Habitat Selection of Temperate Bats at Different Temporal and Spatial Scales

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Le coeur décide yous qu'est sa maison

Pis les étoiles sont claires à soir

Dans l'bois – Édith Butler, Lisa LeBlanc & Lise Aubut

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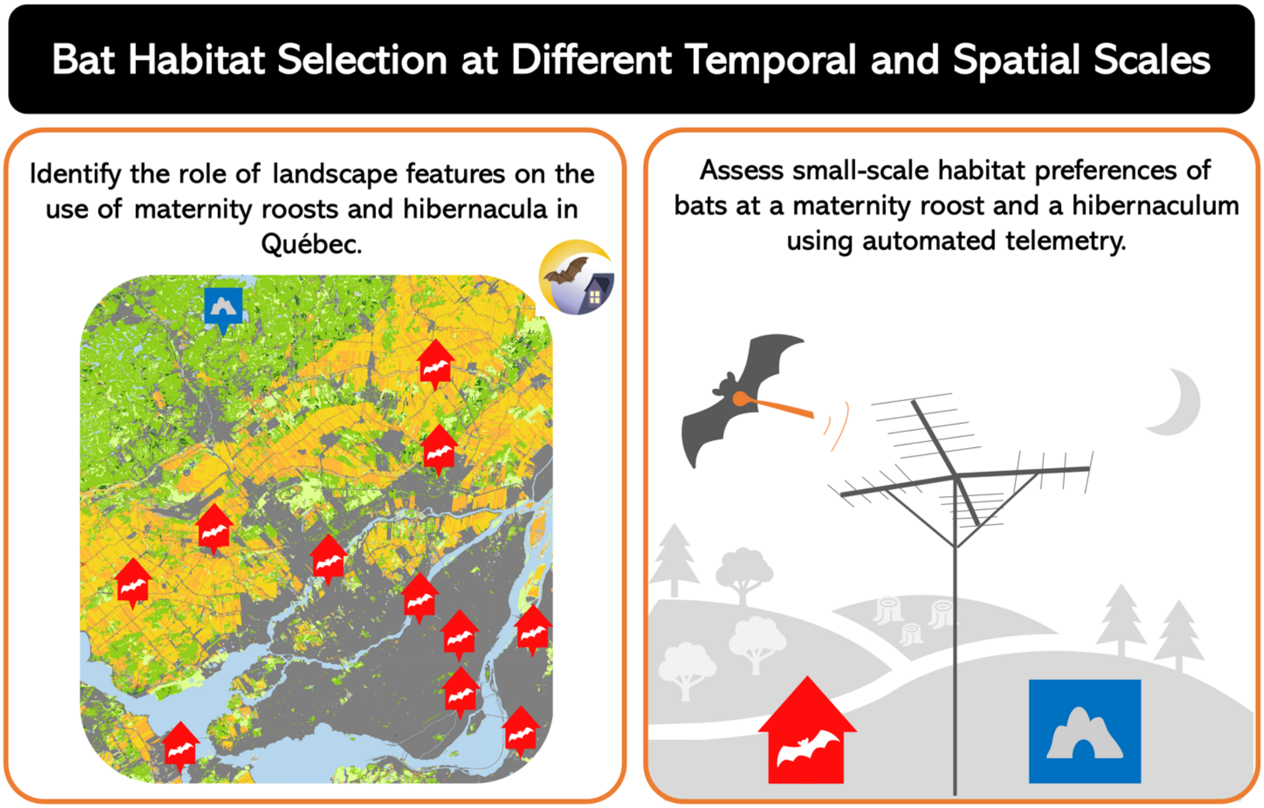
ABSTRACT

Habitat loss is one of the major threats to biodiversity. Hence, protecting essential habitat of endangered species is a key conservation measure. Nevertheless, it remain a challenge to understand habitat requirements of animals, as they can be modulated by several factors including seasonality, physiological state, and scale of observation. It is especially challenging to identify key habitats for small species like bats which are hard to locate and track, and for which data are often rare or scattered. My thesis seeks to use a combination of citizen science, governmental data and new technologies to study habitat requirements of bats in Québec (Canada) around different seasonal roosts ("central place") and over different spatial scales. In Chapter One, I examine the role of landscape composition in the selection of summer and winter roosts in Québec. I used citizen science and data from provincial government surveys to localize roosts and extracted surrounding landscape features at different scales. Summer roosts were associated with human-modified landscapes and landscape elements related to water, whereas winter roosts were associated with forest and not with human-modified landscapes. In Chapter Two, I studied habitat preferences and behaviour of the little brown bat (*Myotis lucifugus*) at two periods of the year. I used automated telemetry to track bats and looked at behaviour and activity levels in different habitats surrounding a summer roost during the lactation period and around a winter roost during the mating period (known as swarming). Bats frequently returned to the summer roost, but during swarming, bats did not frequently return to the winter roost, suggesting different spatial constraints for habitat use in the surroundings as well as the importance of the frequency of returning to a central place (or not). Bat activity was also not distributed uniformly around both roosts, suggesting selection of certain habitats. Many bat populations in North America have suffered substantial declines from the white-nose syndrome. Protecting remnant populations and their habitat might be one of the few effective conservation measures. Together, those two chapters allow identifying key habitats for bats like water and forest edges and seasonal variation in habitat use behaviour. By integrating multiple research methods, including citizen science, data archives, and emerging technologies (e.g., radiotelemetry methods) we show the possibilities to study

habitat selection over multiple period of the annual cycle, even for a small and cryptic mammals, to enhance seasonal management practices.



RÉSUMÉ

La perte d’habitat est l’une des principales menaces pour la biodiversité. Par conséquent, la protection de l’habitat essentiel des espèces menacées est une mesure de conservation primordiale. Néanmoins, il reste difficile de comprendre les exigences des animaux en matière d’habitat, car elles peuvent être modulées par plusieurs facteurs, notamment les saisons, l’état physiologique et l’échelle d’observation. Il est particulièrement difficile d’identifier les habitats essentiels pour les petites espèces comme les chauves-souris, qui sont difficiles à localiser et à suivre, et pour lesquelles les données sont souvent rares. Ma thèse vise à utiliser une combinaison de science citoyenne, de données gouvernementales et de nouvelles technologies pour étudier les habitats des chauves-souris au Québec (Canada) autour de différents gîtes saisonniers ("lieu central") et à différentes échelles spatiales. Dans le premier chapitre, j’examine le rôle de la composition du paysage dans la sélection des gîtes d’été et d’hiver au Québec. J’ai utilisé la science citoyenne et les données du gouvernement provincial pour localiser les gîtes et extraire les caractéristiques du paysage environnant à différentes échelles. Les gîtes d’été étaient associés à des paysages anthropiques et à des éléments du paysage liés à l’eau. Les gîtes d’hiver étaient associés à la forêt et non à des paysages anthropiques. Dans le deuxième chapitre, j’ai étudié les habitats préférentiels et le comportement de la petite chauve-souris brune (*Myotis lucifugus*) à deux périodes de l’année. J’ai utilisé la télémétrie automatisée pour suivre les chauves-souris et examiné le comportement et le niveau d’activité dans différents habitats autour 1) d’un gîte d’été pendant la période de lactation et 2) autour d’un gîte d’hiver pendant la période d’accouplement. Les chauves-souris retournaient fréquemment au gîte d’été, mais pendant la période d’accouplement, elles ne retournaient pas fréquemment au gîte d’hiver. Ce qui suggère des contraintes spatiales différentes pour l’utilisation de l’habitat dans les environs, ainsi que l’importance de la fréquence de retour à un endroit central (ou non). L’activité des chauves-souris n’était pas non plus répartie uniformément autour des deux gîtes, ce qui suggère une sélection de certains habitats. De nombreuses populations de chauves-souris en Amérique du Nord ont subi un déclin important suite à l’introduction du syndrome du nez blanc. La protection des populations restantes et de leur habitat pourrait être l’une des rares mesures de conservation efficaces. Ensemble, ces deux

chapitres permettent d’identifier les habitats clés des chauves-souris, comme les points d’eau et les lisières de forêt, ainsi que les variations saisonnières dans le comportement d’utilisation de l’habitat. En intégrant de multiples méthodes de recherche, y compris la science citoyenne, les archives de données et les technologies émergentes (par exemple, les méthodes de radiotélémétrie), nous montrons qu’il est possible d’étudier la sélection de l’habitat à plusieurs périodes du cycle annuel, même pour un petit mammifère cryptique, afin d’améliorer les pratiques de gestion saisonnière.

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INTRODUCTION

Habitat loss due to urbanization, massive agriculture, and deforestation is one of the major threats to biodiversity worldwide (Newbold et al., 2015; Powers & Jetz, 2019). Identifying important habitat of endangered species is a critical step for any conservation program. However, many aspects need to be considered when studying habitat requirements as it can differ according to the time of the year (e.g., Stanley et al., 2021), physiological state (e.g., Bjørneraas et al., 2012), resource availability (e.g., Geggie & Fenton, 1985) and the scale of observations (is a single tree a habitat or is a whole forest a habitat?; McGarigal et al., 2016). For animals using central or focal places like a residence or a mating site, the habitat available is also constrained by the location of this place. Therefore, understanding habitat selection can be challenging without a solid framework (Lele et al., 2013; McGarigal et al., 2016). Moreover, researchers often need to locate and/or track animals to investigate habitat selection, leading to research gaps on small and cryptic animals like bats.

Bats are an important group in temperate ecosystems where insectivorous species consume large volumes of arthropod biomass, including agricultural pests and disease vectors (Kunz et al., 2011). Unfortunately, bat populations in North America have suffered large declines in last decades because of white-nose syndrome (WNS), a fungal disease affecting hibernating bats (Frick et al., 2010). To date, no treatment has been found for WNS, and limiting the residual mortality caused by other threats, such as habitat loss, might be one of only a few effective conservation measures (Frick et al., 2019; Hoyt et al., 2021). Hibernating bats are long-lived mammals (Wilkinson & Adams, 2019) that migrate locally between summer roosts, where reproductive females aggregate to nurse their pups, and winter roosts where bats mate and hibernate (Davis & Hitchcock, 1965; Dekeukeleire et al., 2016; Fenton, 1969). While previous studies have focused on key characteristics of used roosts and immediate surroundings (Fontaine et al., 2021; Glover & Altringham, 2008; Kerth et al., 2001; Lausen & Barclay, 2006; Perry, 2013), there is still little information on how habitat composition and structure at different spatial scales affect roost selection. As bats are constrained to return periodically to those roosts, surrounding habitat might play a key role in survival and fitness (Frick et al., 2023; Mackie & Racey, 2007). The difficulty while studying small bats is being able to locate and track them to identify essential habitat (O’Mara et al., 2014). Fortunately, technologies such as remote sensing, and new data acquisition methods, such as citizen science, open doors for research on these cryptic animals.

My thesis seeks to explore habitat selection of temperate bats using a framework that encompasses multiple species, multiple scales and different periods of the year. In Chapter One, I investigated the effect of landscape features on summer and winter roost selection in Québec (Canada). I hypothesized that the presence of foraging habitat in the vicinity could drive roost selection. In Chapter Two, I used automated radiotelemetry to investigated behaviour and habitat preferences of little brown bats (*Myotis lucifugus*) at both a summer and a winter roost. I evaluated the return rate pattern and the distribution of bat activity in the surroundings according to habitat types. Together, these two chapters encompass habitat selection at different spatial and temporal scales and contribute to the literature aiming to enhance conservation plans for bats in the context of white-nose syndrome. My project also demonstrates the synergistic potential of citizen science, government databases, and innovative technologies to study small and cryptic animals.

LITERATURE REVIEW

Habitat loss caused by land conversion, climate change and resource exploitation is a major threats to biodiversity (Newbold et al., 2015; Powers & Jetz, 2019; Venter et al., 2006). Survival and breeding success of wildlife being closely linked to the availability of high-quality habitats (King et al., 2006; Long et al., 2016; Mathewson & Morrison, 2015). Habitat conservation is one of the most cost-effective strategies to enhance biodiversity worldwide (Gray et al., 2016; Martin et al., 2018). However, identifying important habitat for endangered species remains a challenge as habitat selection can be modulated by many factors, like seasons (e.g., Beier & McCullough, 1990; Stanley et al., 2021), physiological state (Bjørneraas et al., 2012) and resource availability (Long et al., 2016; Mathewson & Morrison, 2015). Moreover, animals also select habitat at multiple spatial and temporal scales that can range from the selection of a geographic range by a species to the selection of a single leaf by one individual during a specific season. Fully understanding habitat selection processes is important to properly define scales associated with ecological and conservation questions. In this review, I provide a definition of habitat selection and describe new tools that facilitate the understanding of animal habitat requirements. Finally, I describe the importance of habitat selection across the annual cycle of endangered North American bats and highlight research gaps.

Habitat Selection

Multi-level and Multi-scale Habitat Selection

Habitat selection is a behavioural process by which animals search for habitat containing needed resources to optimize fitness (Johnson, 1980; Krausman, 1999). As a result of habitat selection, animals have habitat preferences that can be described as the disproportionate use of a habitat relative to others (e.g., more time passed or higher activity level in a habitat; Garshelis, 2000; Johnson, 1980; Krausman, 1999). Habitat selection occurs at different levels of organization, mainly species, population or individual, which are each reflective of different processes. Johnson (1980) introduced a four-tiered habitat selection hierarchical framework widely used in modern ecology: 1st order, selection of a geographic range by a species; 2nd order, selection of a home range by an individual or a group ; 3rd order, selection of habitats by an individual or a group within its home range ;

and 4th order selection of a resource by an individual. Each selection order represents a different process, as the geographic range will mostly be dictated by climatic conditions, while the home range is likely determined by resource distribution (Johnson, 1980; Figure 1).

Within each order of selection, habitat can be perceived at different spatial scales. Scale of habitat selection can be defined by two components: grain and extent (Thompson & McGarigal, 2002; Figure 1). Grain is the resolution at which the habitat is perceived. For example, with a fine grain, we might perceived an isolated tree in a grassland as a habitat patch, while with a coarse grain, we might perceived the same habitat patch as grassland. Extent is the size of the study area (e.g., buffers on animal locations) or the scope of the habitats influence on an animal. The grain and extent employed to measure habitat selection will constrain the analysis of habitat selection, and it is therefore critical to choose a meaningful scale for the question and organism studied (McGarigal et al., 2016; Thompson & McGarigal, 2002). For example, to answer relevant biological questions on a caterpillar living in a tree, the leaves might be the proper grain to describe a habitat patch and the tree might be the proper extent. As for an owl living in a forest, trees within this forest might be a proper grain and the forest a proper extent.

Multiple studies demonstrated that failure to consider the multi-level and multi-scale nature of habitat selection brought biaised conclusions on animal habitat requirements. A study conducted on an isolated puma (*Puma concolor*) population in California demonstrated that grasslands were more abundant within puma home ranges compared to available habitat, suggesting selection for grassland (3rd order selection). However, grassland was avoided by pumas when moving and foraging within their home range (2nd order selection ; Zeller et al., 2017). Similarly, Schweiger et al. (2021) demonstrated that riparian habitat was strongly selected within Colorado chipmunk (*Neotamias quadrivittatus)* home range (3rd order selection). Nevertheless, by tracking individuals within their home range (2nd order selection) and by reducing the grain of observation, they demonstrated that chipmunks selected and used only certain types of riparian habitat (steep and shady riparian habitat). Without the multi-scale and multi-level framework, those studies would have been misinterpreted, leading to inefficient management plans for those species (Schweiger et al., 2021; Zeller et al., 2017).

Habitat Selection Over Temporal Scale

Because many animals move or change their behaviour through different periods of the year (breeding, migration, etc.; Marra *et al.,* 2015), habitat selection processes should vary over time to fulfill the changing needs and energetic constraints of animals (Andersen et al., 2022; Beier & McCullough, 1990; Lamb et al., 2020; Marra et al., 2015; Figure 1). For migrant songbirds, such as wood thrushes (*Hylocichla mustelina*), individuals are much less selective in terms of habitat during migration than during breeding seasons (Stanley et al., 2021). Indeed, wood thrushes selected mostly forested landscapes during breeding periods, but can be found in diverse habitats at migration stopover sites (Stanley et al., 2021). Difference in habitat selection during migration is potentially due to the importance of minimizing migration time by choosing stopover sites opportunistically (Stanley et al., 2021). Thus, those result suggests that wood thrushes should respond differently to habitat perturbations according to the time of the year (Stanley et al., 2021). Even though different periods of annual cycles are often isolated in time and space, events during one period can create carry-over effects affecting fitness during subsequent periods (Harrison et al., 2011; Marra et al., 2015).

