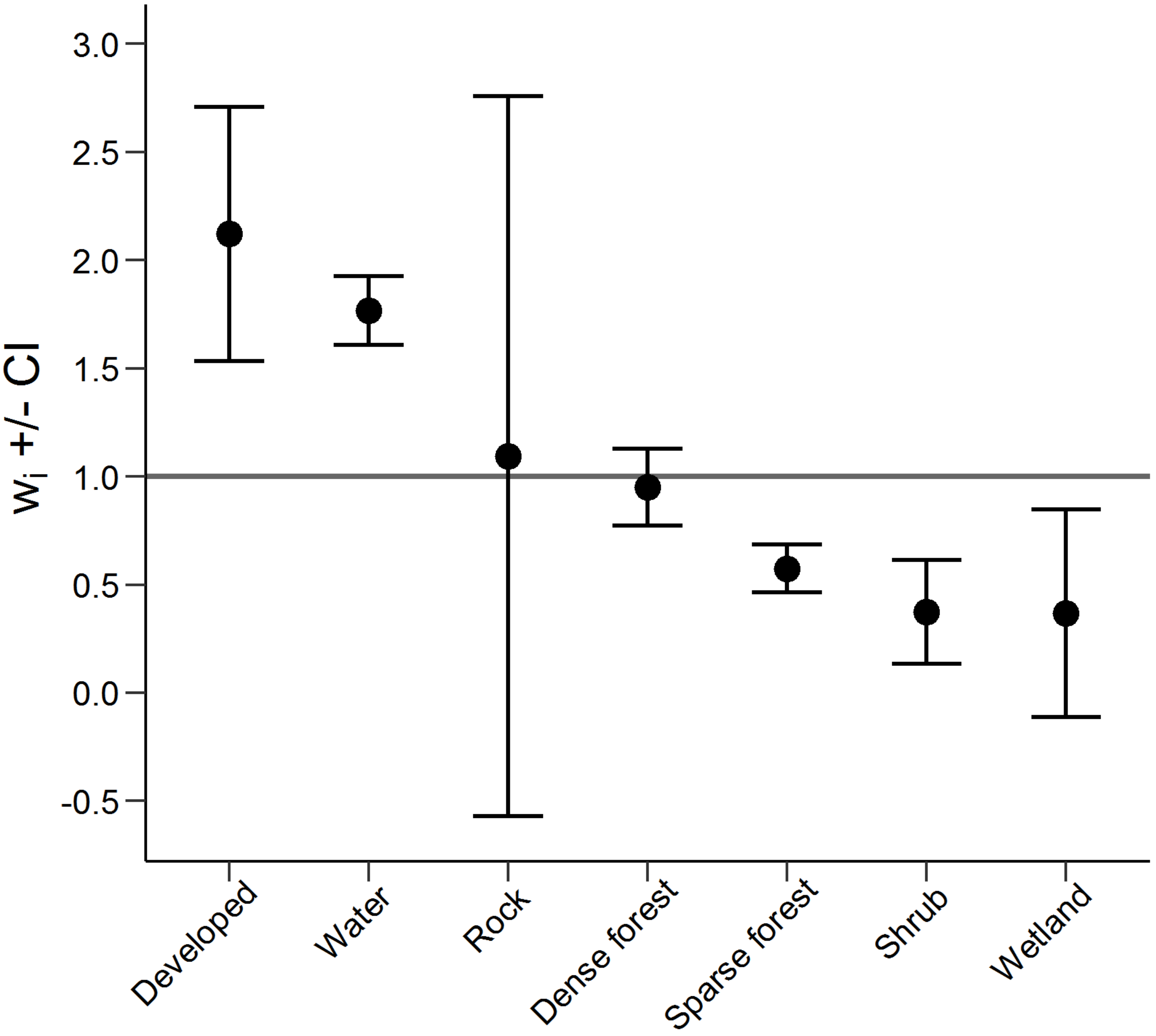

Figure 2.8: Selection ratios (w_i), with Bonferroni confidence intervals, for habitats used by little brown bats in the Laclu region of Kenora county, ON, Canada. Habitats are ranked in descending order by selection ratio. The grey line at $w_i = 1$ shows no preference or avoidance of any habitat type. Values > 1 indicates a preference for a given habitat while values < 1 reflect habitat avoidance.

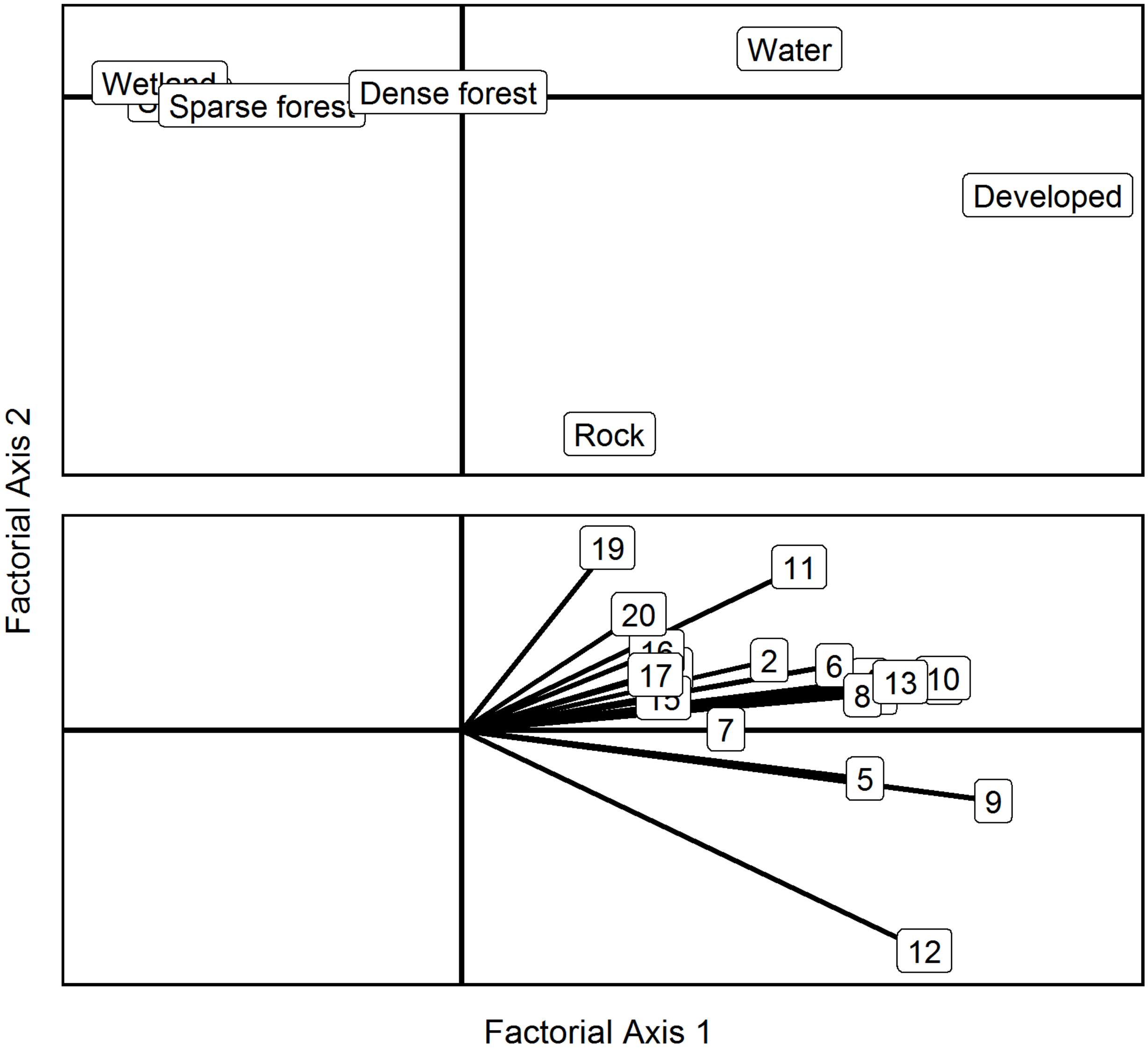

Figure 2.9: Results from eigenanalysis of selection ratios for little brown bats in the Laclu region in Kenora county, Ontario, Canada. The top graph indicates the variation in habitat selection by habitat type for all bats combined along 2 factorial axes. The bottom graph shows the eigenvector of the selection ratio for each of the individual 7 pregnant (labels 1-7) and 13 lactating (labels 8-20) female bats on the factorial axis.