Studying habitat selection across spatial and temporal scales is essential to comprehensively understand habitat requirements of a species. Biologists are increasingly aware of the importance of level and spatial/temporal scales in habitat selection processes. However, multi-scale studies are still underrepresented in the literature, especially for small mammals, and studies often don't consider temporal variation (McGarigal et al. 2016). Indeed, a review of more than 800 papers on habitat selection identified two main clusters: multi-level/single scale studies and single level/multi-scale studies (McGarigal et al. 2016). A multi-level framework reflected different behavioural processes and habitat selection can occur at different scales in each level (McGarigal et al., 2016). Thus the importance looking at multiple levels and scales to infer on animals requirements (McGarigal et al., 2016). Moreover, studies of animal ecology are temporally biased towards the breeding period because of the complexity and logistic challenge of monitoring throughout the annual cycle (Marra et al., 2015). The accessibility of technologies to track animals and the availability of environmental data collected by remote sensing are now precious tools to achieve relevant habitat selection studies at multiple scales, especially for small and cryptic species.

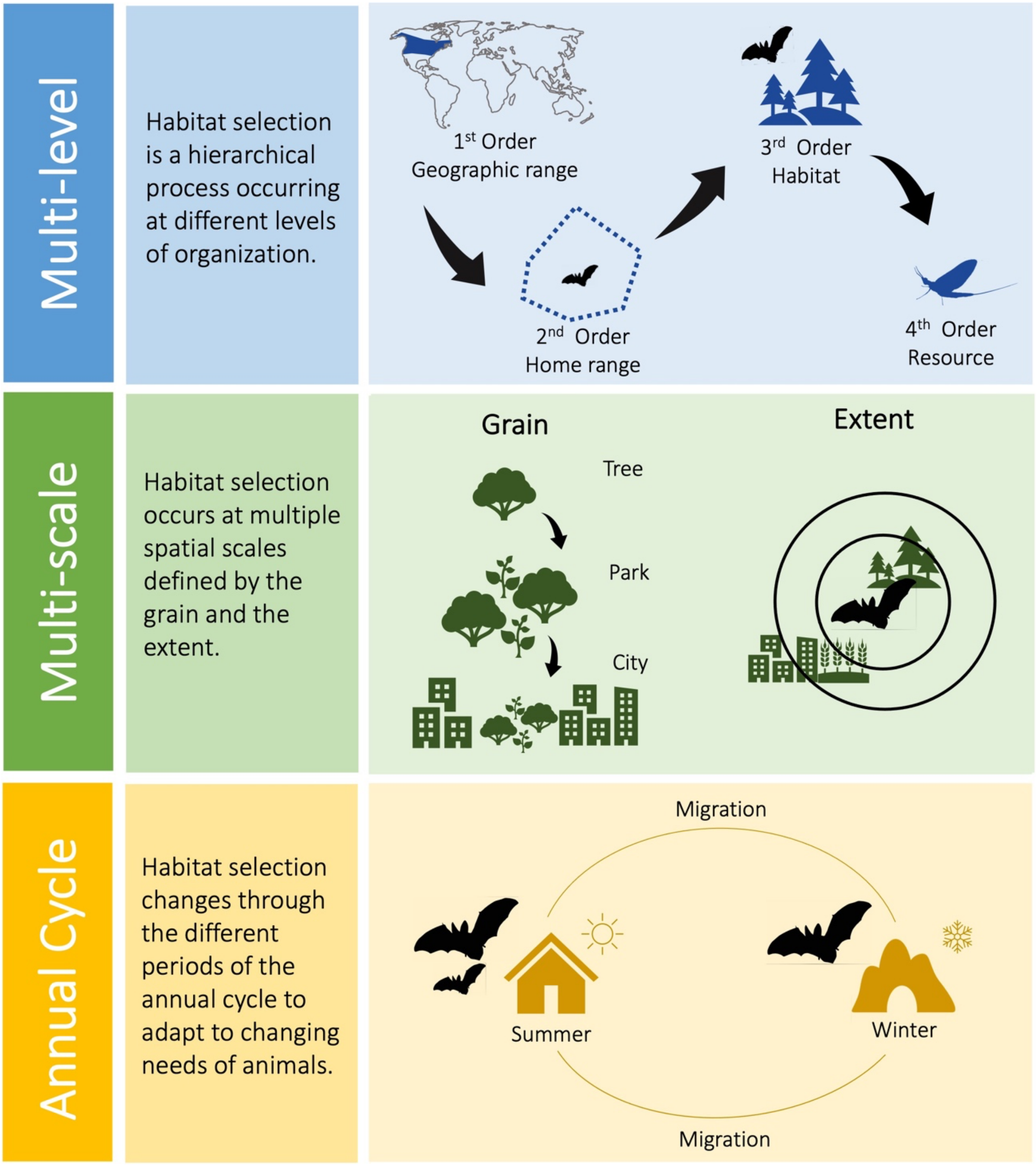

Figure 1. Summary of processes that influence habitat selection.

Citizen Science and Technology in Habitat Selection Studies

The massive contribution of the public in acquiring data on biodiversity has led to enormous citizen science[1] (also call participatory science) geodatabases like eBird (https://ebird.org/home) and iNaturalist (https://www.inaturalist.org). In addition, the increasing availability of remote sensing data has led to a better understanding of landscape ecology globally, including monitoring land use and habitat fragmentation (both concepts are reviewed in Pettorelli et al., 2014). The combination of citizen science and accessibility of land cover data have extended the scope of studies on animal distributions and habitat selection across time and space worldwide (Chandler et al., 2017; Dickinson et al., 2010; Sullivan et al., 2014).

One of the biggest advantages of citizen science is the possibility to collect a significant amount of data on broad scales, in addition to democratizing science and building public support towards conservation (Chandler et al., 2017; Fontaine et al., 2022). It is especially relevant for rare and cryptic species for which data are sometimes scarce (Fontaine et al., 2022). However, the use of citizen science in research projects has received some concern because of reliability of species identification by non-specialists and potential spatial/temporal bias (Dickinson et al., 2010; Johnston et al., 2022). Indeed, incorporating citizen science in research and conservation questions can be challenging, but many studies have demonstrated the robustness, cost-effectiveness, and power of these datasets when potential biases are considered (Farhadinia et al., 2018; Shumba et al., 2018). In habitat selection studies, the often-opportunistic nature of citizen science is more suited to broader levels of habitat selection (selection of geographic range [1st order] or selection of a home range [2nd order]; Fattebert et al., 2018; Shumba et al., 2018). Indeed citizen science is often a good tool to pinpoint animals in time and space, which most of the time can help identify patterns at the species level.

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[1] I note that the term "citizen science" in this review is used to define any person without a scientific background participating in scientific activity, regardless of citizenship. The term citizen science has been criticized because of lack of inclusiveness and sometimes other terms are used like participatory science or community science. I use the term citizen science here as it is the most common one and to avoid confounding definitions with other terms (Cooper et al., 2021).

Studies of movement and fine-scale habitat selection have been facilitated by rapid advances in the development of biologgers in recent decades (Cagnacci et al., 2010; Katzner & Arlettaz, 2020; Kays et al., 2015; Williams et al., 2020; Wilmers et al., 2015). For example, global position system (GPS)-based telemetry can track animals all over the world with an accuracy of ~5 m (Wilmers et al., 2015). Coupled with other sensors, such as accelerometers, GPS devices can give insight into habitat use, movement, behaviour, and physiological performance of animals (Katzner & Arlettaz, 2020; Wilmers et al., 2015). However, the smallest GPS tag available to date is still too heavy to be carried by many small animals without negative impacts (Kissling et al., 2014; Taylor et al., 2017). According to current best practices, researchers often aim to maintain tag weight under 2-5% of the animal body mass (e.g., Aldridge & Brigham, 1988; Canadian Council on Animal Care, 2023). Very small devices exist, like light-level geolocators (GLS) using sunlight to estimate locations, but their small size comes with tradeoffs on spatial accuracy and the need to recover animals (Bridge et al., 2013). Overall, the weight of tags must be a balance between minimizing impacts on animals ,extending battery life, data archiving, retrieval, and resolution (Kays et al., 2015; Kissling et al., 2014; Williams et al., 2020).

Radiotelemetry is a method to track small animals with high temporal and spatial precision without the need to recover tags (Cagnacci et al., 2010; Kays et al., 2015; Kissling et al., 2014; Taylor et al., 2017). Animals as light as butterflies and bumblebees can carry frequency encoded radio transmitters (Fisher et al., 2020; Kissling et al., 2014). However, an intense effort must be deployed to track animal locations using frequency encoded radiotelemetry. Observers must often manually track the radiotransmitter on foot or by car/plane, which requires a substantial investment of time and/or money for a relatively limited amount of data (Kissling et al., 2014; Martin et al., 2009; Taylor et al., 2017). It become especially challenging to track and estimate locations of fast-moving animals from radiotelementry (Lenske & Nocera, 2018).

Recently, the development of digitally-encoded radiotransmitters has led to new automated radiotelemetry systems able to continuously record a large number of animals (Taylor et al., 2017). These systems are composed of digitally-encoded radiotransmitters transmitting on the same frequency, and fixed (or mobile) receiver stations, allowing simultaneous monitoring of any tags within range of the receiver (Taylor et al., 2017). Detection range from fixed receiver towers is highly variable, but in some circumstances it is possible to continuously monitor tags up to 10 km away (Crewe et al., 2019; Taylor et al., 2017) leading to large-scale tracking opportunities. The most ambitious system is the Motus Wildlife Tracking System, a collaborative network composed of >1500 receiver towers distributed across 5 continents that have tracked more than 35,000 individual animals including birds, bats, and insects (Motus Wildlife Tracking, 2022). So far, automated telemetry has mostly been used to track large-scale movement and habitat selection (e.g., stopover or breeding site selection; McGuire et al., 2012; Morningstar & Sandilands, 2019; Taylor et al., 2017). However, automated radiotelemetry is promising to expand local-scale knowledge by concentrating receiver towers in small areas, especially for central place foragers whose movements are restricted around a central point (Lenske & Nocera, 2018). Yet, few studies have tested this design (Nelson & Gillam, 2017).

Central Place Foraging

Central places can be a residence (nest, roost, den, etc.) to which animals regularly return in between foraging trips or station keeping movements (Orians & Pearson, 1979). In the context of habitat selection, the use of a central place creates a spatial dependence, as animals often constrain their movement to their vicinity (Rosenberg & McKelvey, 1999). When foraging animals leave their central place, the cost of commuting to a habitat patch must be worth the gain (MacArthur & Pianka, 1966; Olsson et al., 2008; Orians & Pearson, 1979; Pyke, 2019). The optimal foraging strategy is influenced by the quality of foraging patches (food availability), distance from the central place, loads that needs to be carried back (e.g., food/milk to feed young) and the return frequency to the central places (Lalla et al., 2022; Olsson et al., 2008; Orians & Pearson, 1979; Rosenberg & McKelvey, 1999). As such, the probability of selecting a habitat patch decreases with distance from the central place because of commuting cost (Nilsson et al., 2020; Olsson & Bolin, 2014; Rainho & Palmeirim, 2011; Rosenberg & McKelvey, 1999). Consequently, a habitat patch selected far away from the central place should be highly valuable to offset commuting costs (Elliott et al., 2009; Olsson et al., 2008; Orians & Pearson, 1979), and an animal that returns many times a day may need to stay closer than one that returns only once a day (Daniel et al., 2008; Lalla et al., 2022).

The central places itself needs to provide a certain protection level, microclimate or other requirements depending on its function (hibernation sites, mating sites, breeding sites, etc. ; e.g., Glover & Altringham, 2008; Mainwaring et al., 2014). When optimal central places are abundant, the proximity of high-quality habitat patches might become a driver of selection too (Rosenberg & McKelvey, 1999). The choice of optimal central places and foraging strategies in the surrounding might differ according to availability of optimal central places, availability of optimal foraging habitat patches, predation risk, disturbances and return constraints to the central place (e.g., feeding young or not; Daniel et al., 2008; Lalla et al., 2022; Mainwaring et al., 2014; Olsson & Bolin, 2014; Rosenberg & McKelvey, 1999).

Bats and Threats

Bats are one of most diverse mammal groups, and many species are notable for their sociability (e.g., Kerth, 2008), their use of echolocation (e.g., Bohn & Gillam, 2018), their long life span relatively to their size (Wilkinson & Adams, 2019) and the use of torpor as an energy saving tactics (Jonasson & Willis, 2012; Wojciechowski et al., 2007). Bats offer an interesting opportunity to study movement and habitat selection, as they are able to travel great distances (relative to body size) within (Best & Geluso, 2003; Morningstar & Sandilands, 2019) and among seasons (Alcalde et al., 2021; Fenton, 1969; Norquay et al., 2013; Roby et al., 2019) allowing exploitation of large, fragmented landscapes year round (Gehrt & Chelsvig, 2003). Still, many species remain understudied (and probably even unknown) compared to other groups (Frick et al., 2019).

About 30% of North American bat species are considered at risk, most of which being insectivorous bats concentrated in the northeast (Hammerson et al. 2017). Insectivorous bats in North America consume a great biomass of arthropods and loss of this ecosystem service associated with bat population declines has been estimated to cost millions of dollars (Kunz et al., 2011; Williams-Guillén et al., 2016). Major threats for temperate bats include habitat loss due to human development (Frick et al., 2019; Kurta et al., 1989; Russo

& Ancillotto, 2014), wind energy development (Arnett et al., 2016), climate change (Adams & Hayes, 2008; Festa et al., 2023), and wildlife disease such as the white-nose syndrome (Cheng et al., 2021; Frick et al., 2010; Hammerson et al., 2017)

White-Nose Syndrome

White-nose syndrome (WNS) is a fungal disease that has led to enormous declines in hibernating bat populations across North America in last decades (Cheng et al., 2021; Frick et al., 2010). The European fungal pathogen, *Pseudogymnoascus destructans*, was first detected in North America in New York state in 2006 and is now widely spread (Cheng et al., 2021; Frick et al., 2010; White-Nose Syndrome response team, 2022). The fungus can persist in underground environments where many bat species hibernate (Hoyt et al., 2021; Verant et al., 2012). Hibernating bats reduce body temperature and immune function, which allows the fungus to proliferate on epidermal tissues (Langwig et al., 2015). Fungal infection affects multiple physiological functions causing frequent arousal during hibernation, and ultimately leading to loss of fat stores and potential starvation before the end of hibernation (Hoyt et al., 2021; Langwig et al., 2015; Verant et al., 2014).

Since WNS arrival, declines of >90% in hibernating bat populations have been observed across North America, especially for the little brown bat (*Myotis lucifugus*), northern long-eared bat (*Myotis septentrionalis*) and tricolored bat (*Perimyotis subflavus*; Cheng et al., 2021). Other species like the Indiana bat (*Myotis sodalis*) and big brown bat (*Eptesicus fuscus*) have also been moderately affected (Cheng et al., 2021). Following WNS invasion, there are some evidences of populations stabilizing in some regions (Langwig et al., 2012; Maslo et al., 2015), while declines continue in other populations (Hoyt et al., 2021). White-nose syndrome is still spreading through western North America where the effect on populations is uncertain (Lorch et al., 2016). No effective cure or applicable treatments have been found and protecting remaining populations might be the best conservation strategy to enhance recovery (Frick et al., 2019; Hoyt et al., 2021). Therefore, better understanding of hibernating bat ecology and habitat requirements is needed to develop and strengthen conservation plans.

Ecology of Temperate Hibernating Bats

Temperate bats can either migrate south or use hibernation to survive to winter conditions. Through this review, I focus on hibernating bats. Most hibernating bats use two residences depending on the time of the year: maternity roosts in summer used by reproductive females and hibernacula in winter (Figure 2). Migration between these seasonal residences ranges from travel from a few kilometers to <500 km (Krauel et al., 2018; Norquay et al., 2013; Rivers et al., 2006; Roby et al., 2019; Rockey et al., 2013). Males and females exhibit different seasonal behaviours and mainly coexist during mating and hibernation periods at the hibernaculum, although some males can be found roosting with females in the summer (Davis & Hitchcock, 1965; Fenton, 1969; Senior et al., 2005). Mating is thought to occur mainly in late summer at hibernacula (copulation can also occur during hibernation or in spring), but females only ovulate in spring after hibernation and give birth in summer at maternity roosts (Boyles et al., 2006; Oxberry, 1979; Thomas et al., 1979).

I acknowledge that the phenology of temperate bats and their behaviour at the different period of the annual cycle can differ depending on the latitude (e.g., Jordan, 2020; McGuire et al., 2016). Temperate bat species also have different morphological constraints influencing flight speed, manoeuvrability, and foraging strategy (Jung et al., 2012; Luszcz & Barclay, 2016) and habitat selection is species-dependent (Jung & Threlfall, 2018; Laforge et al., 2021). Therefore, the habitat selection patterns described in the next paragraph may be applicable to many species, but not all (Laforge et al., 2021).

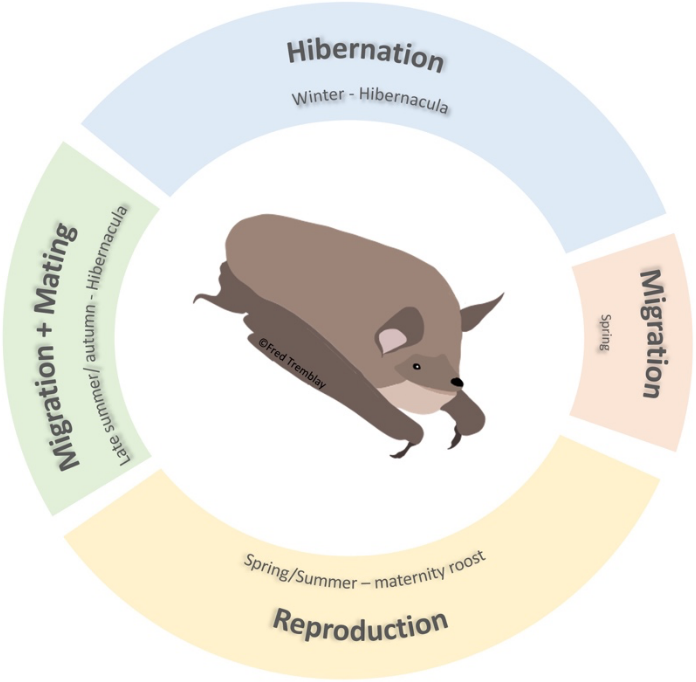

Figure 2. Typical annual cycle of a reproductive female little brown bat

Summer: Parturition and Lactation at the Maternity Colony

When leaving hibernacula after hibernation, males and females occupy different residences and home ranges for the summer (Senior et al., 2005). Males and non-reproductive females rather use different and non-permanent day roosts, while reproductive females gather in maternity colonies (Broders & Forbes, 2004; Davis & Hitchcock, 1965; Fenton, 1969; Senior et al., 2005). Females usually give birth in June or July to one or two pups and then nurse their pup(s) for about a month (Garbino et al., 2021; Kurta et al., 1989). During this period, females are constrained to return to the maternity roost between foraging trips to nurse flightless pups at night (Anthony et al., 1981; Fontaine, 2021; Henry et al., 2002), resulting in central place foraging behaviour (Daniel et al., 2008; Rainho & Palmeirim, 2011). Consequently, lactating females usually decreased foraging distance and time away from the maternity roost compared to pregnant females (Fontaine, 2021; Henry et al., 2002). Lactating females have high energetic and water demands for milk production and flight represents most of the daily energy expenditure (Kunz et al., 1995; Kurta et al., 1989, 1990). Maternity roost selection is therefore a tradeoff between available foraging resources in the surrounding area and, selecting a roost that provides protection from the elements and predators, and conditions to ensure rapid development of pups (e.g. Daniel et al., 2008).

Maternity Roost Selection

Females carefully choose their maternity roosts, to which they show high fidelity between years with a relatively low dispersal rate (Henry, 2001; Lewis, 1995; Norquay et al., 2013). Maternity roosts can be various structures like old trees and snags (e.g., Broders et al., 2006), caves (e.g., McCracken & Gustin, 1991) or human structures (e.g., Neubaum et al., 2010). Temperature inside the roost is a key element for female bats, and is particularly a concern in temperate regions where temperature covers a large range. When temperature decreases below a certain threshold, females are more likely to use torpor (decrease in body temperature, metabolic rate and physiological activity) to offset the energetic cost of euthermia (Henry, 2001; Willis et al., 2006). However, the use of torpor can delay gestation and affect mother and pup survival (O'Shea et al., 2010; Racey & Swift, 1981). On the other hand, roosts can also overheat and cause bats to move to avoid negative effects like dehydration (Crawford & O'Keefe, 2021; Henry, 2001). As a strategy to mitigate temperature fluctuations, tree roosting bats can switch roosts according to weather to find optimal microclimates (Kerth et al., 2001; Patriquin et al., 2016; Ruczyński & Bartoń, 2020). Some species like little brown and big brown bats can also select roost in buildings as anthropogenic structures sometimes provide multiple internal microclimates (Lausen & Barclay, 2006; Voigt et al., 2016).

While suitable conditions inside the roost are required, presence of foraging areas in the surroundings are beneficial. Indeed, during lactation; female home ranges are concentrated around the maternity roost, such that maternity roost selection is not only driven by conditions in the roost but also its surrounding habitats (2nd order selection: selection of a home range). Minimal distances to natural areas such as forest and waterbodies influence roost selection for many species (Balzer et al., 2022; Bellamy & Altringham, 2015; Boughey et al., 2011; Pauli et al., 2015; Rainho & Palmeirim, 2011; Schroder et al., 2017).

For example, the roost occurrence of six European bat species was positively related to broadleaf forest features near the roosts (Boughey et al., 2011). Maternity roost in buildings or trees can be found in highly anthropogenic landscapes and even urban centres (Dietz et al., 2020; Neubaum et al., 2010; Thorne et al., 2021). Old forest patches with snags and mature trees are crucial habitat for the establishment of a maternity roost of tree roosting bats within cities (Dietz et al., 2020; Thorne et al., 2021). Moreover, urban parks and ponds can represent high quality foraging habitat for bats in cities (Avila-Flores & Fenton, 2005; Dietz et al., 2020; Fabianek et al., 2011; Thomas et al., 2021; Uhrin et al., 2017). As such, anthropogenic landscapes may be suitable for the establishment of maternity colonies as long as they provide suitable foraging habitat patches (Geggie & Fenton, 1985; Gehrt & Chelsvig, 2003; Gili et al., 2020; Russo & Ancillotto, 2014; Uhrin et al., 2017).

Many bat species forage (3rd selection order: selection of habitat) over water, in wooded habitat or wetlands (Brooks & Ford, 2005; Ford et al., 2005; Fukui et al., 2006; Holloway & Barclay, 2000; Kniowski & Gehrt, 2014; Krauel et al., 2018; Lookingbill et al., 2010; Ober & Hayes, 2008; Thomas et al., 2021; Walsh & Harris, 1996). Edge features like riparian habitat and forest edges are both highly used by bats (Furmankiewicz & Kucharska, 2009; Grindal & Brigham, 1999; Holloway & Barclay, 2000; Kalcounis-Rueppell et al., 2013). As such, forest harvesting has different impacts on bats. Some practices that favoured the retention of mature forest patches can increase edge density and openings in cluttered forest which can favour bat activity, while preserving potential roosts (Law et al., 2016; Patriquin & Barclay, 2003). However, within harvested patches, bat activity is often minimal (Dodd et al., 2012; Law et al., 2016; Patriquin & Barclay, 2003).

Bats can persist in various human-modified landscapes, including agricultural fields and urban areas, although bats activity is often higher in natural habitat patches within thoses landscapes Jung & Threlfall, 2018). Indeed, Indiana bats select forested patches and waterbodies for foraging more than any other habitat, even if more than 80% of the study area was agricultural fields (Kniowski & Gehrt, 2014). Heterogeneous agricultural landscapes with perennial or organic crops do seem to attract more species and enhance foraging activity (Monck-Whipp et al., 2018; Put et al., 2018). Overall, bats activity in urbanized landscapes has mostly been recorded in vegetated urban parks and around water ponds (Avila-Flores & Fenton, 2005; Dietz et al., 2020; Fabianek et al., 2011; Thomas et al., 2021). Recent studies highlight the influence of other anthropogenic stressors that could negatively impact habitat selection in urban areas like noise pollution (Finch et al., 2020; Lehrer et al., 2021) and artificial light at night, although some species hunt insects at streetlights (Russo & Ancillotto, 2014; Rydell, 1992; Salinas-Ramos et al., 2021; Voigt et al., 2020).

Fall and Winter: Mating and Hibernation at Hibernacula

After the breakup of maternity colonies by the end of July, males and females gather at hibernacula for the mating season. Mating behaviour is called swarming, characterized by flight and vocalization at hibernaculum entrances prior to hibernation (Davis & Hitchcock, 1965; Fenton, 1969; Senior et al., 2005; Thomas et al., 1979). Swarming sites attract bats from many summer colonies in large catchment areas, a behaviour that is likely important for maintaining gene flow in populations that are mostly isolated in summer (Dekeukeleire et al., 2016; Furmankiewicz & Altringham, 2007; Parsons & Jones, 2003; Rivers et al., 2006). Bats seem to ultimately hibernate where they swarm (Van Schaik et al., 2015), although movement among swarming sites has been reported (Dekeukeleire et al., 2016; Fenton, 1969; Rivers et al., 2006). However, during swarming periods, bats do not necessarily visit hibernacula every night (Dekeukeleire et al., 2016; Furmankiewicz, 2008; Lowe, 2012; Parsons & Jones, 2003; Rivers et al., 2006). Bats also need to forage to deposit fat stores before hibernation (Gallant & Broders, 2015; Kunz et al., 1998; McGuire et al., 2009; Thomas et al., 1990). During this period, they may use torpor on colder nights to minimize energy expenditure and maintain fat stores when prey might be declining (McGuire et al., 2016; Speakman & Rowland, 1999). Thus, activity during swarming periods must be balanced spatially and temporally among foraging, swarming, and roosting.

In winter, bats gather in hibernacula where they decrease metabolic rates to cope with cold temperatures and the absence of food (Jonasson & Willis, 2012). Bats arouse from hibernation periodically, returning to normal metabolic rate and euthermic body temperature, potentially to drink, urinate, or copulate (Boyles et al., 2006; Reeder et al., 2012). Periodic arousals are extremely costly during winter (Thomas et al., 1990).

Maximizing fat store deposition pre-hibernation is thus extremely important to ensure winter survival and could be a strategy to offset WNS impact during this period (Cheng et al., 2019; Davis & Hitchcock, 1965; Domashinski, 2022; Jonasson & Willis, 2011)

Sex-Specific Behaviours During the Swarming Period

Many bat mating systems are promiscuous suggesting differences in behaviour between sexes during mating seasons (Furmankiewicz & Altringham, 2007; Thomas et al., 1979). Male-biased behaviour at swarming sites has been reported many times, with higher capture rates for males than females (Burns & Broders, 2015; Dekeukeleire et al., 2016; Fenton, 1969; Furmankiewicz, 2008; Rivers et al., 2006), males visits being more frequent and longer than females (Burns & Broders, 2015; Davis & Hitchcock, 1965), and males roost closer to the swarming site than females (Furmankiewicz, 2008). Sex-specific behaviour might be explained by differences in resource allocation. First, males likely increase mating opportunity by spending more time at swarming sites (Burns & Broders, 2015; Furmankiewicz, 2008; Glover & Altringham, 2008). Second, energetic demands might differ between sexes after reproduction in the summer. At the end of the summer, female little brown bats that weaned young are more energy depleted than males (Burns & Broders, 2015), yet they usually enter hibernation heavier than males, likely to ensure sufficient energy stores to support hibernation and also early spring gestation (Jonasson & Willis, 2012; Norquay & Willis, 2014). Therefore, females would need to allocate more time to foraging before hibernation. Still, many questions remain about sex-specific and inter-individual behaviour during swarming and hibernation periods (Burns & Broders, 2015; Fraser & McGuire, 2023).

Hibernaculum Selection

Hibernacula can occur in caves or mines (e.g., Glover & Altringham, 2008), crevices (e.g., Klüg-Baerwald et al., 2017) or buildings (Neubaum, 2018; Voigt et al., 2016; Whitaker & Gummer, 2000), depending on the species. Suitable hibernation sites typically provide stable temperatures above freezing and high humidity over winter (reviewed in Perry, 2013). Geology and configurations of cave hibernacula usually are the principal drivers of temperature and humidity (Perry, 2013; Randall & Broders, 2014), and the contribution of landscapes seem to be marginal (Glover & Altringham, 2008; McClure et al., 2020; Perry, 2013; Wethington et al., 1997). Still, bats intensively forage nearby hibernacula pre-hibernation and potentially post-hibernation (McGuire et al., 2009; Roby et al., 2019), suggesting the importance of foraging areas in the surroundings. Foraging habitat like waterbodies and rivers in the surrounding area seems to increase the probability of selection of hibernacula (de Boer et al., 2013; Randall & Broders, 2014), but this subject remains understudied.

Day Roosts and Habitat Selection During Pre-and Post-Hibernation

During swarming seasons before hibernation, bats can roost in various structures ranging up to 26 km from the hibernaculum (Brack, 2006; Dekeukeleire et al., 2016; Gallant & Broders, 2015; Lowe, 2012; Parsons & Jones, 2003). A study in England showed that during the swarming period, Natterer's bats (*Myotis nattereri)* selected day roosts (2nd order selection) surrounded by greater proportion of arable and pasture habitat (Parsons & Jones, 2003). In contrast, Bechstein's bat (*Myotis bechsteinii)* roosts in Belgium were mostly found in old forested fragments (Dekeukeleire et al., 2016). In North America, little brown bats and northern long-eared bats roost in trees from coniferous/mixed forest patches (Lowe, 2012). Still, bats can periodically switch roosts during the swarming season (Brack, 2006; Dekeukeleire et al., 2016; Lowe, 2012), therefore, they might be less selective, in terms of habitat, around their day roosts.

Few studies have evaluated foraging habitat selection by bats during swarming period (3rd order selection). In England, Natterer's bats used mostly woodland, pasture and open water for foraging, even though woodland represented only a small proportion of the home range (Parson & Jones 2003). Indiana bats selected open woodland for foraging more than expected during swarming seasons (Brack, 2006). However, such studies of habitat selection during swarming seasons remain scarce (Frick et al., 2023).

Conclusion

To summarize, habitat selection happens at different spatial and temporal scales. Failure to consider these variations can lead to inappropriate or biased conclusions about species ecology and thus insufficient conservation plans. However, it can be hard to study animals along different scales because of the challenge of locating animals over long periods of time. Fortunately, new technologies and data acquisition methods can facilitate localization and tracking, even for small and cryptic animals like bats. Hibernating bats are an interesting group to study habitat selection being local migrants with different residences ("central places") and energetic constraints according to the period of the year. Moreover, important declines in hibernating bats population in recent decades, has led to conservation concerns. Better understanding of bat habitat requirements can enhance both the literature on habitat selection at multiple scales and conservation plans for bats.

NOTE ON CHAPTER 1

This chapter corresponds to a manuscript with the same title that I anticipate will be submitted for publication in the *Canadian Journal of Zoology* soon. The data in this chapter were collected by the MELCCFP and by the Batwatch citizen science project. This chapter was conceptualized by me with the help and supervision from Dr. Anouk Simard (MELCCFP), Dr. Liam P. McGuire (University of Waterloo) and Dr. Kyle H. Elliott (McGill University). Part of this chapter was written and revised by other students in the Scientific Manuscript Writing course given by Dr. Anna L. Hargreaves (McGill University).

CHAPTER 1: The Relative Influence of Landscape Features on Maternity Roost and Hibernaculum Selection in Temperate Bats

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Abstract

Optimal residence selection is key to survival and reproductive success of many species, especially if they are inhabited for extended periods. Resources can be obtained from the surrounding habitat, but are constrained by the requirement to return to their residence (“central place”). Many bat species use permanent roosts during different periods of the year. While most conservation plans aim to protect these roosts, the availability of suitable foraging habitat is also critical. We evaluated the importance of landscape factors at multiple scales surrounding seasonal bat roosts in Québec (Canada), using both citizen science and government databases. In summer, bats selected maternity roosts with higher anthropogenic cover and water edge density in their surroundings at the 150 m and the 2 km scales respectively, with notable differences between southern and northern Québec. In winter, hibernaculum population size was inversely related to human-modified landscape and positively related to forest edge density. However, in both seasons our models explained relatively little of the observed variance, suggesting that, while influential, other factors, such as physical characteristics of the roost, are likely important in roost selection decisions made by bats. Nevertheless, our study shows that the protection of maternity roost and hibernacula themselves should be paired with protection of surrounding habitat. Together, citizen science and professional surveys provided data on a cryptic species that encompass a large temporal and spatial scale, that could not be gathered with either approach alone.

Keywords

Central Place Foragers, Maternity Roost, Hibernacula, Conservation, Landscape, Roost Selection, Multi-scale, White-nose syndrome, Temperate Bats, Citizen Science

Introduction

Selection of an optimal residence (e.g., burrow, den, nest, roost, etc.) can increase the fitness of an animal by providing functions like protection and a microclimate that minimizes thermoregulatory costs. As an animal's requirements vary across their annual cycle, factors influencing residence selection are expected to vary too. Many conservation plans thus forbid destroying or damaging the physical structure of residences or the critical habitat of endangered species (e.g., Species at Risk Act, 2002). Yet, the immediate habitats surrounding the residence is also significant for providing resources, especially in central place foragers constrained to return periodically to their residence (i.e. parents provisioning young; Olsson & Bolin, 2014; Orians & Pearson, 1979; Rosenberg & McKelvey, 1999). Characteristics of both the physical residence and the surrounding landscape are determinant for residence selection (Rosenberg & McKelvey, 1999). As the availability of suitable residences increases, habitat surrounding the residence might become the principal driver of selection (Oakeley & Jones, 1998; Rosenberg & McKelvey, 1999). For species of conservation concern that rely on residences as central places, understanding the influence of the surrounding habitat is an essential component of comprehensive management plans.