Discussion

My results from this chapter support the time constraints hypothesis, which suggests that time needed for provisioning offspring exerts a stronger influence than energetic limitations on patterns of home range size, space use and activity for pregnant versus lactating bats. Lactating bats had dramatically smaller home ranges, centred on the maternity roost, and made many more visits to the maternity roost throughout the night, presumably to nurse YOY between foraging trips. Pregnant bats, on the other hand, had much larger home ranges, travelled further from the maternity colony during the night, and made fewer visits back to the maternity colony. Although I did not find evidence that energetic constraints affected changes in home range size between pregnancy and lactation, I did find evidence of an energetic carryover effect of WNS on home range and space use. Both pregnant and lactating bats I studied used home ranges that were vastly larger than pre-WNS bats studied by Henry et al. (2002), despite similar latitudes and climate conditions between studies, suggesting that the energetic constraints associated with WNS likely influences space use.

The reduction in home range size that I observed between pregnancy and lactation was similar to that reported by Henry et al. (2002). Mammalian lactation is energetically expensive, especially for small mammals which may need to drastically increase food consumption to meet energetic demands (Anthony and Kunz 1977; Kurta et al. 1989). Despite these high energetic demands, time constraints associated with YOY care appeared to limit foraging behaviour during lactation suggesting an optimization between foraging and parental care in this species (Mitchell and Powell 2012). Although T_a did not differ between pregnancy and lactation in my studies, it is possible that synchronization of flying insect abundance with lactation in the middle of summer (Mackay and Kalff 1969; Paetzold and Tockner 2005) could allow lactating bats to maintain energy balance despite a reduction in home range size. The abundance of lakes near the maternity colony may also provide habitat for the development of aquatic insect prey that little brown bats tend to feed on during lactation (Anthony and Kunz 1977; Fenton and Barclay 1980).

Contrary to the energetic constraints hypothesis, home range size did not increase as energetic demands increased, suggesting that energy limitation is not as important in structuring home range size as other constraints. Furthermore, there was no significant relationship between T_a and home range size, despite the fact that T_a affects the abundance of flying insects as well as thermoregulatory costs (Anthony et al. 1981, Negraeff and Brigham 1995, Meyer et al. 2016). However, this could reflect the low variation in average night-time T_a experienced by bats in my study (13.9-15.6 °C). This low variability in T_a may have been too small to drive a relationship between energetic costs, foraging behaviour and home range size (Lacki 1984). Despite the difference in home range size between pregnant and lactating bats, I did not find a significant difference in habitat selection between groups. Both pregnant and lactating bats showed a preference for habitats developed for human use, including roads and buildings, which often had street lamps in my study area. Artificial lighting along roads in my study could have attracted flying insects, increasing food density relative to other neighbouring habitat patches (Furlonger et al. 1987; Rydell 2006). Bats also showed a tendency to forage over water. Previous studies using acoustic methods to record echolocation calls, have shown a preference of little brown bats for edge habitats near water sources (Nelson and Gillam 2016). The combination of road edges and buildings with artificial lighting, as well as abundantly available aquatic habitat for insect development in my study site may result in high local insect densities.

A potential limitation of my comparisons of both habitat selection and home range size is a relatively small sample size for both the pregnant and lactating groups. However, based on post-hoc power analysis and effect size between groups (Cohen’s d = 1.34), the sample size for both groups were large enough to yield sufficient power (power = 0.86) to detect a difference between groups.

My results also provide evidence of a carryover effect of WNS on habitat selection during reproduction. Bats recently affected by WNS in my study had home range sizes approximately 60 times larger than previous estimates of home range for a pre-WNS population of little brown bats (Henry et al. 2002). It is likely that surviving WNS, among other factors, is a component contributing to this vast difference in spatial scale. Reduced foraging efficiency because of damaged wing tissues, at least during pregnancy before wings have mostly recovered, or increasing energetic demands of supporting recovery from WNS during reproduction may influence total space requirements, leading to this difference in home range sizes. Compared to healthy bats, individuals recovering from WNS may be forced to travel further and forage over larger areas to meet their heightened energetic demands (Anthony et al. 1981). Interestingly, pregnant bats with higher wing damage scores made more return visits to the colony than less damaged pregnant individuals. This pattern was not apparent with lactating bats, all of which generally showed a lower extent of wing damage than pregnant bats. This difference in effects between pregnant and lactating bats may be explained by the extent of WNS-induced wing damage and length of recovery time after emerging from hibernation (Fuller et al. 2011). After emerging from hibernation, pregnant bats with greater wing damage may be more inclined to return to the roost throughout the night, possibly to rest, digest acquired food and save energy on thermoregulation by huddling (Kerth 2008; Pretzlaff et al. 2010). Energy saved in this method could then be spent on tissue recovery.

It is possible that differences in home range size between my study and Henry et al.'s (2002) data reflect factors other than WNS carryover effects (Meteyer et al. 2012, Davy et al. 2017). For one, the colony studied by Henry et al. (2002) was found on an island where space use may have been limited by island size. This could explain some of the difference I observed, given that home ranges I quantified were much larger than the total island size (~200 ha) at Henry et al's field site. However, bats studied by Henry et al. (2002) still had home ranges of 30 ha during pregnancy and 17.6 ha during lactation, vastly smaller than the total island size. Thus, they were still able to maintain energy balance despite foraging over an area about 60 times smaller than bats in my study. Different home range sizes could also reflect population-based differences between studies. However, both Henry et al.'s (2002) colony and the colony I studied are at similar latitudes with similar summer T_a and generally similar environmental conditions and habitat composition. This suggests that the enormous difference in home range size I observed was at least partly by the recent invasion of WNS in the population followed in this study. If the colony on Grosse Île still exists, I recommend that researchers return to this study site to quantify post-WNS home range.

Healthy female little brown bats experience a multitude of constraints on both energy and time budgets during the reproductive season, that affect torpor use and foraging behaviours (Anthony et al. 1981; Dzal and Brigham 2013). WNS survivors experience greater constraints on their energy and time use than healthy bats, and likely face carryover effects of the disease as heightened energetic demands associated with healing from tissue damage (Fuller et al. 2011, Meteyer et al. 2012, Davy et al. 2017). At a local scale, my study suggests that time constraints associated with non-foraging activities are the primary factor influencing variation in home range size between pregnancy and lactation. However, at a much larger regional scale, my data suggestion that carryover effects of WNS on energetics may lead to a dramatic increase in overall energetic demands and home range size for surviving populations. I recommend that future studies quantify home ranges and habitat selection in little brown bats and aim to estimate home range size of healthy populations in the western range of this species before the arrival of WNS. Quantifying home range size for the same colonies before and after invasion by WNS will allow future studies to directly compare the impact of WNS and estimate energetic carryover effects to help devise management strategies to help conserve endangered bats in the face of WNS and other threats.

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Chapter 3

Sex and age-specific rates of pre-white-nose syndrome survival for two northern populations of little brown bats (*Myotis lucifugus*)

Abstract

Peripheral populations near the limit of a species' range often exhibit lower vital rates than central populations. Understanding how these vital rates change over time is essential for managing these potentially vulnerable populations. I used seven years (2011-2017) of mark-recapture data for 4932 individual little brown bats (*Myotis lucifugus*) to test the hypothesis that demographic characteristics, such as sex and age, along with seasonal environmental factors, affect variation in annual survival of little brown bats. I used Cormack-Jolly-Seber models and model selection to account for permanent emigration from the populations and included both summer and winter weather parameters as predictor variables. I found mixed evidence for my hypothesis, and annual survival varied by demographic characteristics, but not environmental factors. At both hibernacula, annual survival varied over time with both age and sex of bats but did not vary with either summer or winter climatic variables. At 'The Abyss' males consistently had higher average annual survival rates (0.75 ± 0.035 (SE)) than females (0.61 ± 0.04. First-year survival of young-of-the-year (YOY) was higher for males (0.23 ± 0.01) than for females (0.13 ± 0.01) but was dramatically lower than adult survival. At St. George Bat Cave male survival (0.67 ± 0.07) was not significantly different from that of females (0.65 ± 0.07). First-year survival for YOY was similar for males (0.47 ± 0.13) and females (0.44 ± 0.13), although there was high inter-annual variation with estimates of apparent survival ranging from 0.07-0.59. Interestingly, my estimates of survival were consistently lower than estimates from lower latitude populations of this species and variation was independent of climatic variables.