Hibernating bat populations in eastern North America (hereafter referred to as "bats") have experienced large declines, exceeding 90 % in certain populations, since the introduction of white-nose syndrome (WNS) to North America in 2006 (Cheng et al., 2021; Frick et al., 2010). This fungal disease affects bats during hibernation, causing frequent arousal and rapid depletion of fat stores (Frick et al., 2010; Reeder et al., 2012). Population recovery is expected to be slow as bats are long-lived mammals and females give birth to one or two pups per year (Garbino et al., 2021; Hoyt et al., 2021; Wilkinson & Adams, 2019). To date, no treatment has been found for WNS, but persisting populations suggest a possible tolerance to the disease (Langwig et al., 2017). Limiting the residual mortality caused by other threats, such as habitat loss, might then be one of the few effective conservation measures (Frick et al., 2019; Hoyt et al., 2021). Multi-species and large-scale conservation guidelines are needed to promote efficient and cost-effective plans that can be promptly applied by managers (Cable et al., 2021; Donaldson et al., 2017; Pauli et al., 2015).

Hibernating bats alternate seasonally between residences. In summer, reproductive females gather in maternity colonies to raise their pups (Davis & Hitchcock, 1965), often roosting in buildings (Lausen & Barclay, 2006; Voigt et al., 2016). While suitable conditions inside the maternity roost are required, the availability of foraging habitat in the surrounding area is also important (Henry, 2001; Thomas et al., 2021). Indeed, to offset the cost of pregnancy and lactation, insectivorous females consume their own body mass in insects per night (Kunz et al., 2011; Kurta et al., 1989a), all while regularly returning to the roost to nurse pups (Fontaine, 2021; Henry, 2001). In that sense, high quality foraging areas close to the maternity roost could promote female fitness through reduced foraging effort and consequently enhance offspring survival and fattening before hibernation (e.g., Mackie & Racey, 2007).

Prior to hibernation, males and females converge at winter roosts (hibernacula) for mating season (Fraser and McGuire, 2023). During the pre-hibernation season, bats may face a tradeoff between copulation at the hibernaculum and building fat stores for hibernation (Gallant and Broders, 2015; McGuire et al., 2009; Thomas et al., 1990). Consequently, the landscape surrounding hibernacula serve for both foraging and roosting during this period (Brack, 2006; Gallant and Broders, 2015). Although not a central place in the sense of central place foraging theory, hibernacula represent important focal sites for pre-hibernation activity as they are repeatedly revisited (Brack, 2006; Gallant and Broders, 2015). Bats may not be spatially constrained by the hibernaculum, but minimizing commuting distance between roosting, foraging, and mating sites likely provides a fitness advantage (Muthersbaugh et al., 2019; Raesly and Gates, 1987). Moreover, bats with higher fat stores at the beginning of hibernation could be more resistant to WNS in winter (Cheng et al., 2019; Jonasson and Willis, 2011). Maximizing energy intake near the hibernaculum during pre-and post-hibernation periods could offset the energy cost of WNS.

Conservation plans limited to protecting only the physical structure of maternity roosts and hibernacula are likely insufficient, as they need to integrate the surrounding foraging habitats. However, there is a limited understanding of how landscape composition is related to roost selection, and the scale at which different landscape elements influence bats. We aimed to identify the importance of landscape features around maternity roosts and hibernacula of temperate bat species including *Eptesicus fuscus* (big brown bat; Beauvois, 1796), *Myotis lucifugus* (little brown bat; Le Conte, 1831) and *Myotis septentrionalis* (northern long-eared bat; Trouessart, 1897). We used citizen science and provincial government data to locate maternity roosts and hibernacula in Québec (Canada). By combining those two data sources, we gather data across Québec that encompass two period of the annual cycle of bats, enhancing spatial and temporal coverage of this study. We extracted landscape features surrounding maternity roost and hibernacula at different ecologically relevant scales. Our specific objectives were to evaluate the impact of landscape features 1) on the selection of maternity roosts by comparing used versus available roosts, 2) on the population size of hibernacula prior to the arrival of WNS, and 3) on the population declines caused by WNS in hibernacula. We predicted a positive influence of natural landscapes on the selection of maternity roosts and hibernation population sizes (e.g., Thomas et al., 2021). A full description of specific predictions is included in Table 1.1.

Methods

Study Region

Bats in Québec are found in the southern region, characterized by a wet continental climate and a high level of human activity, and in the northern region, characterized by the boreal forest and scattered human activity (Institut de la statistique du Québec, 2021). White-nose Syndrome arrived in southern Québec in 2009-2010 and reached northern regions between 2012 and 2015 (Faure-Lacroix et al., 2020). The disease spread eastward until 2019, when it reached Anticosti Island, thus becoming widespread throughout the province (White-Nose Syndrome response team, 2022).

We obtained summer roost locations from the Neighbourhood Batwatch citizen science project (https://batwatch.ca/; hereafter referred to as “Batwatch”). As of 2021, participants registered 593 bat summer colonies in Québec (Neighbourhood Bat Watch, 2021). We considered only colonies with a confirmed occupied roost and confirmed coordinates. Roosts in buildings represented most observations (> 60%) from the Batwatch database, and consequently, we only included those roosts in the analyses (i.e., excluding bat boxes and tree roosts) for a total of 311 summer roosts. Although summer roosts are sometimes occupied by males or non-reproductive females (e.g., Davis & Hitchcock, 1965), we expected that most building roosts were used by reproductive females, and we refer to them as maternity roosts hereafter. Our datasets identified the species for 44% of the maternity roosts (mostly identified with acoustic detectors): 20% were occupied by *E. fuscus*, 15% by *Myotis spp.* and 9% by mixed *Myotis spp.* and *E. fuscus*. *Myotis septentrionalis*, *M. lucifugus* and *E. fuscus* are the only three species known to roost in buildings in Québec (Soper & Fenton, 2007), and we are thus confident that our data encompass only those species. The Batwatch database also included count data for certain roosts, but monitoring started after the arrival of WNS in most regions of Québec. As population size fluctuated considerably post-WNS, and we had few pre-WNS counts, we did not use count data.

For hibernacula, we used historical and recent hibernaculum count data from the Québec government (Ministère des Forêts, de la Faune et des Parcs, unpublished data). Sites were surveyed during hibernation, between November and March hibernation season, and in cases where there were multiple surveys reported for one season, we used the highest count in our analysis. We noted whether each count was conducted before or after WNS regional arrival (Faure-Lacroix et al., 2020; White-Nose Syndrome response team, 2022). We assumed counts to be representative of the hibernating population and comparable among years. Our dataset includes counts from 38 hibernacula where *M. lucifugus* and *M. septentrionalis* were the dominant species (Ministère des Forêts, de la Faune et des Parcs, unpublished data).

Framework

To evaluate the role of landscape features on maternity roost selection, we chose a *used vs. available* framework (Manly et al., 2002). We compared landscape features around used maternity roosts to those around random available roosts. We selected available roosts by generating random coordinates proportional to the number of used roosts within each ecological region of Québec and selecting the nearest building using satellite imagery (Google, 2022; U.S. Geological Survey, 2022). This method ensured that 1) we compared used roosts with available roosts within the same geographical distribution and that 2) available roosts were in buildings that could potentially serve as maternity roosts, although buildings were not evaluated for their roosting potential. As available roosts are not guaranteed to be true negatives, such framework can only infer relative probability of selection (Johnson et al., 2006; Manly et al., 2002).

To evaluate the role of landscape features on hibernaculum selection pre-WNS, we used population size as a proxy for selection. We used the greatest count registered per hibernaculum pre-WNS to evaluate the selection of hibernacula in relation to landscape features. To evaluate how landscape features could have mitigated declines in hibernacula post-WNS, we estimated the largest decline per hibernaculum by using the maximum count pre-WNS and the minimum count post-WNS, when sampling had occurred before and after WNS.

We defined foraging ranges based on previous studies on our species, which reported foraging distances from the maternity roost from < 2 km to 5 km (Brigham, 1991; Broders et al., 2006; Henry et al., 2002; Menzel et al., 2001) and distance from the hibernaculum generally from < 2 km to >10 km (Brack, 2006; Gallant & Broders, 2015). To ensure independence, we removed maternity roosts and hibernacula for which foraging range (5 km and 10 km radius circular buffer respectively) overlapped by more than 30%. We used a hierarchical framework to remove overlapping maternity roost and hibernacula (Figure S1.1) based on information accuracy and reliability (i.e., sites with more detailed or more reliable data were selectively retained).With this method we avoid overrepresenting some areas where roost density is high because bats switch roosts or because there are more observers in the region. This step resulted in removing 97 maternity roosts and 5 hibernacula from the dataset. When generating available roost coordinates, we also avoided overlaps with other used or available roosts.

There are pronounced landscape differences between northern and southern Québec because of climatic and antrohopogenic activity gradient. Therefore we expected selection pressures, trade-offs, and constraints to be different between the two regions. We separated southern and northern maternity roosts (i.e., south and north of the boreal forest line respectively; Figure 1.1), but not hibernacula because of low sample size.

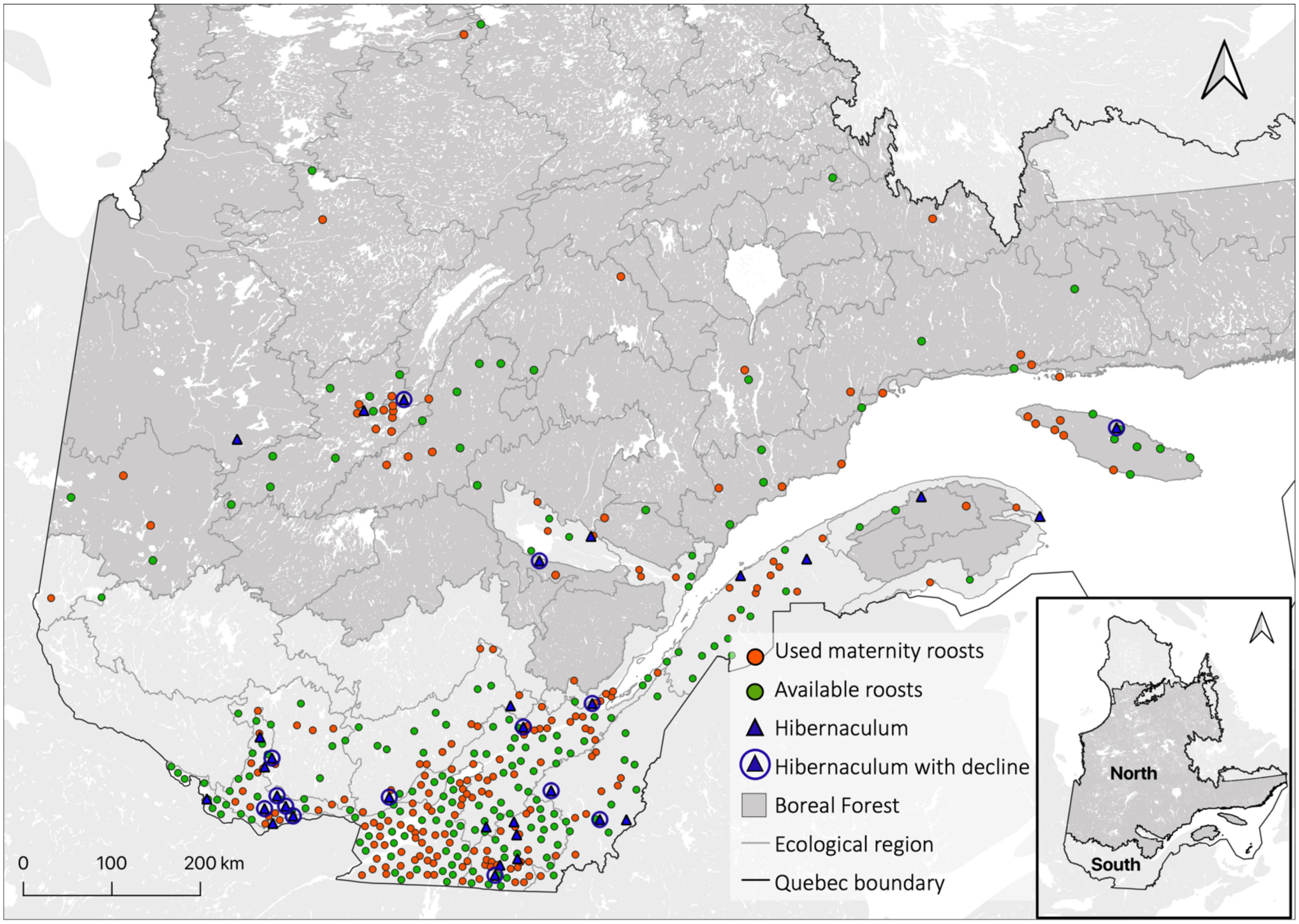

Figure 1.1. Distribution of used and available maternity roosts and hibernacula in southern and northern Québec (Canada), this division being delimited by the boreal forest line.

We used the latest version (2018) of the land use classification of Québec (30 m resolution) to characterize landscapes around maternity roosts and hibernacula (Ministère de l'Environnement et de la Lutte contre les changements climatiques, 2018). We derived 12 landscape features documented to affect maternity roost selection (see predictions in Table 1.1). Our dataset included a comparatively small sample size for hibernacula, and thus we considered only eight landscape features (Table 1.1). We also used latest hydrographic layers of Canadian waterways and water bodies (50k scale; Government of Canada, 2019) and road layer of Québec (Ministère de l'Énergie et des Ressources Naturelles, 2018) to compute minimum Euclidean distance between these features and maternity roosts/hibernacula (Table 1.1). Finally, we used the *landscapemetrics* package (Hesselbarth et al., 2019) in R (version 4.2.2; R Core Team, 2022) to extract values from these datasets.

Table 1.1. Landscape feature descriptions and their predicted effect on selection of maternity roosts and hibernacula.

Hibernaculum		**Maternity roost**				
Landscape features	**Effect**	**Landscape features**	**Effect**	**Description**	**Mechanism**	**References**
Human-modified	-	Annual Crop	-	% cover of annual crop	Intensive agriculture reduces diversity and abundance of insects.	(Cable et al., 2021; Kniowski & Gehrt, 2014; Thomas et al., 2021)
		Perennial Crop	+	% cover of perennial and specialized crop	Perennial agriculture offers diversity of habitat and high diversity of insects.	(Lentini et al., 2012; Put et al., 2019; Wickramasinghe et al., 2003)
		Anthropogenic	-	% cover of anthropogenic surfaces including urban, industrial, roads and paved areas	Bat activity decreased in highly anthropogenic habitat such as city centres.	(Hale et al., 2012; Jung & Threlfall, 2016; Krauel & LeBuhn, 2016; Russo & Ancillotto, 2014)
		Harvested forest	+	% cover of harvested forest	Certain harvesting activity may create edge habitat and habitat heterogeneity favourable for bats.	(Law et al., 2016; Patriquin & Barclay, 2003)
Forest	+	Broadleaf Forest	+	% cover of broadleaf or mixed forest	Forest provides diverse foraging habitat and diversity of insects.	(Boughey et al., 2011; Gili et al., 2020; Kniowski & Gehrt, 2014; Pauli et al., 2015)
		Coniferous Forest	+	% cover of coniferous forest	Bat activity is generally lower in coniferous forest than in broadleaf forest, but some species do use coniferous forest especially mature stands.	(Broders et al., 2006; Broders & Forbes, 2004; Kalcounis et al., 1999)
Wetlands	+	Wetlands	+	% cover of wetlands	Wetlands provide high abundance and diversity of insects.	(Balzer et al., 2022; Lookingbill et al., 2010)
Water	+	Water	+	% cover of freshwater	Waterbodies are good foraging habitat for bats.	(Gili et al., 2020; Kniowski & Gehrt, 2014)
Forest edge	+	Forest edge	+	Density of forested edge	Forest edges are good foraging and commuting habitats.	(Kalcounis-Rueppell et al., 2013; Krauel & LeBuhn, 2016; Law et al., 2016)
Water edge	+	Water edge	+	Density of freshwater edge	Water edges are good foraging and commuting habitats.	(Barr et al., 2021; Gorman et al., 2022; Kniowski & Gehrt, 2014)
Distance to roads	+	Distance to roads	+	Minimum Euclidian distance to major roads (national and regional highway)	Roads may act as barriers to bat movements and traffic noise can impact foraging behaviour.	(Bennett et al., 2013; Berthinussen & Altringham, 2012; Finch et al., 2020; Lehrer et al., 2021)
Distance to water	-	Distance to water	-	Minimum Euclidian distance to freshwater body or permanent watercourse	Water is an important resource for drinking and foraging	(Bellamy & Altringham, 2015; Davis & Hitchcock, 1965, 1965; Krauel & LeBuhn, 2016; Lehrer et al., 2021; Pauli et al., 2015; Thomas et al., 2021)

We extracted landscape features using different buffer sizes to test the effect of scale on the selection of maternity roosts and hibernacula. First, we defined a roosting scale (150 m radius) to represent the direct environment of the roosting site (Broders et al., 2006). Second, we defined a core scale (2 km radius) to encompass the average foraging range of reproductive females at maternity roosts (Bergeson et al., 2013; Brigham, 1991; Broders et al., 2006; Henry et al., 2002) and average foraging range at hibernacula (Gallant & Broders, 2015; Muthersbaugh et al., 2019). Third, we defined a foraging scale (5 km radius) to represent the maximum foraging distance of the studied species in the summer (Brigham, 1991; Menzel et al., 2001; Randall et al., 2014). We also included a 10 km scale for hibernaculum analyses as previous studies demonstrated that bats can fly up to 10 km from hibernacula and probably farther (Brack, 2006; Gallant & Broders, 2015).