Understanding long-term changes in vital rates of healthy little brown bat populations is critical as White-Nose Syndrome (WNS) continues to advance across North America. My data will assist in development of management plans and provide baseline estimates of pre-WNS survival to allow future evaluation of conservation and management strategies.

Introduction:

Long-term monitoring of wildlife populations and communities can provide crucial information for wildlife and ecosystem conservation, especially for species and populations facing major conservation threats from habitat loss, climate change and anthropogenic impacts (Magurran et al. 2010). Population monitoring is essential for identifying and managing impacts of invasive species on native species and ecosystems. For example, a long-term monitoring program allowed managers to quantify demographics of the invasive sea lamprey (*Petromyzon marinus*) in the Great Lakes region of North America and develop management strategies to minimize lamprey impacts on native fish species (Marsden et al. 2003; Shear 2006). Long-term population monitoring can also provide up-to-date information on wildlife health, enabling preventative measures to minimize the spread and impacts of wildlife diseases. Surveillance for rabies in striped skunks (*Mephitis mephitis*), for example, has helped reduce the risk of rabies for both people and animals (Greenwood et al. 1997; Childs et al. 2007).

In a disease context, population monitoring has most often been successful for zoonotic wildlife pathogens (i.e., pathogens that can jump from wildlife to people), like rabies, because of mobilization of public health resources. However, monitoring programs are also essential to the success of management plans for endangered species in response to non-zoonotic wildlife disease and other threats (Block et al. 2001). Long-term monitoring programs enable estimation of vital rates (e.g., survival, reproduction), which are crucial for quantifying and predicting population dynamics. Long-term monitoring played an essential role in tracking the demographic decline of the threatened Greater Prairie-Chicken (*Tympanuchus cupido*) and enabled timely management to prevent extirpation of the population in question (Westemeier et al. 1998). Long-term population monitoring is also a critical component of adaptive management (Schreiber et al.

2004). With good monitoring, within an adaptive management framework, the effectiveness of different management options, such as habitat protection and enhancement, or captive breeding for population supplementation, can be compared and iteratively improved (Runge 2011). Therefore, establishment of long-term monitoring is important for informed decision making and continual improvement of endangered species management plans (Beissinger and Westphal 1998; Morris and Doak 2002; Chirakkal and Gerber 2010).

North American bats provide a number of important ecosystem services, (e.g., Boyles et al. 2011) and face a wide range of conservation threats but, because of their cryptic nature, long-term monitoring programs for bats (Order Chiroptera), generally, are often difficult to design and implement (O'Shea et al. 2003). Because of their ecological importance combined with the severity of recent threats to bats, considerable effort has been expended to monitor bat populations and population responses to anthropogenic and natural disturbances. Long-term monitoring has been used to assess vital rates and population dynamics of insect-eating bats in the United States to assess responses to inter-annual variation in weather patterns (Frick et al. 2010b) and to inform predictive models of bat population responses to climate change (Hayes and Adams 2017). Long-term monitoring has also been used to determine how bat populations respond to timber harvesting in Australia (Law et al. 2018). Despite the difficulty in implementation, long-term monitoring of bat species can provide data that can be used for a variety of purposes.

Long-term monitoring to quantify vital rates has become especially important for hibernating bat species in North America because of infectious disease. White-nose syndrome (WNS) is caused by the fungal pathogen *Pseudogymnoascus destructans* (Gargas et al. 2009, Lorch et al. 2011, Warnecke et al. 2012) and has caused enormous declines of several hibernating bat species since its discovery in naïve populations of eastern North America in 2007 (Frick et al. 2010a; Langwig et al. 2015; Hayman et al. 2016). These declines have led to the listing of three hibernating bat species as endangered in Canada (COSEWIC 2013), and one species as threatened in the U.S.A (U.S. Fish and Wildlife Service 2016). *Pseudogymnoascus destructans* is adapted for growth at cold temperatures typical of bat skin during hibernation (Verant et al. 2014) and, therefore, causes enormous rates of mortality for some hibernating species by causing them to deplete their hibernation fat reserves prematurely. It also appears to cause seasonal carryover effects, impacting individuals even if they survive infection (Harrison et al. 2011; Davy et al. 2017; Chapter 2). Surviving bats emerge from hibernation with severely depleted fat stores and must then recover damaged tissues in spring at a time when the weather is still cold, and females would normally initiate pregnancy. Females rely on residual fat reserves as an energy capital to invest into pregnancy and may be particularly vulnerable to mortality if WNS depletes these fat reserves prematurely. As capital breeders, female bats rely on fat stores to support reproduction; however, if they use their fat stores instead to support healing and WNS recovery, females may not be able to maintain pregnancy or may have to delay birth until later in the season (Jonasson and Willis 2011). Young-of-the-year (YOY) born later in the season have less time for growth and fat accumulation and consequently have a lower chance of surviving the following winter. Reduced fecundity of surviving females may have long-term impacts and prevent populations from recovering from initial population decline. With the ongoing expansion of WNS across North America, there is a need to quantify population-specific vital rates in both healthy and infected populations. Identification of these vital rates across the geographic range of affected species will contribute to more accurate prediction of WNS impacts and potential for population recovery.

Populations affected by WNS experience drastic declines, but some individuals survive winter with the disease. These bats may possess heritable traits that reduce susceptibility to winter mortality from WNS. Although population modelling projections suggest that affected populations are unlikely to reach pre-WNS numbers (Russell et al. 2015), survivors with heritable survival traits could contribute to an evolutionary rescue effect, helping reduce extinction risk and enhance population recoveries (Maslo et al. 2015; Maslo and Fefferman 2015; Dobony and Johnson 2018). Maslo et al. (2015) used sensitivity analysis to show that maximizing adult and YOY survival, as opposed to fecundity, is essential for population stability but, to date, only one study by Frick et al. (2010b) provides reliable estimates of annual survival for a WNS-affected species based on mark-recapture analyses. Therefore, quantifying baseline vital rates prior to the arrival of WNS is critical for estimating recovery potential of populations. These vital rate estimates could also be useful as a concrete numerical target for evaluation of different management strategies.

The little brown bat (*Myotis lucifugus*) is a small (7-12 g), historically widespread insectivorous bat found throughout North America, whose geographic range extends from Alaska to Mexico. Prior to the spread of WNS in North America, the little brown bat was also one of the most common species on the continent and has served as a model organism for studying sociality and social behaviour in vertebrates, life history of mammals, and phenology of mammalian hibernation (Davis and Hitchcock 1965; Barclay et al. 1979; Thomas et al. 1979; Fenton and Barclay 1980). During the fall swarming period, males and females gather at hibernaculum entrances in large numbers each night, presumably for mating and other social functions while also building fat reserves for hibernation. However, YOY often are unable to accumulate as much fat reserves as adults and may suffer reduced survival (Davis and Hitchcock

1965; Kunz et al. 1998, Frick et al. 2010b). In the spring, females emerge early from hibernation and form maternity colonies to initiate gestation and maximize time during the summer season for YOY growth. Males, however, emerge from hibernation weeks after females, likely to minimize risk of bad spring weather and synchronize emergence with increasing insect abundance (Norquay and Willis 2014; Czenze and Willis 2015). Ongoing research on population-specific vital rates for this species is focused primarily on estimating potential recoveries of WNS-affected populations (e.g., Maslo et al. 2015; Dobony and Johnson 2018) and few data exist to estimate pre-WNS vital rates (but see Humphrey and Cope 1976; Keen and Hitchcock 1980; Frick et al. 2010b). Moreover, all previous estimates of vital rates for little brown bats have been from the eastern United States near the latitudinal centre of the species' range. This regional bias could limit our inference when it comes to estimating the potential for population recoveries because many species have higher variability in survival near their range limits (Sievert and Keith 1985; Sexton et al. 2009). Peripheral populations may experience reduced survival due to the combination of reduced resource availability, higher intra- or inter-species competition, and heightened predation risk (Sexton et al. 2009). Data on little brown bat populations in the northern part of their range are lacking, despite the importance of peripheral populations for understanding the relative influence of biological and environmental factors on survival.