Our datasets included observations of maternity roosts from 2001 – 2021 and of hibernacula from 1970 to 2021. Landscape changes over this period could bias the results of our study. Therefore, we tested for a correlation between landscapes using the oldest (2012) and the latest (2018) available land use classification of Québec, a time period which encompassed > 80% of the observations in our dataset (i.e., < 20% of observations are from before 2012). Pearson's correlation coefficient was > 0.9 for all landscape cover extracted around maternity roosts (5 km buffer) between 2012 and 2018, except for coniferous forest cover ($r = 0.78$) and harvested forest cover ($r = 0.26$). Similarly, Pearson's r was > 0.9 for landscape cover extracted around hibernacula (10 km buffer). Harvested forest cover is expected to vary among years, but strong correlation among other landscape features suggesting no drastic changes in land use over the timescale of the data available to us.

Statistical Analyses

We used a pseudo-optimized multi-scale approach that considered each landscape feature at a specific scale in univariate models before assessing the final multi-scale model for all analyses (McGarigal et al., 2016). We compared univariate models and selected the scale that fit best as the relevant scale for each landscape feature when building the multi-scale model. In case of equivalent models among all scales, we selected the 2 km scale as the most relevant for maternity roosts and the 10 km scale for hibernacula.

We used generalized linear models with a binomial family to evaluate maternity roost selection for all species combined (with used or available roost as the dependent variable). We measured effect size and significance of landscape features included in the final multi-scale model by odds ratios and 95% confidence intervals for odds ratios. We estimated model performance using McFadden's pseudo-R^2, a ratio between the likelihood of the fitted model and the null model. Pseudo-R^2 values for generalized linear models are generally lower than R^2 values in linear models, and a good rule of thumb suggests that McFadden R^2 values between 0.2 – 0.4 indicate a good fit (McFadden, 1979).

We used linear models to evaluate hibernaculum selection (here evaluated as population sizes) pre-WNS. Population sizes were log transformed before analyses to ensure model assumptions were not violated. We measured effect size of landscape features included in the final multi-scale model using model coefficient estimates and their 95% confidence intervals. We assessed model performance using adjusted R^2. Hibernacula in our dataset experienced drastic population decline post-WNS (mean = 85%; median = 96%). Given the lack of variance, the skewed distribution and the small sample size ($n = 14$), a linear regression analysis was not feasible to evaluate hibernaculum declines related to landscape features. We instead used nonparametric Spearman rank correlation to evaluate the relationship between hibernaculum decline post-WNS and landscape features at all studied scales. Significance threshold was set to $\alpha = 0.05$.

We used the Akaike information criterion corrected for small sample size (AICc; Burnham et al., 2011) for model selection. We used the *MuMin* package (Bartoń, 2022) in R to create a model selection table from full models. We considered all models with ΔAICc < 2.0 as equivalent and we selected the most parsimonious as the best fitted model. As expected, we found strong correlations among landscape features in our analyses. When Pearson correlation coefficient > 0.6 or < -0.6, we computed alternative models keeping apart correlated landscape features separate and selected models with the best fit. All percentage landscape features (% cover) were logit transformed (Warton & Hui, 2011) and all variables were standardized using Z-standardization before analyses.

Results

Maternity Roost Selection

Our final dataset included 196 used maternity roosts (159 southern and 37 northern) reported between 2001 and 2021, with 69 % of roosts having confirmed bat presence between 2018 and 2021. The surroundings of southern maternity roosts were characterized by broadleaf forest, agriculture (annual and perennial combined) and anthropogenic cover (average cover of 31%, 31% and 12% respectively at the 5 km scale; Figure S1.2). Northern used maternity roosts were characterized by coniferous forest, wetland and waterbody cover (average cover of 30%, 21% and 13% respectively at the 5 km scale; Figure S1.2). The proportion of human-modified landscapes (anthropogenic, annual crops, perennial crops and harvested forest combined; Table 1.1) around southern maternity roosts was 20 times higher than around northern maternity roosts. We excluded annual and perennial crop cover for the northern analyses as we observed only a small percentage of those around used and available roosts (mean < 3% at all scales).

In southern Québec, bats selected maternity roosts with higher anthropogenic cover within 150 m (Odds Ratio (OR) = 1.986 ; OR 95% C.I. =[1.495, 2.638]; Table 1.2), and higher water edge density within 2 km (OR = 1.54; OR 95% C.I. =[1.142, 2.076]; Table 1.2), compared to available roosts (Figure 1.2). The final model also indicated that used maternity roosts were closer to water sources (on average 107 m closer; OR= 0.743; OR 95% C.I. =[0.562, 0.983]) and closer to major roads (on average 2,330 m closer; OR=0.063; OR 95% C.I. = [0.009, 0.427]) compared to available buildings roosts (Table 1.2). The model explained 14.2% of the variance in the selection of maternity roosts (Table 1.2). Seven subset models fell within ΔAICc < 2.0, and the most parsimonious model had ΔAICc= 0.969 (Table S1.2). An equivalent model (absolute lowest AICc) also indicated a positive effect of annual crop cover (Table S1.2). Water cover and water edge variables were correlated (Pearson correlation coefficient = 0.65) and were therefore included in separate models.

Table 1.2. Effect of landscape features at their relevant scales on maternity roost selection by bats in southern Québec (Canada). Best fit model output from generalized linear models with binomial family including coefficient estimates (ß), standard error (SE), odds ratio (OR), 95% confidence interval on odds ratio (OR 95% C.I.), and model McFadden Pseudo R^2. All landscape features were standardized prior to analyses and cover landscape features were logit transformed.

Landscape features	**ß**	**SE**	**OR**	**OR 95% C.I.**	**Pseudo R^2**
Anthropogenic (150 m)	0.686	0.145	1.986	1.495, 2.638	0.142
Distance to major roads	-2.769	0.979	0.063	0.009, 0.427	
Distance to water	-0.296	0.143	0.743	0.562, 0.983	
Water edge (2 km)	0.432	0.152	1.54	1.142, 2.076	

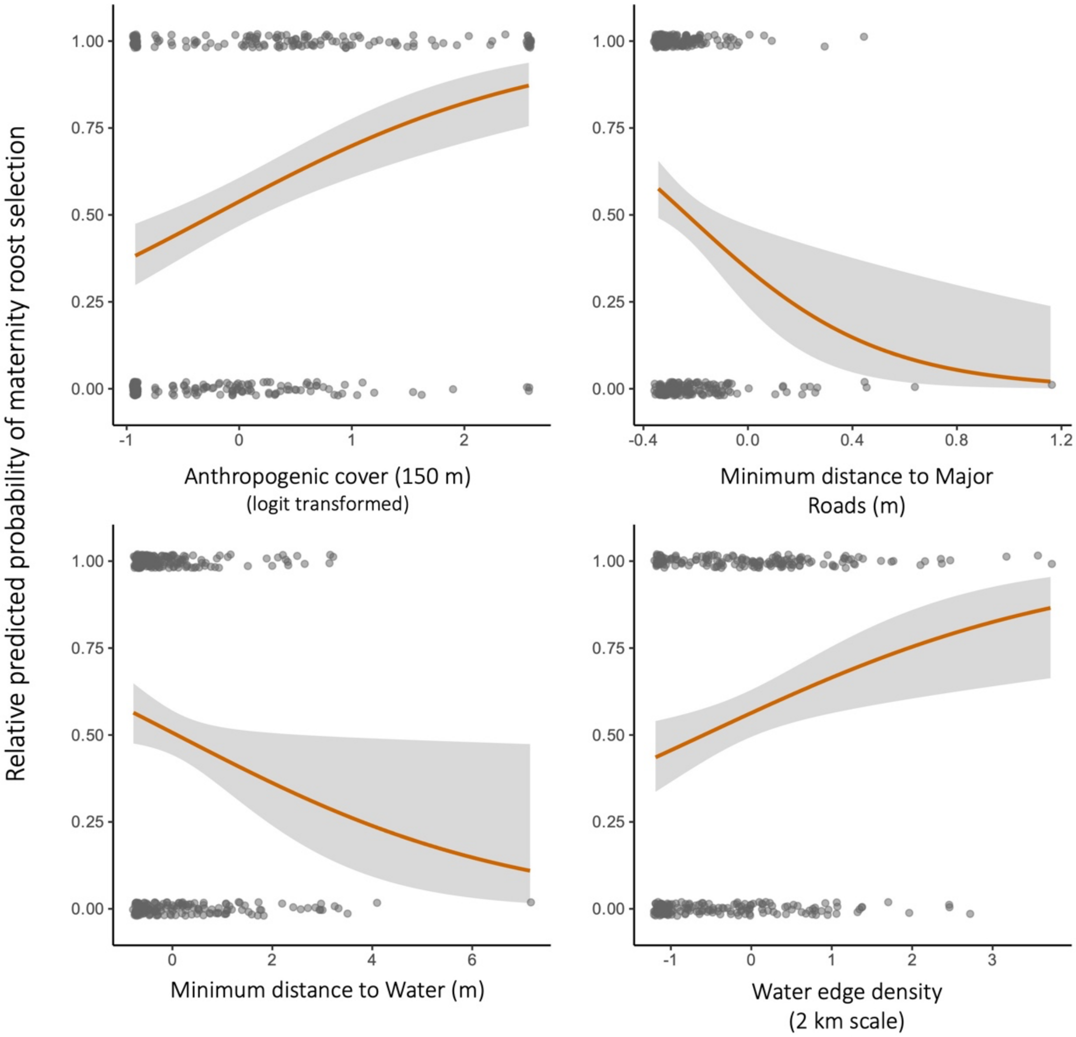

Figure 1.2. Relative predicted probability of summer maternity roost selection by bats in relation to landscape features in southern Québec (Canada). Prediction curves from generalized linear models with binomial family in orange and 95% confidence intervals in grey.

In northern Québec, landscape features could not predict maternity roost selection, as the null model was included in the equivalent models sets. However, among equivalent models, the absolute lowest AICc indicated a positive effect of water cover and water edge density on maternity roost selection (Table S1.3).

Hibernaculum Selection

Our final dataset included 32 hibernacula with population counts pre-WNS (mean = 1 073 bats; min= 2; max=9 300 bats) recorded between 1970 and 2015. About 70% of hibernacula were cavities created following human activities (mining or digging). Forest cover (mixed, broadleaf, and coniferous) dominated the landscape around hibernacula with a mean > 55% at all scales followed by human-modified landscape cover with a mean > 15% at all scales (Figure S1.3). Population size negatively correlated with human-modified cover within 2 km (ß=-1.025; 95% C.I. = [-1.819, -0.23]) and positively correlated with density of forest edges within 10 km (ß=0.828; 95% C.I. = [0.034, 1.622]; Table 1.3; Figure 1.4). This model containing an effect of both human-modified landscape and forest edges was the only one within ΔAICc < 2.0 in the model selection table (Table S1.5). Wetlands cover and forest edge variables were correlated (Pearson correlation coefficient= 0.61) and were therefore included in separate models.

The relationship between hibernaculum population size and forest edge density was biased by one hibernaculum that could be considered an outlier (Figure 1.4). Yet, after removing the hibernaculum with the absolute lowest forest edge density from the analysis, the effect of forest edge density was still present in the equivalent sets of four models although not in the most parsimonious one. The effect of forest edges density on population should thus be interpreted with caution.

Table 1.3. Effect of landscape features at their relevant scales on population size in hibernacula in Québec (Canada) pre-WNS. Best fit model output from linear model including coefficient estimates (ß), standard error (SE), 95% confidence interval on coefficient estimate (95% C.I.) and adjusted R^2. All landscape features were standardized prior to analyses and cover landscape features were logit transformed.

Landscape features	**ß**	**SE**	**95% CI**	**Adjusted R^2**
Human modified (2 km)	-1.025	0.3881	-1.819, -0.231	0.180
Forested edge density (10 km)	0.828	0.3881	0.034, 1.622	

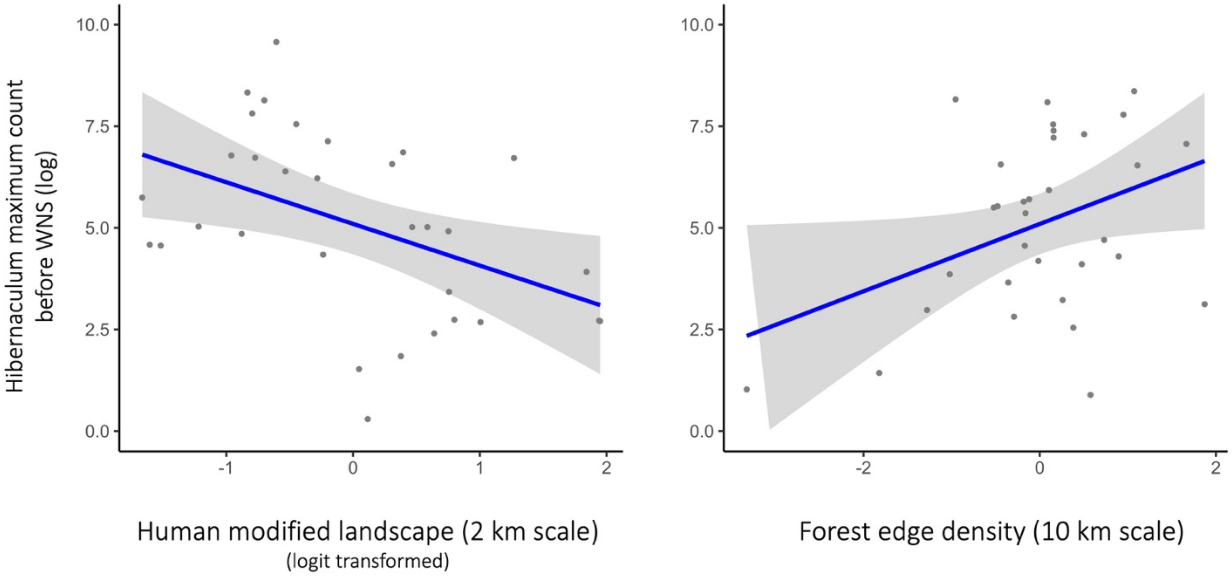

Figure 1.3. Hibernaculum population size pre-WNS in relation to landscape features in Québec (Canada). Prediction curve from linear model in blue and 95% confidence interval in grey.

Our dataset included 14 hibernacula with at least one count pre- and post-WNS enabling us to compute decline (mean = 85% decline; median= 96%; range = 39% — 100%). Hibernacula with the lowest declines had higher water edge density at the 10 km, 5 km and 2 km scales (Table 1.4; Figure 1.4), although this relationship was the strongest at the 2 km scale (Spearman correlation coefficient or ρ=-0.647, p val.=0.012). Similarly, hibernacula with the lowest declines had the highest water cover at the 2 km scale (ρ=-0.6473, p val.=0.008; Table 1.4; Figure 1.4).

Table 1.4. Population decline (%) in hibernacula post-WNS in Québec (Canada) ranked with landscape features at different scales. Spearman correlation coefficient (ρ) and p-value are reported for each landscape feature, tested at the four scales. Distance to water and distance to roads were tested but nonsignificant. Significant results highlighted in grey.