My objective was to quantify variation in apparent annual survival (Φ) of little brown bats in the northern part of the species' range. I used seven years (2011-2017) of mark-recapture data obtained from two hibernacula in Manitoba, Canada, to test the hypothesis that demographic characteristics (i.e., sex and age) along with seasonal environmental factors (i.e., precipitation and temperature) impact annual survival. I predicted that: (1) female bats would exhibit lower apparent survival than males because they emerge earlier from hibernation putting them at a greater risk from harsh spring weather (Norquay and Willis 2014; Czenze and Willis 2015); (2) First-year survival of YOY should be lower than adult survival because YOY are often naïve and unable to build as large fat reserves for hibernation compared to adults (Davis and Hitchcock 1965; Sendor and Simon 2003); (3) survival would be lower after long, harsh winters because energy reserves might not last until spring; and (4) survival would be lower after hot dry summers because of reduced availability of insect prey (Frick et al. 2010b).

Materials and Methods

I used mark-recapture data from ‘The Abyss’ cave near Grand Rapids (Lat 51.307; Long -97.654) and ‘St. George Bat Cave’ near Fisher River First Nation (Lat 51.444; Long -97.361) from 2011 to 2017. Both hibernacula have approximately 1 m diameter entrance openings on level terrain which open into limestone caverns housing hundreds (The Abyss) to thousands (St. George Bat Cave) of little brown bats each winter. Bats were captured during the night throughout the late summer and fall swarming period (early August to late September) using harp traps placed at the cave entrance. Sex of all bats was recorded, and relative age was assessed as either adult or YOY based on the degree of fusion in the metacarpal epiphyses, where complete fusion indicated adult status (Kunz and Anthony 1982). Morphometric data on body mass and forearm length were also recorded. All individuals caught at hibernaculum entrances during the fall swarming period (i.e., August 1st to October 8th) in a given year were considered part of the same cohort for analysis. I obtained weather data from the closest Environment Canada Weather station located in Grand Rapids (~60 km from The Abyss) and Hodgson (~45 km from St. George Bat Cave). I chose to include seasonal temperature and total precipitation as explanatory variables because summer temperature and precipitation can influence insect abundance, bat activity (Anthony et al. 1981) and survival (Frick et al. 2010b), while winter temperature and snowfall can influence energy expenditure and water availability at emergence (Speakman and Racey 1989).

Individual bats were tagged using uniquely coded passive integrated transponders (PIT tags; Trovan Ltd. ID 100-01 Douglas, UK). PIT tags were inserted sub-dermally in the scapular region using a single-use disposable syringe. PIT tags have been used for many studies of insectivorous bats with no reports of negative effects (O'Shea et al. 2004; Neubaum et al. 2005; Ellison et al. 2007; Rigby et al. 2012) and theoretically function for the lifetime of the individual (O'Shea et al. 2004). Tagged individuals were detected using a 475 x 400 x 40mm square panel antenna (ANT-612 Large Panel Antenna, Trovan Ltd., Douglas U.K.) placed perpendicular to the flight path of emerging bats to maximize detection (Kunz et al. 1988). The flight path of bats was directed to within the 20-30 cm range of the panel antennas using plastic window screening. Panel antennas were attached to a PIT tag decoder/datalogger (LID650n, Dorset ID, Aalten, The Netherlands) which automatically recorded date, time, and unique identification tag of any marked bats that passed within range of the antenna. Decoders were housed in weather-resistant plastic bins along with two 12-volt, 40 amp-hour batteries charged by a 64-watt solar panel (EWS-85M Enerwatt Solar Module, Enerwatt CA). PIT-tag systems were checked opportunistically throughout the year to ensure systems were functional and to download any stored data onto a laptop. The systems allowed for automated, non-invasive detections (hereafter recaptures) of hundreds of PIT-tagged bats within and among years.

To estimate population-specific survival rate, I constructed encounter histories based on PIT-tag recaptures for six cohorts of marked bats, one for each year from 2011-2017. Individuals were given a '1' if they were detected in a given year, including at their initial capture, and '0' if there were not recaptured, for all years throughout the study. Individuals caught in year one of the study were assigned encounter histories with seven years of encounters, individuals captured in year two had six years of encounter and so on. As an example, an individual with an encounter history of 1001001 would have been detected three times in total, once in each of the first, fourth and seventh years of the study.

I used program MARK (White and Burnham 1999) to construct Cormack-Jolly-Seber (CJS) models of apparent annual survival based on PIT-tag encounter histories. These mark-recapture models estimate apparent survival and not actual survival, because CJS models are incapable of disentangling actual mortality from emigration, both of which appear as if the individual had left the population (Cooch and White 2006, Barbour et al. 2013). CJS models have the following four assumptions: (1) Every animal from a demographic sub-group within a cohort (i.e., the group of bats detected in a given year) has the same probability of being recaptured in subsequent years; (2) Every animal from a given demographic sub-group within a cohort has the same probability of survival to the next year; (3) Marks are not lost over time; and (4) All individuals are marked within a short timeframe and are released immediately after marking. PIT tags are permanent marks and all bats were released immediately after capture, so the data met assumptions 3 and 4. I tested for deviation from assumptions 1 and 2 by estimating goodness-of-fit (GOF) using the program U-CARE (Choquet et al. 2009). Test 2CT in U-CARE assesses the presence of potential positive/negative trap responses (i.e., “trap-happiness” or “trap-shyness”) which violate assumption 1 that individuals have equal recapture probability. Test 3SR allows for detection of effects of emigrant individuals within a demographic group. The presence of emigrant individuals in a cohort violates assumption 2, because emigrants are never redetected after the initial capture. Their encounter histories would consequently suggest zero survival relative to resident individuals, artificially increasing mortality estimates and thereby violate the second assumption of CJS models. I also used GOF testing in U-CARE to determine the variance inflation factor, $\hat{c}$, which can be used to adjust for a potential lack of fit during model selection. Significance for all null-hypothesis testing was assessed at the $p = 0.05$ level and all values reported represent the mean ± standard error.

I used Akaike's Information Criterion (AIC) to compare CJS models incorporating my predictor variables (i.e., demographics of bats and annual variation in climatic variables) (Akaike 1974). When $\hat{c} \neq 1$, I used the quasi-AIC (QAIC) to identify the best fit model (Lebreton et al. 1992). Otherwise I used AIC adjusted for small sample size (AIC_c) (Hurvich and Tsai 1989; Cooch and White 2006). I used package 'RMark' (Laake 2013) in R (R Development Core Team 2018), which uses the framework of program MARK to construct CJS models. Models within 2 ΔAIC_c points were considered to have equivalent model support, and final model estimates were obtained using model averaging with parameter estimates averaged according to model weighting (Symonds and Moussalli 2011).

In my study system, some bats are never detected after their initial capture during fall swarm because they emigrate from the swarm at that hibernaculum to other hibernacula for hibernation (henceforth transient individuals). However, once an individual is detected entering or exiting a given hibernaculum after its release (i.e., its second encounter of its encounter history) it can be considered a resident, because little brown bats exhibit extremely high hibernaculum fidelity (Norquay et al. 2013). To account for this pattern, I used a time-since-marking (TSM) model to distinguish between newly marked cohorts (containing a mixture of transient and resident individuals) and cohorts marked in previous years and seen again in subsequent years (which are almost completely composed of resident individuals). To test my hypothesis that demographics and climatic variables influence apparent annual survival, I included both sex and age structure into the TSM model. I also included weather variables (mean temperature and total precipitation) from both summer and winter as potentially explanatory covariates of survival. I did not include individual morphometric covariates (e.g., body mass) because body mass can vary dramatically within individual bats throughout their lives and I only had a single measurement obtained at initial capture (Schwarz and Seber 1999). Moreover, most bats in a given cohort were captured during late swarming when bats rapidly increase fat stores (Fenton and Barclay 1980; McGuire et al. 2009; McGuire et al. 2016)

I calculated group-specific expected mean life span (MLS) using mean annual survival estimates from the best fit model(s) following Seber (1982) and Sendor and Simon (2003) with the equation:

$$Mean\ Life\ Span = \frac{-1}{ln\Phi}$$

Results:

A total of 4932 individual bats were captured and tagged between 2011 and 2017 at The Abyss (n = 963) and St. George Bat Cave (n = 3969). Tagging efforts across both sites were spread approximately equally by sex but were biased towards adults compared to YOY. Mean redetection rates of individuals detected at least once after marking was 26% at The Abyss and 28% at St. George Bat Cave (Table 3.1).

The goodness-of-fit test 2CT suggested no evidence of either trap-shyness or trap-happiness for any demographic at either cave (Table 3.2). Test 3SR for The Abyss suggested evidence of transience for males, but not females with evidence of transience for both males and females at St. George Bat Cave (Table 3.2). The estimate of $\hat{c}$ for The Abyss was not over-dispersed ($\hat{c} = 1$), so I used AICc for subsequent model selection. Estimates of $\hat{c}$ for St. George Bat Cave indicated that the saturated model was mildly over-dispersed ($\hat{c} = 1.6$) so I corrected for overdispersion in model selection by using QAIC.

The top 10 models for both sites included a combination of sex and age in their model structure (Table 3.3). Model selection showed that no model that included summer environmental variables ranked in the top 10 for model fit. Similarly, models that included winter environmental variables ranked at highest in 7th place in the top 10, and all models with winter environmental variables ranked below those with environmental variables excluded. Furthermore, models that included environmental variables had low Akaike weights (Table 3.3).

Table 3.1: Summary of mark-recapture data for little brown bats marked at The Abyss and St. George Bat Cave per year between 2011-2017 by age and sex. Recap represents the total number of marked bats redetected at least once after their initial capture.

Abyss									
Group	2011	2012	2013	2014	2015	2016	Marked	Recap	% recap.
Adult females	37	16	175	27	2	21	278	75	26.98
YOY females	60	8	32	0	9	4	113	8	7.08
Adult males	69	16	253	34	2	29	403	140	34.74
YOY males	108	10	35	0	14	2	169	35	20.71
TOTAL	**274**	**50**	**495**	**61**	**27**	**56**	**963**	**258**	**26.79**
St. George									
Adult females	66	131	891	286	27	93	1494	440	29.45
YOY females	57	65	98	34	31	1	286	52	18.18
Adult males	87	253	1277	248	20	69	1954	676	34.60
YOY males	66	55	138	32	37	0	325	87	26.77
TOTAL	**276**	**504**	**2404**	**600**	**115**	**163**	**3969**	**1255**	**31.62**

Table 3.2: Results of goodness-of-fit tests from program U-CARE for mark-recapture data from The Abyss and St. George Bat Cave. Test 3SR evaluates the presence of transient individuals in the group. Test 2CT evaluates the prediction of unequal capture rate, suggestive of trap-shyness or trap-happiness. Statistically significant ($P < 0.05$) results are presented in bold.

Hibernaculum	Group	Test	χ^2	df	p
Abyss	Adult female	3.SR	7.30	5	0.20
	YOY female	3.SR	5.75	3	0.12
	Adult male	3.SR	**30.83**	**4**	**<0.001**
	YOY male	3.SR	**52.13**	**3**	**<0.001**
	Adult female	2.CT	0.001	2	>0.99
	YOY female	2.CT	0.71	2	0.70
	Adult male	2.CT	2.58	4	0.63
	YOY male	2.CT	1.92	4	0.75
St. George	Adult female	3.SR	**61.70**	**5**	**<0.001**
	YOY female	3.SR	**27.63**	**5**	**<0.001**
	Adult male	3.SR	**46.26**	**5**	**<0.001**
	YOY male	3.SR	**13.24**	**4**	**<0.001**
	Adult female	2.CT	1.08	3	0.78
	YOY female	2.CT	0.001	3	>0.99
	Adult male	2.CT	5.85	3	0.12
	YOY male	2.CT	0.11	3	0.99

Table 3.3: Results of model selection for predictors of apparent survival (Φ) based on mark-recapture data from The Abyss and St. George Bat Cave showing the top 10 models, sorted in descending order of fit, based on AIC (QAIC) scores. The null model (Φ(t), P(t), without demographic and environmental factors) is included for comparison. P = recapture probability, t = time dependence, • = estimate for groups constant between years, age = marked as adult/YOY, sex = male/female, Winter temp. = mean annual winter temperature, snow = total winter snowfall. (Quasi) Akaike's information criterion = QAICc, differences in (Q)AIC = ΔAIC, proportion of model support = AIC weight, number of model parameters (n.p.). Note: Models have large numbers of parameters because CJS models estimate a parameter for each year for every group separately

Abyss				
Model	AICc	ΔAICc	AIC weight	n.p.
Φ(~sex(•) + age (•)) P(~sex(t))	1904.76	0	0.740	16
Φ(~sex(t) + age(t)) P(~t)	1907.49	2.73	0.189	25
Φ(~sex(t) + age(t) + migrants (t) P(~t)	1910.98	6.22	0.033	30
Φ(~sex(t) + age(t)) P(~sex(t))	1912.02	7.26	0.020	31
Φ(~sex(t) + age(t)) P(~age(t))	1913.82	9.05	0.008	31
Φ(~sex(t) + age(t)) P(~sex(t))	1915.01	10.25	0.004	36
Φ(~sex(t) + age(t)) + Winter temp. + snow) P(~t)	1915.16	10.40	0.004	32
Φ(~sex(t) + age(t)) P(~age(t))	1917.40	12.64	0.001	36
Φ(~sex(t) + age(t) + Winter temp. + snow) P(~sex(t))	1919.22	14.46	<0.001	38
Φ(~sex(t) + age(t) + Winter temp. + snow) P(~age(t))	1921.72	16.95	<0.001	38
Φ(t), P(t)	2053.54	148.8	<0.001	12
St. George				
Model	QAICc	ΔQAICc	AIC weight	n.p.
Φ(~sex(t) + age(t)) P(~t)	6374.609	0	0.451	25
Φ(~sex(t) + age(t)) P(~age(t))	6375.212	0.603	0.334	31
Φ(~sex(t) + age(t)) P(~sex(t))	6378.415	3.807	0.067	31
Φ(~age(t)) P(~age(t))	6379.841	5.232	0.033	30
Φ(~sex(t) + age(t)) P(~t)	6380.141	5.532	0.028	30
Φ(~sex(t) + age(t)) P(~age(t))	6380.804	6.195	0.020	36
Φ(~age(t)) P(~t)	6381.107	6.498	0.017	24
Φ(~age(t)) P(~sex(t))	6381.175	6.566	0.016	30
Φ(~sex(t) + age(t)) P(~sex(t))	6381.411	6.803	0.015	36
Φ(~sex(t) + age(t) + Winter temp. + snow) P(~age(t))	6382.316	7.707	0.014	38
Φ(t), P(t)	6474.158	99.55	<0.001	12

For The Abyss, the definitive top model included effects of sex and age that were constant over time, with little variation in survival estimates between years within demographic sub-groups. This suggests a consistent effect of these factors on survival independent of the year of data collection. Parameter estimates from the top model suggested consistently higher average annual survival for males ($\Phi = 0.745 \pm 0.034$) compared to females ($\Phi = 0.610 \pm 0.038$) and this sex difference was consistent during adulthood regardless of whether bats were marked as adults or YOY ($t = -2.64$, $df = 8$, $p = 0.03$) (Figure 3.1A, B). Average annual survival of YOY in their first year was also higher for males ($\Phi = 0.226 \pm 0.014$) than for females ($\Phi = 0.127 \pm 0.007$) but was dramatically lower than adult survival (Figure 3.1C).