	150 m		**2 km**		**5 km**		**10 km**	
Landscape features	**ρ**	**p val.**	**ρ**	**p val.**	**ρ**	**p val.**	**ρ**	**p val.**
%Forest	0.234	0.421	-0.073	0.805	-0.321	0.263	-0.169	0.563
Forest edge density	-0.202	0.488	0.233	0.422	0.293	0.310	0.246	0.396
%Wetlands	-0.278	0.336	-0.110	0.708	0.282	0.329	0.396	0.161
%Human modified	-0.336	0.240	-0.084	0.776	-0.123	0.675	0.051	0.864
%Water	-0.274	0.342	-0.673	0.008	-0.249	0.391	-0.334	0.242
Water edge density	-0.290	0.315	-0.647	0.012	-0.583	0.029	-0.598	0.024

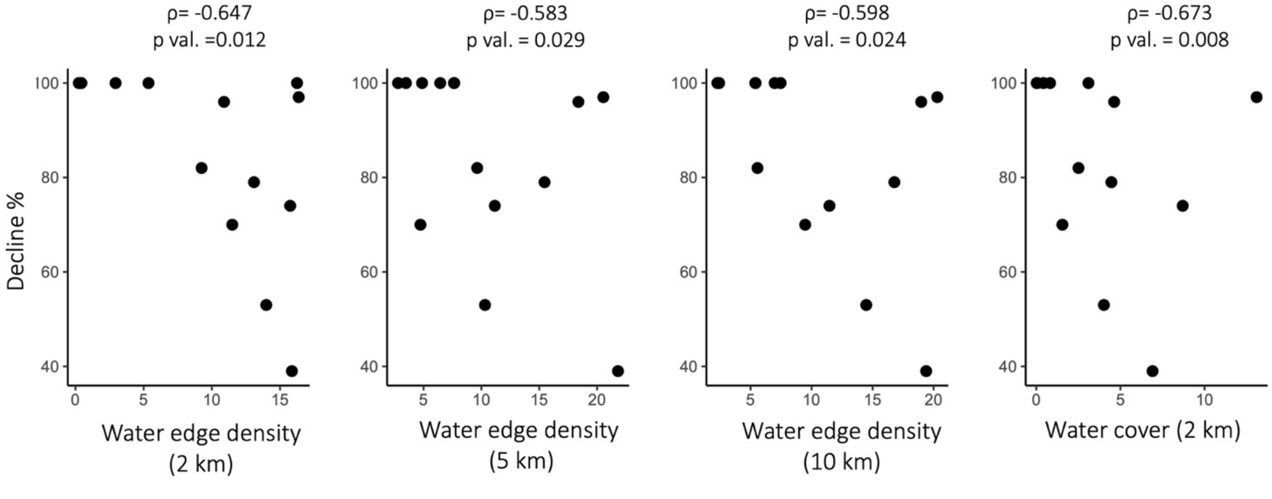

Figure 1.4. Population decline (%) in hibernacula post-WNS in Québec (Canada) in relation to landscape features with nonparametric Spearman's rank correlation coefficient (ρ) and associated p-value (p val.). Only significant relations (p val. < 0.05) shown.

Discussion

Bats are constrained on different levels to exploit habitats in the surroundings of their residences throughout the year (maternity roost or hibernacula). We evaluated the impact of landscape features on the selection of maternity roosts and hibernacula in the context of WNS. Human-modified and natural landscape features affected selection of maternity roosts and hibernacula, although with different effects. Identifying important landscapes around bat residences year-round could complement the protection of the residence itself, enhance population recovery, and contribute to conservation guidelines for bats.

Maternity Roost Selection

Bat foraging behaviour and habitat preferences may differ depending on habitat and prey availability (e.g., Geggie & Fenton, 1985). Consequently, maternity roosts in different landscapes might also have different selection pressures. In our study, we observed a difference in landscape composition around southern and northern maternity roosts, consistent with human activity gradients in Québec (Institut de la statistique du Québec, 2021 ; Jobin et al., 2020). Preferred foraging areas (i.e., waterbodies; Thomas & Jung, 2019) may be more available in northern regions, which could contribute to the weaker landscape effects on maternity roost selection in this region. Anthropogenic areas in the boreal forests may act as refuges for building-roosting bats whereas natural roosts are limited by tree diameters and low temperature (Randall et al., 2014; Thomas & Jung, 2019). Most northern maternity roosts were indeed in small or medium human settlements, but by generating available roosts in the same ecological region, we might have blurred the effect of anthropogenic landscapes on roost selection.

Anthropogenic landscape positively influenced maternity roost selection in southern Québec. In univariate models, the anthropogenic landscape at the smallest scale (150 m) alone could explain maternity roost selection better than any other scales, since 2 km and 5 km scales had ΔAICc>13 and ΔAICc> 20 respectively (Table S1.1). This result might seem contrary to our predictions (Table 1.1), but suggests that bats tolerate anthropogenic landscapes for their roosting sites, while foraging landscapes are a secondary consideration. Many studies on bats roosting in buildings support a decrease in bat foraging activity in urban centers and an increase in natural parks or in outskirts (Avila-Flores & Fenton, 2005; Krauel & LeBuhn, 2016; Thomas & Jung, 2019). Bats might be faced with the trade-off of roosting in buildings that provide better microclimates (Lausen & Barclay, 2006), but with the counter effect of being farther from suitable foraging habitats (Geggie & Fenton, 1985; Russo & Ancillotto, 2014). Similarly, used maternity roosts were closer to major roads than available roosts, denoting a proximity to human settlements. Even though bat activity usually decreases near highways, maternity roosts were on average 3,370 m away from major roads compared to 5,700 m for available roosts, which might be far enough to avoid the negative effects (e.g., noise and barriers to movement; Bennett et al., 2013; Berthinussen & Altringham, 2012). Moreover, this effect could be an artefact of citizen science that tends to produce spatially biased observation towards inhabited areas.

Landscape associated with water are important for insectivorous bats (Gili et al., 2020; Thomas et al., 1990; Walsh & Harris, 1996). Reproductive females have high energy demands and water loss rates during pregnancy and lactation with flight, representing over 60% of daily energy expenditure (Kurta et al., 1989a, 1989b). Choosing roosts close to water and foraging areas during those periods might be a strategy to cope with these challenges (Adams & Hayes, 2008). Water edge is an important feature for bats, providing drinking water, high insect density, and good flight paths to commute, especially when vegetated (Ford et al., 2005; Fukui et al., 2006; Holloway & Barclay, 2000). Consequently, proximity to water sources is also an important predictor of roost selection for many insectivorous bats (Bellamy & Altringham, 2015; Lewis et al., 2022; Schroder et al., 2017).

Hibernaculum Selection pre-WNS and Decline post-WNS

In comparison to maternity roosts, the impact of landscape features on hibernacula has received little attention (but see Wethington et al., 1997), and report mostly on the internal conditions of hibernacula (Glover & Altringham, 2008; McClure et al., 2020; Raesly & Gates, 1987). We provide evidence that land managers should not disregard the impact of surrounding habitat on hibernaculum selection (here evaluated by population size). Indeed, hibernacula with less human-modified landscapes and higher density of forested edge hosted more bats. Consistent with this pattern, *Myotis sodalis* (Miller & Allen, 1928), during the mating season, maximized foraging opportunities by using developed/urban area less than expected and open forest edges more than expected (Brack, 2006).

During mating seasons, bats are less selective of their day roost and use different structures like trees (Brack, 2006; Gallant & Broders, 2015), buildings (Furmankiewicz, 2008; Lowe, 2012), or the hibernaculum itself (Fenton, 1969; Rivers et al., 2006), often switching among days (Brack, 2006; Lowe, 2012). Thus, human modified landscapes might be less attractive to bats during mating and hibernation periods, contrary to the summer when bats might be attracted to potential building roosts in developed areas (de Boer et al., 2013). As foraging activity must be maximized in preparation for hibernation, bats might be less attracted to hibernacula in human-modified landscapes associated with decreased foraging activity (Geggie & Fenton, 1985; Russo & Ancillotto, 2014). This idea is supported by the 2km relevant scale of human-modified landscape (Table S1.4), which corresponds to the radius where foraging and roosting activity is generally highest around hibernacula (Brack, 2006; Gallant & Broders, 2015; Muthersbaugh et al., 2019). In our study, human-modified landscapes also included harvested forest (Table 1.1), a landscape with mixed effects on bats. Harvest activity sometimes enhance the habitat matrix by creating edges, which favour foraging and commuting activity (Krauel & LeBuhn, 2016; Law et al., 2016; Patriquin & Barclay, 2003). Still, harvested forest represented < 2% of the landscape around hibernacula, and therefore likely has only a marginal effect in our study.

In the context of WNS, greater foraging opportunities in the surroundings of hibernacula might enhance fat store deposition pre- and post-hibernation, a key factor for WNS tolerance (Cheng et al., 2019). Declines were lowest at hibernacula with high water edge density and water cover. These features could favour foraging activity close to hibernacula (de Boer et al., 2013; Randall & Broders, 2014) and offset the cost of WNS. Due to small sample size (n=14) and skewed distribution of declines, we could not conduct parametric statistics with this data. Nonetheless, we provide preliminary evidence that protection of habitat surrounding hibernacula could be an effective conservation measure to counter WNS.

Importance of Multi-Species and Multi-Scale Framework

We highlight the opportunity brought by multiple data sources like citizen science and government databases to monitor cryptic species on a large scale. We acknowledge the lack of species-level information in our study and potential spatial bias, a challenge of citizen science data (Dickinson et al., 2010). Indeed, *E. fuscus* is more a generalist species for which habitat might be less of a concern (Agosta, 2002) compare to *M. lucifugus* and *M. septentrionalis* (Broders et al., 2006; Fabianek et al., 2011). However, differentiating those three species without direct access to the colony or acoustics materials is challenging, especially for sites only having historical reports. Yet, understanding multi-species patterns allow to support large-scale conservation plans. Although locations of maternity roosts in our study might be biased towards inhabited areas, those data are concentrated at places where bats might be more vulnerable to habitat loss (Russo and Ancillotto, 2014). Our result and the underlying conservation guidelines should thus be considered in the context of a antrhopogenic landscape matrix.

Implications

Multiple factors can impact selection of maternity roosts and hibernacula, as implied by the relatively low explanatory powers of our models. Indeed, buildings and caves are not all equally good for bats, and choosing roosts/hibernacula with optimal physical structure can increase fitness and tolerance to WNS (Glover & Altringham, 2008; Neubaum et al., 2010; Verant et al., 2012; Voigt et al., 2016). While conservation guidelines need to incorporate the protection of residences, we demonstrate the significance of surrounding landscape features. For maternity roosts, we recommend the protection of natural water edges within 2 km, especially in cities, where roost availability is high but foraging habitat scarce. For hibernacula, we suggest limiting human—modified landscape development and enhancing the protection of different forest structures to promote edge habitat within at least 10 km.

References

Adams, R. A., & Hayes, M. A. (2008). Water Availability and Successful Lactation by Bats as Related to Climate Change in Arid Regions of Western North America. *Journal of Animal Ecology*, *77*(6), 1115–1121.

Agosta, S. J. (2002). Habitat use, diet and roost selection by the big brown bat (Eptesicus fuscus) in North America: A case for conserving an abundant species. *Mammal Review*, *32*(3), 179–198. https://doi.org/10.1046/j.1365-2907.2002.00103.x

Avila-Flores, R., & Fenton, M. B. (2005). Use of spatial features by foraging insectivorous bats in a large urban landscape. *Journal of Mammalogy*, *86*(6), 1193–1204. https://doi.org/10.1644/04-MAMM-A-085R1.1

Balzer, E. W., McBurney, T. S., & Broders, H. G. (2022). Little brown Myotis roosts are spatially associated with foraging resources on Prince Edward Island. *Wildlife Society Bulletin*. https://doi.org/10.1002/wsb.1405

Barr, E. L., Silvis, A., Armstrong, M. P., & Ford, W. M. (2021). White-nose Syndrome and Environmental Correlates to Landscape-Scale Bat Presence. *Wildlife Society Bulletin*, *45*(3), 410–421. https://doi.org/10.1002/wsb.1215

Bartoń, K. (2022). *MuMIn: Multi-Model Inference* (1.47.1).

Bellamy, C., & Altringham, J. (2015). Predicting species distributions using record centre data: Multi-scale modelling of habitat suitability for bat roosts. *PLoS ONE*, *10*(6). https://doi.org/10.1371/journal.pone.0128440

Bennett, V. J., Sparks, D. W., & Zollner, P. A. (2013). Modeling the indirect effects of road networks on the foraging activities of bats. *Landscape Ecology*, *28*(5), 979–991. https://doi.org/10.1007/s10980-013-9874-0

Bergeson, S. M., Carter, T. C., & Whitby, M. D. (2013). Partitioning of foraging resources between sympatric Indiana and little brown bats. *Journal of Mammalogy*, *94*(6), 1311–1320. https://doi.org/10.1644/12-MAMM-A-311

Berthinussen, A., & Altringham, J. (2012). The effect of a major road on bat activity and diversity. *Journal of Applied Ecology*, *49*(1), 82–89. https://doi.org/10.1111/j.1365-2664.2011.02068.x

Boughey, K. L., Lake, I. R., Haysom, K. A., & Dolman, P. M. (2011). Effects of landscape-scale broadleaved woodland configuration and extent on roost location for six bat species across the UK. *Biological Conservation*, *144*(9), 2300–2310. https://doi.org/10.1016/j.biocon.2011.06.008

Boyles, J. G., & Willis, C. K. (2010). Could localized warm areas inside cold caves reduce mortality of hibernating bats affected by white-nose syndrome? *Frontiers in Ecology and the Environment*, *8*(2), 92–98. https://doi.org/10.1890/080187

Brack, V. (2006). Autumn Activity of Myotis sodalis (Indiana Bat) in Bland County, Virginia. *Northeastern Naturalist*, *13*(3), 421–434. https://doi.org/10.1656/1092-6194(2006)13[421:AAOMSI]2.0.CO;2

Brigham, R. M. (1991). Flexibility in foraging and roosting behaviour by the big brown bat (Eptesicus fuscus). *Canadian Journal of Zoology*, *69*(1), 117–121. https://doi.org/10.1139/z91-017

Broders, H. G., & Forbes, G. J. (2004). Interspecific and Intersexual Variation in Roost-Site Selection of Northern Long-Eared and Little Brown Bats in the Greater Fundy National Park Ecosystem. *The Journal of Wildlife Management*, *68*(3), 602–610.

Broders, H. G., Forbes, G. J., Woodley, S., & Thompson, I. D. (2006). Range Extent and Stand Selection for Roosting and Foraging in Forest-Dwelling Northern Long-Eared Bats and Little Brown Bats in the Greater Fundy Ecosystem, New Brunswick. *Journal of Wildlife Management*, *70*(5), 1174–1184. https://doi.org/10.2193/0022-541x(2006)70[1174:reassf]2.0.co;2

Burnham, K. P., Anderson, D. R., & Huyvaert, K. P. (2011). AIC model selection and multimodel inference in behavioral ecology: Some background, observations, and comparisons. *Behavioral Ecology and Sociobiology*, *65*(1), 23–35. https://doi.org/10.1007/s00265-010-1029-6

Cable, A. B., O'Keefe, J. M., Deppe, J. L., Hohoff, T. C., Taylor, S. J., & Davis, M. A. (2021). Habitat suitability and connectivity modeling reveal priority areas for Indiana bat (Myotis sodalis) conservation in a complex habitat mosaic. *Landscape Ecology*, *36*(1), 119–137. https://doi.org/10.1007/s10980-020-01125-2

Cheng, T. L., Gerson, A., Moore, M. S., Reichard, J. D., DeSimone, J., Willis, C. K. R., Frick, W. F., & Kilpatrick, A. M. (2019). Higher fat stores contribute to persistence of little brown bat populations with white-nose syndrome. *Journal of Animal Ecology*, *88*(4), 591–600. https://doi.org/10.1111/1365-2656.12954

Cheng, T. L., Reichard, J. D., Coleman, J. T. H., & Weller, T. J. (2021). The scope and severity of white-nose syndrome on hibernating bats in North America. *Conservation Biology*, *35*, 1586–1597. https://doi.org/DOI: 10.1111/cobi.13739

Davis, W. H., & Hitchcock, H. (1965). Biology and migration of the bat, Myotis lucifugus , in New England. *Journal of Mammalogy*, *46*(2), 296–313.

de Boer, W. F., de Koppel, S. van, de Knegt, H. J., & Dekker, J. J. A. (2013). Hibernation site requirements of bats in man-made hibernacula in a spatial context. *Ecological Applications*, *23*(2), 502–514. https://doi.org/10.1890/1051-0761-23.2.502

Dekeukeleire, D., Janssen, R., Haarsma, A. J., Bosch, T., & Van Schaik, J. (2016). Swarming Behaviour, Catchment Area and Seasonal Movement Patterns of the Bechstein's Bats: Implications for Conservation. *Acta Chiropterologica*, *18*(2), 349–358. https://doi.org/10.3161/15081109ACC2016.18.2.004

Dickinson, J. L., Zuckerberg, B., & Bonter, D. N. (2010). Citizen Science as an Ecological Research Tool: Challenges and Benefits. *Annual Review of Ecology, Evolution, and Systematics*, *41*(1), 149–172. https://doi.org/10.1146/annurev-ecolsys-102209-144636

Donaldson, L., Wilson, R. J., & Maclean, I. M. D. (2017). Old concepts, new challenges: Adapting landscape-scale conservation to the twenty-first century. *Biodiversity and Conservation*, *26*(3), 527–552. https://doi.org/10.1007/s10531-016-1257-9

Fabianek, F., Gagnon, D., & Delorme, M. (2011). Bat distribution and activity in Montrél Island green spaces: Responses to multi-scale habitat effects in a densely urbanized area. *Ecoscience*, *18*(1), 9–17. https://doi.org/10.2980/18-1-3373

Faure-Lacroix, J., Desrochers, A., Imbeau, L., & Simard, A. (2020). Long-term changes in bat activity in Quebec suggest climatic responses and summer niche partitioning associated with white-nose syndrome. *Ecology and Evolution*, *10*(12), 5226–5239. https://doi.org/10.1002/ece3.6194

Fenton, M. B. (1969). Summer activity of M. lucifugus at hibernacula in Ontario and Quebec. *Canadian Journal of Zoology*, *47*, 597–602.