At St. George Bat Cave, the top two models were within 0.7 ΔAIC of each other indicating that both models performed well at explaining variation in the data. Both top models had identical structure for survival, with variation in survival over time and different rates of survival for males and females, and adults and YOY, across years. This suggests that inter-annual survival is structured by demographic groups by both age and sex. Parameter estimates showed that inter-annual variation in survival was greater at St. George Bat Cave compared to The Abyss, and there was no significant effect of sex on survival at St. George Bat Cave. For adults, male survival ($\Phi = 0.668 \pm 0.065$) was only marginally, and not significantly, higher ($t = -0.22$, $df = 8$, $p = 0.83$) than that of females (0.648, SE = 0.068) (Figure 3.2; A, B). Average rate of survival for YOY in their first year was similar for males (0.468, SE= 0.125) and females (0.441, SE = 0.127) although there was high annual variation with estimates of apparent survival ranging from 0.07-0.58 between years (Figure 3-2C, excluding 2017 as an outlier).

Recapture probability at both caves varied with time and did not covary with either summer or winter environmental factors. Recapture probability at The Abyss varied with sex and ranged from 0.26-0.95 for males and 0.29-0.97 for females. Recapture probability for females was lower than that of males in 2012 and 2016 but was similar to that of males in every other year. At St. George Bat Cave recapture probability ranged from 0.16-0.95, with no difference between sexes and a non-significant trend for higher recapture probabilities of adults compared to YOY (Figure 3.3).

Mean lifespan for resident adults at The Abyss varied by sex and ranged from 2 years for females to 3.4 years for males (Table 3.4). Of the 324 individuals marked in the first two years at The Abyss, only 21 individuals survived until the last year of the study. At St. George Bat Cave, the difference in mean lifespan for resident adults was smaller between sexes, with an estimated life span of 2.3 years for females and 2.4 years for males (Table 3.4). At St. George Bat Cave, out of 780 individuals marked in the first two years of the study, only 75 individuals survived until the end of the study.

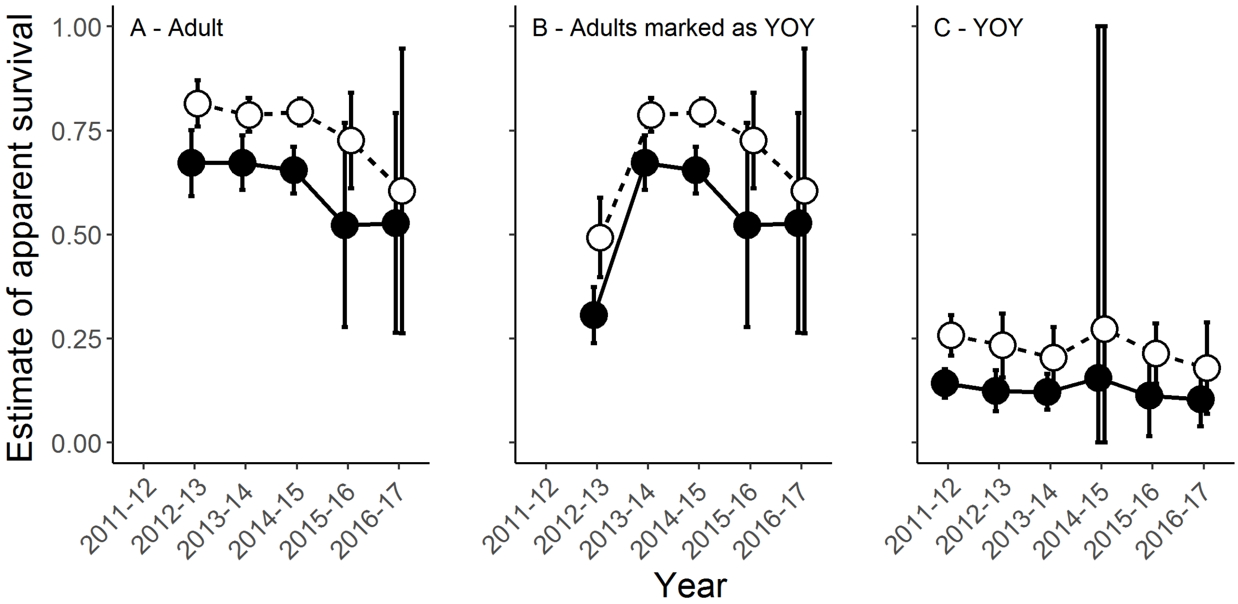

Figure 3.1: Estimates of apparent annual survival (ϕ) ± SE at The Abyss cave between 2011 and 2017 for males (white) and females (black) A: Apparent survival for individuals marked as adults; B: Apparent survival in adulthood for individual marked as YOY; C: First-year YOY survival.

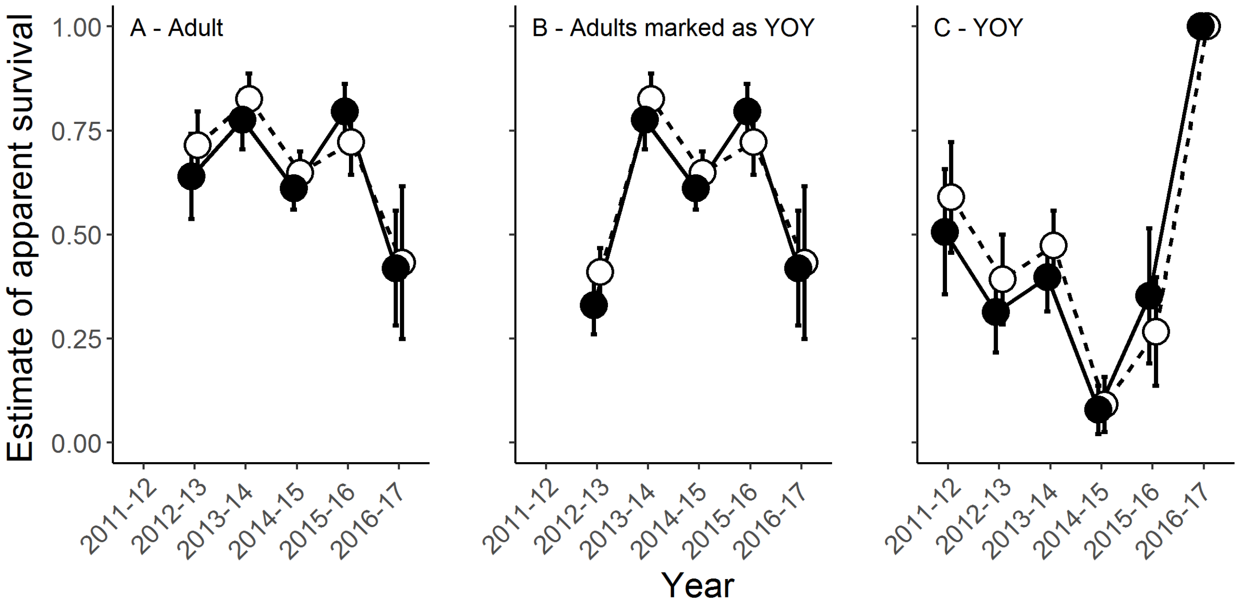

Figure 3.2: Estimates of apparent annual survival (ϕ) ± SE at St. George Bat Cave between 2011 and 2017 for males (white) and females (black) A: Apparent survival for individuals marked as adults. B: Apparent survival in adulthood for individual marked as YOY. C: First-year YOY survival.