Finch, D., Schofield, H., & Mathews, F. (2020). Traffic noise playback reduces the activity and feeding behaviour of free-living bats. *Environmental Pollution*, *263*. https://doi.org/10.1016/j.envpol.2020.114405

Fontaine, A. (2021). *Citizen science and development of innovative tools to improve conservation of threatened bats*. McGill University.

Ford, W. M., Menzel, M. A., Rodrigue, J. L., Menzel, J. M., & Johnson, J. B. (2005). Relating bat species presence to simple habitat measures in a central Appalachian forest. *Biological Conservation*, *126*(4), 528–539. https://doi.org/10.1016/j.biocon.2005.07.003

Frick, W. F., Dzal, Y. A., Jonasson, K. A., Whitby, M. D., Adams, A. M., Long, C., Depue, J. E., Newman, C. M., Willis, C. K. R., & Cheng, T. L. (2023). Bats increased foraging activity at experimental prey patches near hibernacula. *Ecological Solutions and Evidence*, *4*(1), 2688-8319.12217. https://doi.org/10.1002/2688-8319.12217

Frick, W. F., Johnson, E., Cheng, T. L., Lankton, J. S., Warne, R., Dallas, J., Parise, K. L., Foster, J. T., Boyles, J. G., & McGuire, L. P. (2022). Experimental inoculation trial to determine the effects of temperature and humidity on White-nose Syndrome in hibernating bats. *Scientific Reports*, *12*(1), 971. https://doi.org/10.1038/s41598-022-04965-x

Fraser, E. E. and McGuire L. P. (2023) Prehibernation swarming in temperate bats: a critical transition between summer activity and hibernation. *Canadian Journal of Zoology*. https://doi.org/10.1139/cjz-2022-0129

Frick, W. F., Kingston, T., & Flanders, J. (2019). A review of the major threats and challenges to global bat conservation. *Annals of the New York Academy of Sciences*. https://doi.org/10.1111/nyas.14045 CITATIONS

Frick, W. F., Pollock, J. F., Hicks, A. C., Langwig, K. E., Reynolds, D. S., Turner, G. G., Butchkoski, C. M., & Kunz, T. H. (2010). An emerging disease causes regional population collapse of a common North American bat species. *Science*, *329*(5992), 679–682. https://doi.org/10.1126/science.1188594

Fukui, D., Murakami, M., Nakano, S., & Aoi, T. (2006). Effect of emergent aquatic insects on bat foraging in a riparian forest. *Journal of Animal Ecology*, *75*(6), 1252–1258. https://doi.org/10.1111/j.1365-2656.2006.01146.x

Furmankiewicz, J. (2008). Population size, catchment area, and sex-influenced differences in autumn and spring swarming of the brown long-eared bat (Plecotus auritus). *Canadian Journal of Zoology*, *86*(3), 207–216. https://doi.org/10.1139/Z07-134

Gallant, A. J., & Broders, H. G. (2015). Body condition explains little of the interindividual variation in the swarming behaviour of adult male little brown myotis (*Myotis lucifugus*) in Nova Scotia, Canada. *Canadian Journal of Zoology*, *93*(6), 469–476. https://doi.org/10.1139/cjz-2014-0249

Garbino, G. S. T., Feijó, A., Beltrão-Mendes, R., & Da Rocha, P. A. (2021). Evolution of litter size in bats and its influence on longevity and roosting ecology. *Biological Journal of the Linnean Society*, *132*(3), 676–684. https://doi.org/10.1093/biolinnean/blaa203

Geggie, J. F., & Fenton, M. B. (1985). A comparison of foraging by *Eptesicus fuscus* (Chiroptera: Vespertilionidae) in urban and rural environments. *Canadian Journal of Zoology*, *63*(2), 263–266. https://doi.org/10.1139/z85-040

Gili, F., Newson, S. E., Gillings, S., Chamberlain, D. E., & Border, J. A. (2020). Bats in urbanising landscapes: Habitat selection and recommendations for a sustainable future. *Biological Conservation*, *241*. https://doi.org/10.1016/j.biocon.2019.108343

Glover, A. M., & Altringham, J. D. (2008). Cave selection and use by swarming bat species. *Biological Conservation*, *141*(6), 1493–1504. https://doi.org/10.1016/j.biocon.2008.03.012

Google. (2022). *Google satelite imagery*. https://www.google.com/maps/@51.5623841,-72.4437617,1945570m/data=!3m1!1e3

Gorman, K., Deeley, S., Barr, E., Freeze, S., Kalen, N., Muthersbaugh, M., & Ford, W. (2022). Broad-scale geographic and temporal assessment of northern long-eared bat (Myotis septentrionalis) maternity colony-landscape association. *Endangered Species Research*, *47*, 119–130. https://doi.org/10.3354/esr01170

Species at Risk Act, (2002). https://laws-lois.justice.gc.ca/eng/acts/S-15.3/FullText.html

Government of Canada. (2019). *Lakes, Rivers and Glaciers in Canada—CanVec Series—Hydrographic Features*. https://open.canada.ca/data/en/dataset/9d96e8c9-22fe-4ad2-b5e8-94a6991b744b

Hale, J. D., Fairbrass, A. J., Matthews, T. J., & Sadler, J. P. (2012). Habitat composition and connectivity predicts bat presence and activity at foraging sites in a large uk conurbation. *PLoS ONE*, *7*(3). https://doi.org/10.1371/journal.pone.0033300

Henry, M. (2001). *Étude de l'écologie d'une population de petites chauves-souris brunes (Myotis Lucifugus Leconte) en vue d'un programme de conservation*. Sherbrooke University.

Henry, M., Thomas, D. W., Vaudry, R., & Carrier, M. (2002). Foraging distances and home range of pregnant and lactating little brown bats (Myotis lucifugus). *Journal of Mammalogy*, *83*(3), 767–774. https://doi.org/10.1644/1545-1542(2002)083<0767:FDAHRO>2.0.CO;2

Hesselbarth, M. H. K., Sciaini, M., With, K. A., Wiegand, K., & Nowosad, J. (2019). landscapemetrics: An open-source R tool to calculate landscape metrics. *Ecography*, *42*(10), 1648–1657. https://doi.org/10.1111/ecog.04617

Holloway, G. L., & Barclay, R. M. (2000). Importance of prairie riparian zones to bats in southeastern Alberta. *Écoscience*, *7*(2), 115–122. https://doi.org/10.1080/11956860.2000.11682579

Hoyt, J. R., Kilpatrick, A. M., & Langwig, K. E. (2021). Ecology and impacts of white-nose syndrome on bats. *Nature Reviews Microbiology*, *19*(3), 196–210. https://doi.org/10.1038/s41579-020-00493-5

Institut de la statistique du Québec. (2021). *Le Québec chiffres en main 2021* (p. 74).

Jobin, B., Gratton, L., Côté, M.-J., Pfister, O., Lachance, D., Mingelbier, M., Blais, D., Blais, A., & Leclair, D. (2020). L'atlas des territoires d'intérêt pour la conservation dans les basses-terres du Saint-Laurent: Un outil pour orienter la conservation des milieux naturels dans le sud du Québec. *Le Naturaliste canadien*, *144*(2), 47–64. https://doi.org/10.7202/1073990ar

Johnson, C. J., Nielsen, E., Merrill, E. H., Mcdonald, T. L., & Boyce, M. S. (2006). Resource Selection Functions Based on Use–Availability Data: Theoretical Motivation and Evaluation Methods. *Journal of Wildlife Management*, *70*(2), 347–357. https://doi.org/10.2193/0022-541x(2006)70[347:rsfbou]2.0.co;2

Jonasson, K. A., & Willis, C. K. R. (2011). Changes in Body Condition of Hibernating Bats Support the Thrifty Female Hypothesis and Predict Consequences for Populations with White-Nose Syndrome. *PLoS ONE*, *6*(6), e21061. https://doi.org/10.1371/journal.pone.0021061

Jung, K., & Threlfall, C. G. (2016). Urbanisation and Its Effects on Bats—A Global Meta-Analysis. In C. C. Voigt & T. Kingston (Eds.), *Bats in the Anthropocene: Conservation of Bats in a Changing World* (pp. 13–33). Springer International Publishing. https://doi.org/10.1007/978-3-319-25220-9_2

Kalcounis, M. C., Hobson, K. A., Brigham, R. M., & Hecker, K. R. (1999). Bat Activity in the Boreal Forest: Importance of Stand Type and Vertical Strata. *Journal of Mammalogy*, *80*(2), 673–682. https://doi.org/10.2307/1383311

Kalcounis-Rueppell, M. C., Briones, K. M., Homyack, J. A., Petric, R., Marshall, M. M., & Miller, D. A. (2013). Hard forest edges act as conduits, not filters, for bats. *Wildlife Society Bulletin*, *37*(3), 571–576. https://doi.org/10.1002/wsb.289

Kniowski, A. B., & Gehrt, S. D. (2014). Home range and habitat selection of the Indiana bat in an agricultural landscape. *Journal of Wildlife Management*, *78*(3), 503–512. https://doi.org/10.1002/jwmg.677

Krauel, J. J., & LeBuhn, G. (2016). Patterns of bat distribution and foraging activity in a highly urbanized temperate environment. *PLoS ONE*, *11*(12), 1–18. https://doi.org/10.1371/journal.pone.0168927

Kunz, T. H., de Torrez, E. B., Bauer, D., Lobova, T., & Fleming, T. H. (2011). Ecosystem services provided by bats. *Annals of the New York Academy of Sciences*, *1223*(1), 1–38. https://doi.org/10.1111/j.1749-6632.2011.06004.x

Kurta, A., Bell, G. P., Nagy, K. A., & Kunz, T. H. (1989a). Energetics of pregnancy and lactation in free-ranging little brown bats (Myotis lucifugus). *Physiological Zoology*, *62*(3), 804–818. https://doi.org/10.1086/physzool.62.3.30157928

Kurta, A., Bell, G. P., Nagy, K. A., & Kunz, T. H. (1989b). Water balance of free-ranging little brown bats (*Myotis lucifugus*) during pregnancy and lactation. *Canadian Journal of Zoology*, *67*(10), 2468–2472. https://doi.org/10.1139/z89-348

Langwig, K. E., Hoyt, J. R., Parise, K. L., Frick, W. F., Foster, J. T., & Kilpatrick, A. M. (2017). Resistance in persisting bat populations after white-nose syndrome invasion. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *372*(1712), 20160044. https://doi.org/10.1098/rstb.2016.0044

Lausen, C. L., & Barclay, R. M. R. (2006). Benefits of living in a building: Big brown bats (Eptesicus fuscus) in rocks versus buildings. *Journal of Mammalogy*, *87*(2), 362–370. https://doi.org/10.1644/05-MAMM-A-127R1.1

Law, B., Park, K. J., & Lacki, M. J. (2016). Insectivorous Bats and Silviculture: Balancing Timber Production and Bat Conservation. In C. C. Voigt & T. Kingston (Eds.), *Bats in the Anthropocene: Conservation of Bats in a Changing World* (pp. 105–150). Springer International Publishing. https://doi.org/10.1007/978-3-319-25220-9_5

Lehrer, E. W., Gallo, T., Fidino, M., Kilgour, R. J., Wolff, P. J., & Magle, B. (2021). Landscape and Urban Planning Urban bat occupancy is highly influenced by noise and the location of water: Considerations for nature-based urban planning. *Landscape and Urban Planning*, *210*. https://doi.org/10.1016/j.landurbplan.2021.104063

Lentini, P. E., Gibbons, P., Fischer, J., Law, B., Hanspach, J., & Martin, T. G. (2012). Bats in a Farming Landscape Benefit from Linear Remnants and Unimproved Pastures. *PLoS ONE*, *7*(11). https://doi.org/10.1371/journal.pone.0048201

Lewis, M. A., Turner, G. G., Scafini, M. R., & Johnson, J. S. (2022). Seasonal roost selection and activity of a remnant population of northern myotis in Pennsylvania. *PLoS ONE*, *17*(7), e0270478. https://doi.org/10.1371/journal.pone.0270478

Lookingbill, T. R., Elmore, A. J., Engelhardt, K. A. M., Churchill, J. B., Edward Gates, J., & Johnson, J. B. (2010). Influence of wetland networks on bat activity in mixed-use landscapes. *Biological Conservation*, *143*(4), 974–983. https://doi.org/10.1016/j.biocon.2010.01.011

Lowe, A. J. (2012). *Swarming behaviour and fall roost-use of little brown (Myotis lucifugus), and northern long-eared bats (Myotis septentrionalis) in Nova Scotia, Canada*. St. Mary's University.

Mackie, I. J., & Racey, P. A. (2007). Habitat use varies with reproductive state in noctule bats (Nyctalus noctula): Implications for conservation. *Biological Conservation*, *140*(1–2), 70–77. https://doi.org/10.1016/j.biocon.2007.07.031

Manly, B. F. J., McDonald, L. L., Thomas, D. L., McDonald, T. L., & Erickson, W. P. (2002). *Resource Selection by Animals: Statistical Design and Analysis for Field Studies* (Second Edition). Kluwer Academic Publisher.

McClure, M. L., Crowley, D., Haase, C. G., McGuire, L. P., Fuller, N. W., Hayman, D. T. S., Lausen, C. L., Plowright, R. K., Dickson, B. G., & Olson, S. H. (2020). Linking surface and subterranean climate: Implications for the study of hibernating bats and other cave dwellers. *Ecosphere*, *11*(10). https://doi.org/10.1002/ecs2.3274

McFadden, D. (1979). Quantitative Methdos for Analysing Travel Behaviour of Individuals: Some Recent Developments. In *Behavioural Travel Modelling* (David A. Hensher and Peter R. Stopher, p. 872).

McGarigal, K., Wan, H. Y., Zeller, K. A., Timm, B. C., & Cushman, S. A. (2016). Multi-scale habitat selection modeling: A review and outlook. *Landscape Ecology*, *31*(6), 1161–1175. https://doi.org/10.1007/s10980-016-0374-x

McGuire, L. P., Fenton, M. B., & Guglielmo, C. G. (2009). Effect of age on energy storage during prehibernation swarming in little brown bats (Myotis lucifugus). *Canadian Journal of Zoology*, *87*(6), 515–519. https://doi.org/10.1139/Z09-041

Menzel, M. A., Carter, T. C., Jablonowski, L. R., Mitchell, B. L., Menzel, J. M., & Chapman, B. R. (2001). Home Range Size and Habitat Use of Big Brown Bats (Eptesicus fuscus) in a Maternity Colony Located on a Rural-Urban Interface in the Southeast. *The Journal of the Elisha Mitchell Scientific Society*, *117*(1), 36–45.

ministère de l'Environnement et de la Lutte contre les changements climatiques. (2018). *Utilisation du territoire*. https://www.donneesquebec.ca/recherche/dataset/utilisation-du-territoire

Muthersbaugh, M. S., Ford, W. M., Silvis, A., & Powers, K. E. (2019). Activity Patterns of Cave-Dwelling Bat Species during Pre-Hibernation Swarming and Post-Hibernation Emergence in the Central Appalachian. *Diversity*, *11*(159), 1–24.

Neighbourhood Bat Watch. (2021). *Neighbourhood Bat Watch*. https://batwatch.ca/

Neubaum, D. J., Wilson, K. R., & O'Shea, T. J. (2010). Urban Maternity-Roost Selection by Big Brown Bats in Colorado. *The Journal of Wildlife Management*, *71*(3), 728–736.