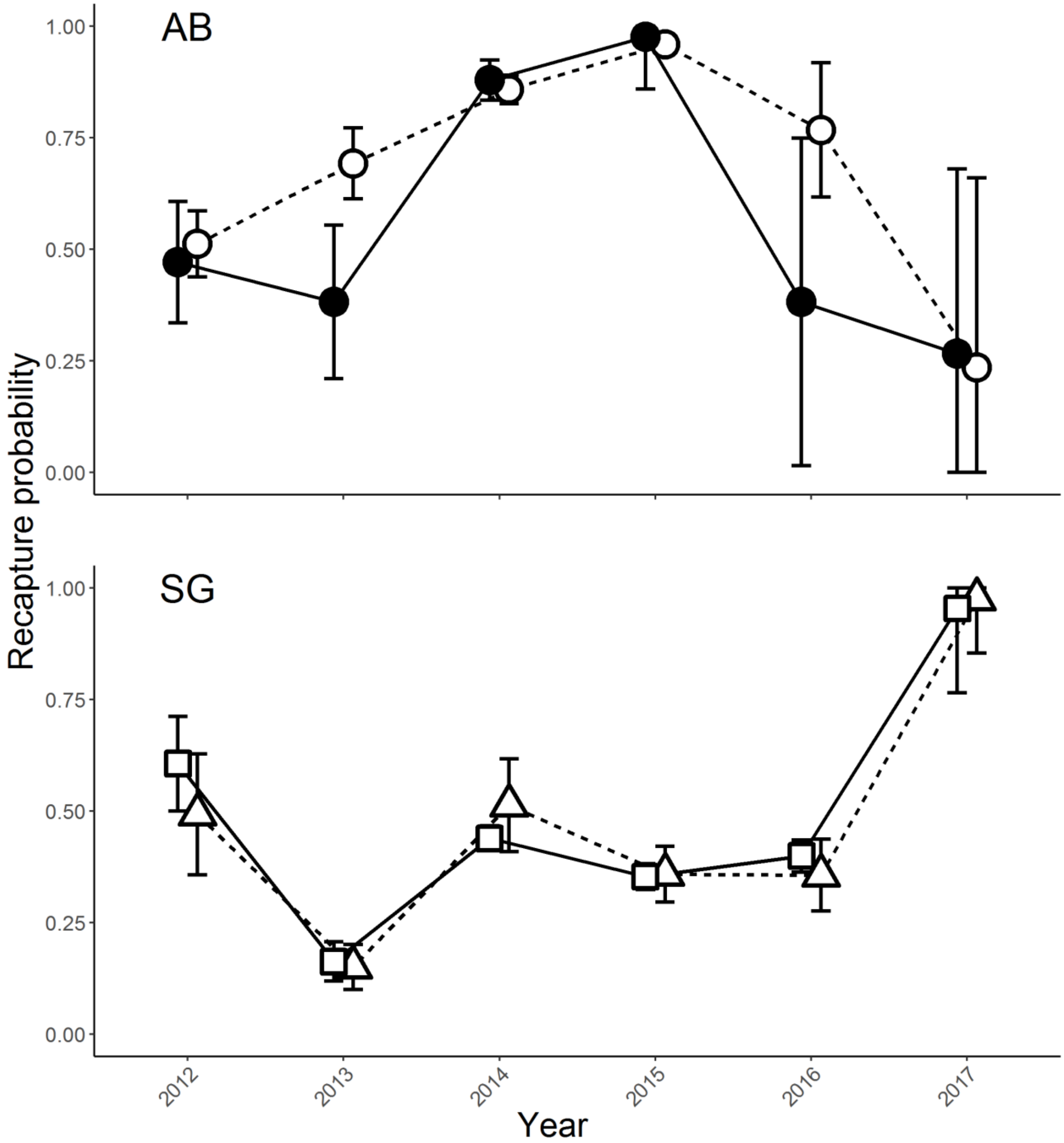

Figure 3.3: Recapture probability ± SE at The Abyss cave (AB) and St. George Bat Cave (SG) between 2012-2017. Recapture probability at AB varied over time by sex (black = female, white = male), while recapture probability at SG varied over time by relative age (square = adult, triangle = YOY).

Table 3-4: Estimates of mean annual apparent survival (± standard error) based on model averaging and the estimated mean life span for male and female little brown bats in The Abyss and St. George Bat Cave. Mean life span (MLS) was estimated using the formula: MLS = -1/ln Φ

Abyss	Year						
	2012-13	2013-14	2014-15	2015-16	2016-17	Mean annual Φ	Mean life span (years)
Female	0.672	0.672	0.654	0.523	0.528	0.610 ± 0.034	2.022 ± 0.023
Male	0.815	0.787	0.795	0.726	0.605	0.745 ± 0.038	3.404 ± 0.026
St. George							
Female	0.640	0.776	0.611	0.796	0.419	0.648 ± 0.068	2.307 ± 0.046
Male	0.715	0.826	0.648	0.722	0.432	0.669 ± 0.065	2.484 ± 0.044

Discussion

My results lend mixed support to my hypothesis that demographics and environmental conditions affect rates of apparent annual survival in little brown bats in the northern part of their range. I found strong support for an effect of demography on survival with greater survival for adults than YOY and greater survival for males than females at one of my two sites (i.e., the Abyss). However, contrary to my predictions, the environmental variables I included in my analysis had no effect on annual survival for bats from these hibernacula. The lack of influence of climatic variables on inter-annual survival, compared to estimates from other populations of insectivorous bat species, suggest other factors such as latitude or population genetics may influence survival and mean life expectancy. Estimates of annual adult survival ranged from 0.30 to 0.82 across both sites, which are lower than survival estimates found for other temperate bats (Sendor and Simon 2003; Frick et al. 2010b; O'Shea et al. 2011).

I found some evidence of an effect of sex on inter-annual survival, with males having higher survival than females at The Abyss. This result is consistent with my prediction that female little brown bats experience lower survival rates than males because of differences in the timing of reproductive investment although the fact I did not detect this effect at St. George Bat Cave indicates that the difference in sex-based survival is site-specific. Males invest energy into reproduction during the fall swarming season, when food is still available, prior to entering hibernation (Barclay et al. 1979). Females store sperm over the winter and then make the vast majority of their reproductive investment after emerging from hibernation in the spring (Buchanan 1987). In my study area, females often emerge in spring when conditions are still cold, and food is unavailable (Norquay and Willis 2014). Female bats must initiate gestation to maximize the time YOY have to grow and store fat reserves before their first winter (Racey and

Swift 1981) and, during much of this gestation period must rely entirely on residual energy reserves stored the previous fall before hibernation. By emerging from hibernation so early, reproductive females may trade-off the benefits of early spring reproduction and rapid offspring growth, against the risk of experiencing harsh, inclement spring weather. This weather can increase thermoregulatory demands during a period when individuals already face high energetic costs of reproduction, substantially increasing mortality risk. Male bats, which emerge much later in the spring, have reduced chances of experiencing harsh spring weather and appear to synchronize emergence with conditions favourable for flying insects (Norquay and Willis 2014, Czenze and Willis 2015). This could explain higher annual survival of males compared to females.

I also found support for my prediction that YOY would have lower survival in their first year than adults. At St. George Bat Cave, the only year in which I did not observe this pattern was 2017 but this is almost certainly attributable to a low sample size of YOY marked the previous year (n = 1 individual). Therefore, it is unlikely that the estimate of survival for 2017 represents normal rates for YOY in the population. Similarly, there was no difference in survival estimates between adults and YOY at The Abyss in 2014-2015 but, again, no YOY were caught at this site the previous year, which means values for that year reflect an extrapolation from the model, reflected in high predicted error associated with this estimate (Figure 3.1). Despite these outliers, the general pattern of lower annual survival for YOY compared to adults is consistent with observations for other species of insectivorous bats (Sendor and Simon 2003; Frick et al. 2010b; O'Shea et al. 2011) and birds (Loery et al. 1987; Newton et al. 2016). YOY experience higher overwintering mortality than adults (Davis and Hitchcock 1965) because they enter hibernation with lesser fat reserves than adults (Schowalter 1980; Kunz et al. 1998).

Additionally, any disturbances during hibernation can cause excess energy expenditure and may disproportionately affect YOY more severely than adults (Boyles and Brack 2009). YOY with limited fat reserves may be more susceptible to premature depletion and consequently overwintering mortality. Furthermore, YOY in their first year are inexperienced in foraging and predator avoidance behaviours (Anthony and Kunz 1977). This inexperience may lead to excessive risk-taking behaviour or inappropriate behavioural responses to predator cues, increasing the risk of predation and mortality (Baxter et al. 2006; Roth et al. 2005).

Another factor that may contribute to overwintering mortality is severity of environmental conditions in the winter. However, I found little evidence that winter climatic variation affected annual survival for these two hibernacula in Manitoba. Hibernacula provide highly stable microclimates throughout winter, and variation in ambient temperature and snowfall have little impact on conditions within hibernacula (Perry 2013). Winter conditions are poor predictors of overwinter survival for other insectivorous bat species as well (Sendor and Simon 2003). While winter environmental conditions may not affect survival, there is some evidence that summer weather conditions, such as rainfall and temperature may affect survival in little brown bats (Frick et al. 2010b). Summer weather conditions can influence flying insect abundance (Williams 1951) and could affect food availability during the swarming period when little brown bats store energy for hibernation. Therefore, environmental conditions during the active season may significantly affect survival (Frick et al. 2011b). However, I did not find any support for this prediction and neither ambient summer temperature or rainfall during the active season were significant predictors of variation in survival at either hibernaculum. As a caveat, however, it my results indicate that short-term seasonal climate variation appears to have no impact. It is possible that climate variation on a long-term (i.e. decades or centuries) may still potentially influence survival trends in these populations. In habitats with low standing water availability, precipitation and freshwater pools are often the limiting factors affecting insect abundance (Wallner 1987). The abundance of freshwater lakes in central Manitoba may act as a buffer, reducing the impact of precipitation on insect abundance and, in contrast to the colony studied by Frick et al. (2010b), provide more stable insect breeding habitat even in hot dry years.

As a result of low survival rates, the mean lifespan recorded for adults at these two hibernacula (2.48 ± 0.03 years) is shorter than the average life expectancy of 5 years reported by Keen and Hitchcock (1980), and dramatically shorter than the longest recorded life span of 34 years for this species (Davis and Hitchcock 1995). Increased winter duration and reduced food abundance near the northern range limit for insect-eating bats in North America, may cause energetic constraints that result in higher mortality and shorter life expectancy (Kunz et al. 1998; Humphries et al. 2004; Gaston 2009). These findings highlight the importance of obtaining population-specific vital rates of wildlife to better understand geographic variation in population dynamics.

My results indicate that seasonal environmental conditions do not have predicable effects on interannual survival in these two little brown bat populations at in the northern range of the species. This research also provides further evidence for the effectiveness of passive detection methods using PIT tags in long-term monitoring programs of bat populations. The redetection rate of marked individuals in this study were consistent with other estimates of recapture rates for other species (Morley 2002; Gibbons and Andrews 2004). My results suggest that the demographic structure of the population influences the population-specific survival rates in little brown bat populations at northern latitudes more strongly than environmental conditions. Furthermore, survival rates of these little brown bat populations were lower than those of populations at lower latitudes. Low YOY survival indicates that recruitment in these populations will be low. The combination of low recruitment rate, along with higher mortality of females compared to males, suggest that WNS impacts may have significant implications on long term population dynamics. As a result of generally lower survival, these northern populations may recover more slowly than populations at lower latitudes. Knowing these population-specific survival rates is an important step for understanding how WNS might impact northern populations and for developing effective recovery management plans.

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Chapter 4

General conclusions

The best plans for management of threatened or endangered wildlife populations have quantitative goals and incorporate species- and often population-specific biological information (Clark et al. 2002; Tear et al. 2005). Thus, understanding basic aspects of natural history, such as habitat requirements and demographic characteristics, is important for effective management. Knowledge of space requirements and habitat preferences of species and populations can be used to designate critical habitat that should be protected (Arvisais et al. 2002; Hagen and Hodges 2006). Similarly, knowledge of vital rates, such as survival, mortality, and fecundity, are critical in estimating the potential impact of climate change or wildlife disease on populations (Morris and Doak 2002; Grosbois et al. 2008). However, for many endangered species, basic information may be lacking, affecting the effectiveness of conservation efforts.

For many species of hibernating bats, this kind of basic biological information is still lacking, especially for peripheral populations near the extent of species' ranges. Hibernating bats in North America are being threatened by an infectious disease known as White-Nose Syndrome (WNS). WNS has caused massive die offs in populations of little brown bat (*Myotis lucifugus*) (Frick et al. 2010; Langwig et al. 2015; Hayman et al. 2016). Due to these population declines, the need to identify basic species information for the little brown bat has become more urgent. With the ongoing spread of WNS and the innate vulnerability of peripheral populations, identifying habitat requirements and vital rates in the endangered little brown bat is important to the success of management and recovery efforts. The main objective of my thesis was to fill some of the knowledge gaps that might affect the successful management and recovery of this endangered species. My thesis provides baseline information that could be used to devise quantitative management goals and be used for comparison and assessment of the effectiveness of different management options.

In chapter 2, I examined home range size and habitat use of female little brown bats from a maternity colony recently affected by WNS. I tested the predictions of two alternative hypothesis about the relative influence of time and energy constraints on space use. The first hypothesis, which I called the ‘time constraints’ hypothesis, predicts that home-range size should decline during lactation compared to pregnancy. Home range size will primarily be constrained by the time required for parental care and not the increased energetic demand of lactation. Alternatively, the ‘energetic constraints’ hypothesis, predicts that instead of time constraints, the high energetic demands associated with pregnancy, lactation, and carryover effects of WNS will primarily constrain home-range size.

I found that lactating bats had reduced home range size and made significantly more roost visits than pregnant bats, providing support for the time constraints hypothesis. However, the estimates of home range sizes for both pregnant and lactating bats I found were drastically larger than home range sizes previously quantified for pre-WNS female little brown bats (Henry et al. 2002). WNS survivors at maternity colonies must reconcile the energetic demands of tissue recovery, daily metabolic activity, and milk production/fetal growth within relatively short summer night lengths. While time constraints appear to be the primary factor affecting the difference in home-range size between pregnancy and lactation, carryover effects of WNS appear to dramatically increase home range size, consistent with increased energetic demands of bats recovering from WNS. My findings suggest that, at the local scale within a maternity colony, time constraints associated with reproduction, limit space use among individuals but that energetic constraints imposed by WNS drastically influence space requirements within and among populations. This chapter also identifies preferred foraging habitats of reproductive female little brown bats and provides information about the type of habitats and amount of space that should be protected around maternity colonies for management of vulnerable little brown bat populations.

In chapter 3, my goal was to estimate vital rates at two hibernacula near the northern geographic range limit of little brown bats. This is important from a conservation standpoint because peripheral populations near the boundary of their geographic range may experience shorter active seasons and greater physiological stress (Humphries et al. 2002; Gaston 2009). I tested the hypothesis that demographic characteristics, such as sex and age, and seasonal environmental variables affect annual survival at these two hibernacula. I predicted that females would have lower survival than males, because of their earlier emergence from hibernation, and that YOY would have lower survival than adults. Furthermore, I predicted that survival would be lower in hot dry years, and cold years with a lot of snow, because of their negative impacts on food availability and energy demand.

I found mixed evidence for these predictions. Annual survival varied over time and differed for both age and sex classes but did not vary with either summer nor winter climatic variables at either hibernaculum. My results suggest that the demographic structure of these populations influences the population-specific survival rates in little brown bat populations at northern latitudes more strongly than environmental conditions. I also found rates of survival that were considerably lower than those reported for more southern populations of this, and other, hibernating bat species. This suggests the possibility of pronounced impacts on these populations from WNS. Knowing population specific survival rates is critical to development of management plans that target enhancement of YOY and female survival. These estimates of survival can also be used as a baseline comparison to determine the relative effectiveness of different recovery options if WNS arrives at these populations. Continuing to monitor the long-term changes in vital rates in these populations will be critically important for future management with ongoing expansion of WNS in North America.

My project provides information to fill knowledge gaps for this species about space use and survival. My research suggests that populations of little brown bats near the northern limit of their geographic range experience higher mortality rates than populations found at lower latitudes. Due to long hibernation durations and low YOY and female survival, these northern populations may be particularly vulnerable to WNS. The fact that fecundity in these population will also be low, implies that recovery from WNS could be particularly slow in these populations which is worrying for a species which already has a slow life history and low rates of population growth. Surviving individuals in these populations may also need to increase their home range sizes, making optimal foraging during the short active periods more important for survival. My research contributes to a greater understanding of vital rates and space use in these vulnerable populations and is important to successful implementation of management of this endangered species.

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