Oakeley, S. F., & Jones, G. (1998). Habitat around maternity roosts of the 55 kHz phonic type of pipistrelle bats (Pipistrellus pipistrellus). *Journal of Zoology*, *245*(2), 222–228. https://doi.org/10.1017/S095283699826609X

Olsson, O., & Bolin, A. (2014). A model for habitat selection and species distribution derived from central place foraging theory. *Oecologia*, *175*(2), 537–548. https://doi.org/10.1007/s00442-014-2931-9

Orians & Pearson. (1979). On the theory of central place foraging. In J. Horn, R. Srairs, & R. D. Mitchell (Eds.), *Analysis of Ecological Systems* (pp. 155–177). Ohio State Press.

Patriquin, K. J., & Barclay, R. M. R. (2003). Foraging by bats in cleared, thinned and unharvested boreal forest. *Journal of Applied Ecology*, *40*(4), 646–657. https://doi.org/10.1046/j.1365-2664.2003.00831.x

Pauli, B. P., Badin, H. A., Haulton, G. S., Zollner, P. A., & Carter, T. C. (2015). Landscape features associated with the roosting habitat of Indiana bats and northern long-eared bats. *Landscape Ecology*, *30*(10), 2015–2029. https://doi.org/10.1007/s10980-015-0228-y

Put, J. E., Fahrig, L., & Mitchell, G. W. (2019). Bats respond negatively to increases in the amount and homogenization of agricultural land cover. *Landscape Ecology*, *34*(8), 1889–1903. https://doi.org/10.1007/s10980-019-00855-2

R Studio Team. (2022). *RStudio: Integrated Development Environment for R.* http://www.rstudio.com/

Raesly, R. L., & Gates, J. E. (1987). Winter Habitat Selection by North Temperate Cave Bats. *American Midland Naturalist*, *118*(1), 15. https://doi.org/10.2307/2425624

Randall, J., & Broders, H. G. (2014). Identification and Characterization of Swarming Sites used by Bats in Nova Scotia, Canada. *Acta Chiropterologica*, *16*(1), 109–116. https://doi.org/10.3161/150811014X683327

Randall, L. A., Jung, T. S., & Barclay, R. M. (2014). Roost-Site Selection and Movements of Little Brown Myotis (Myotis lucifugus) in Southwestern Yukon. *Northwestern Naturalist*, *95*(3), 312–317. https://doi.org/10.1898/13-02.1

Reeder, D. A. M., Frank, C. L., Turner, G. G., Meteyer, C. U., Kurta, A., Britzke, E. R., Vodzak, M. E., Darling, S. R., Stihler, C. W., Hicks, A. C., Jacob, R., Grieneisen, L. E., Brownlee, S. A., Muller, L. K., & Blehert, D. S. (2012). Frequent arousal from hibernation linked to severity of infection and mortality in bats with white-nose syndrome. *PLoS ONE*, *7*(6). https://doi.org/10.1371/journal.pone.0038920

Rivers, N. M., Butlin, R. K., & Altringham, J. D. (2006). Autumn swarming behaviour of Natterer's bats in the UK: Population size, catchment area and dispersal. *Biological Conservation*, *127*(2), 215–226. https://doi.org/10.1016/j.biocon.2005.08.010

Rosenberg, D. K., & McKelvey, K. S. (1999). Estimation of Habitat Selection for Central-Place Foraging Animals. *The Journal of Wildlife Management*, *63*(3), 1028–1038. https://doi.org/10.2307/3802818

Russo, D., & Ancillotto, L. (2014). Sensitivity of bats to urbanization: A review. *Mammalian Biology*, *80*(3), 205–212. https://doi.org/10.1016/j.mambio.2014.10.003

Schroder, E. S., Ekanayake, D. B., & Romano, S. P. (2017). Indiana bat maternity roost habitat preference within Midwestern United States upland Oak-Hickory (Quercus-Carya) forests. *Forest Ecology and Management*, *404*, 65–74. https://doi.org/10.1016/j.foreco.2017.08.032

Soper, K. D., & Fenton, M. B. (2007). Availability of building roosts for bats in four towns in southwestern Ontario, Canada. *Acta Chiropterologica*, *9*(2), 542–546. https://doi.org/10.3161/1733-5329(2007)9[542:AOBRFB]2.0.CO;2

Thomas, D. W., Dorais, M., & Bergeron, J.-M. (1990). Winter Energy Budgets and Cost of Arousals for Hibernating Little Brown Bats, Myotis lucifugus. *Journal of Mammalogy*, *71*(3), 475–479. https://doi.org/10.2307/1381967

Thomas, J. P., & Jung, T. S. (2019). Life in a northern town: Rural villages in the boreal forest are islands of habitat for an endangered bat. *Ecosphere*, *10*(1). https://doi.org/10.1002/ecs2.2563

Thomas, J. P., Kukka, P. M., Benjamin, J. E., Barclay, R. M. R., Johnson, C. J., Schmiegelow, F. K. A., & Jung, T. S. (2021). Foraging habitat drives the distribution of an endangered bat in an urbanizing boreal landscape. *Ecosphere*, *12*(3). https://doi.org/10.1002/ecs2.3457

Turner, G. G., Sewall, B. J., Scafini, M. R., Lilley, T. M., Bitz, D., & Johnson, J. S. (2022). Cooling of bat hibernacula to mitigate white-nose syndrome. *Conservation Biology*, *36*(2), e13803. https://doi.org/10.1111/cobi.13803

U.S. Geological Survey. (2022). *EarthExplorer*. https://earthexplorer.usgs.gov/

Verant, M. L., Boyles, J. G., Waldrep, W., Wibbelt, G., & Blehert, D. S. (2012). Temperature-Dependent Growth of Geomyces destructans, the Fungus That Causes Bat White-Nose Syndrome. *PLoS ONE*, *7*(9), e46280. https://doi.org/10.1371/journal.pone.0046280

Voigt, C. C., Phelps, K. L., Aguirre, L. F., Corrie Schoeman, M., Vanitharani, J., & Zubaid, A. (2016). Bats and Buildings: The Conservation of Synanthropic Bats. In C. C. Voigt & T. Kingston (Eds.), *Bats in the Anthropocene: Conservation of Bats in a Changing World* (pp. 427–462). Springer International Publishing. https://doi.org/10.1007/978-3-319-25220-9_14

Walsh, A. L., & Harris, S. (1996). Foraging Habitat Preferences of Vespertilionid Bats in Britain. *British Ecological Society*, *33*(3), 508–518.

Warton, D. I., & Hui, F. K. C. (2011). The arcsine is asinine: The analysis of proportions in ecology. *Ecology*, *92*(1), 3–10.

Wethington, T. A., Leslie, D. M., Gregory, M. S., & Wethington, M. K. (1997). Vegetative structure and land use relative to cave selection by endangered Ozark big-eared bats (Corynorhinus townsendii ingens). *Southwestern Naturalist*, *42*(2), 177–181.

White-Nose Syndrome response team. (2022). *Where is WNS Now?* https://www.whitenosesyndrome.org/where-is-wns

Wickramasinghe, L. P., Harris, S., Jones, G., & Vaughan, N. (2003). Bat activity and species richness on organic and conventional farms: Impact of agricultural intensification. *Journal of Applied Ecology*, *40*, 984–993.

Wilkinson, G. S., & Adams, D. M. (2019). Recurrent evolution of extreme longevity in bats. *Biology Letters*, *15*(4), 20180860. https://doi.org/10.1098/rsbl.2018.0860

CHAPTER 1 : SUPPLEMENTARY MATERIALS

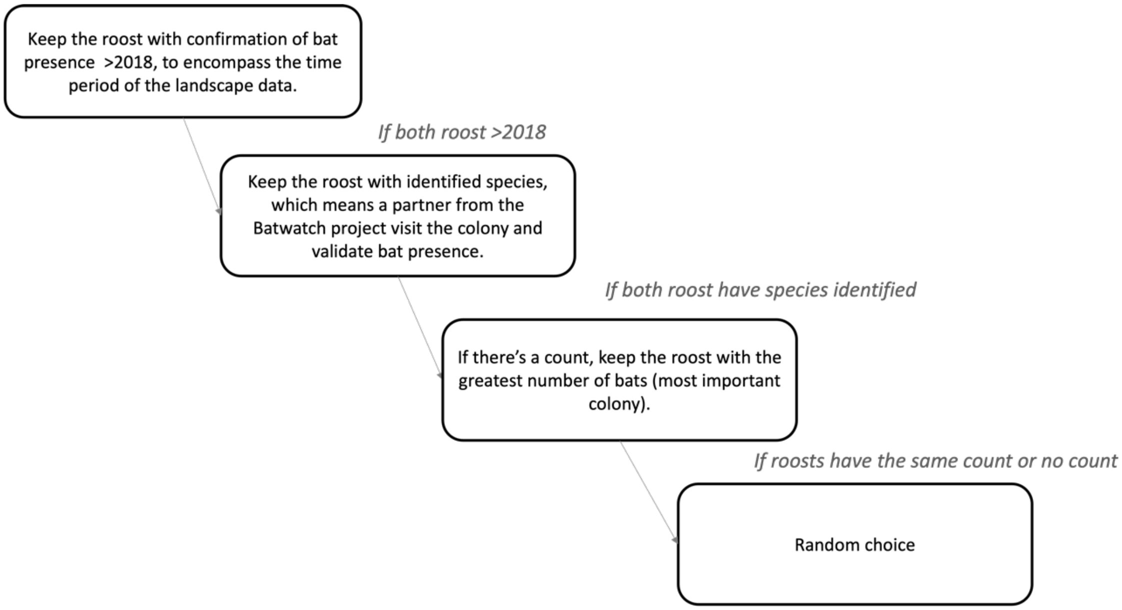

Figure S1.1. Decision tree to choose which roost to keep in between maternity roost overlapping >30% within a 5,000 m buffer in Québec

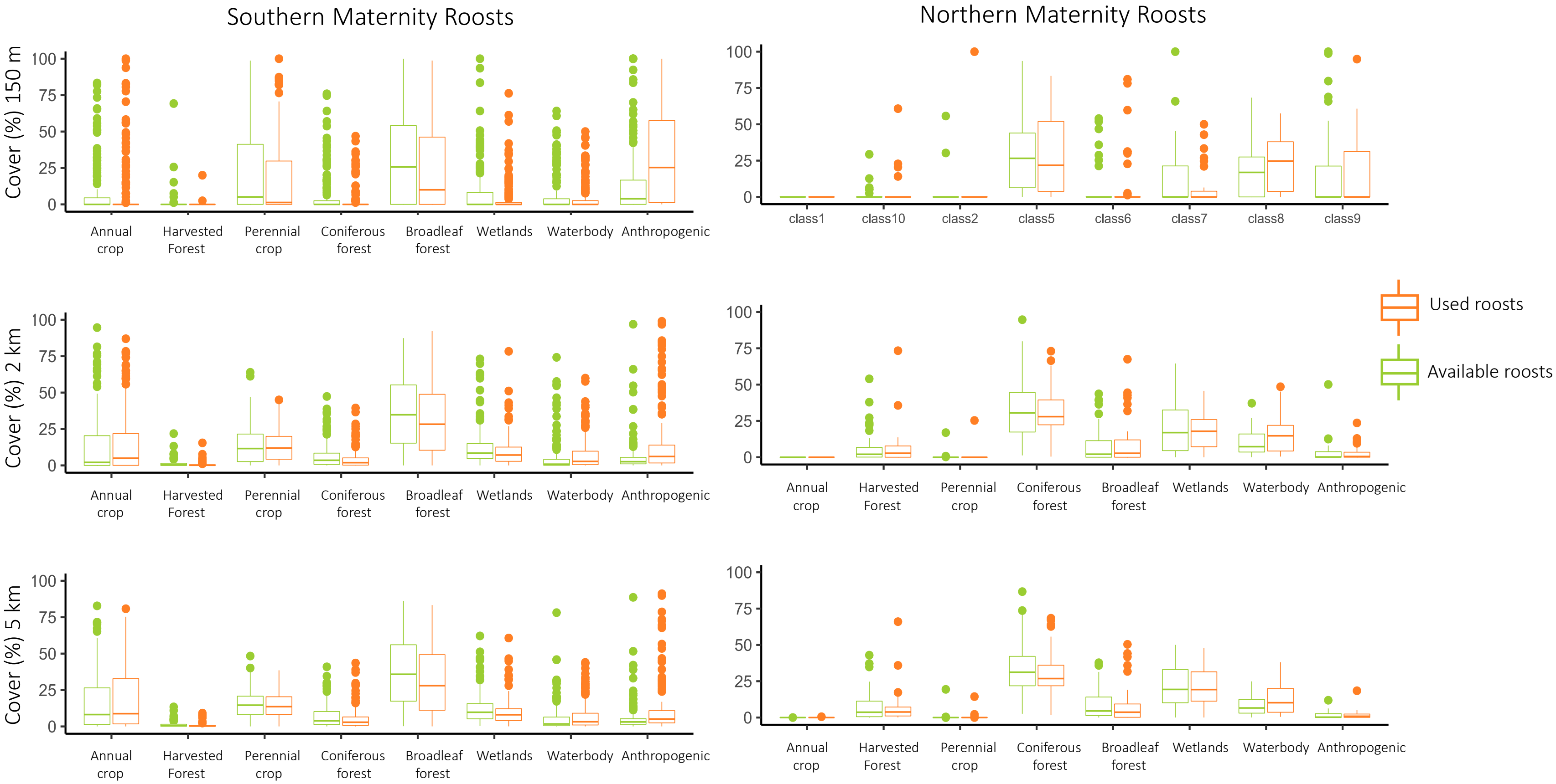

Figure S1.2. Landscape cover (%) around southern and northern used maternity roost in Québec using different buffer sizes.

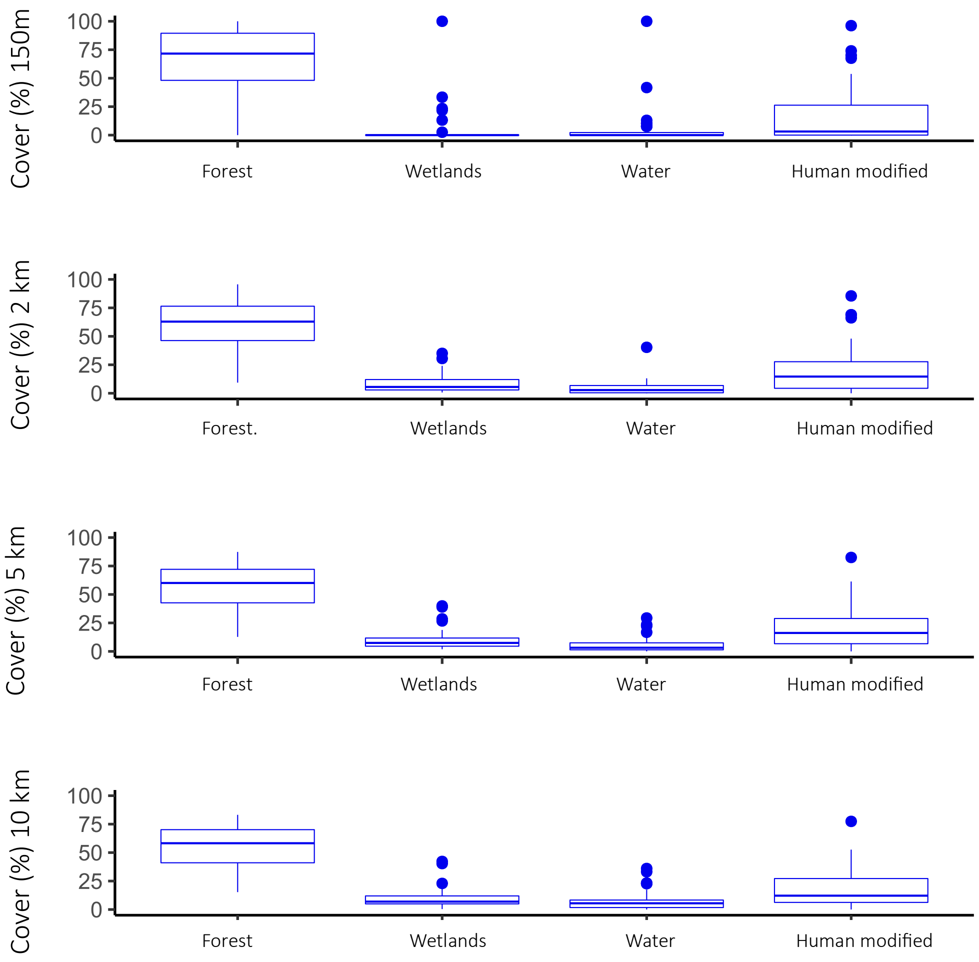

Figure S1.3. Landscape cover (%) around hibernacula in Québec using different buffer sizes.

Table S1.1. Southern and northern maternity roost selection in Québec based on landscape features at each studied scales in univariate models. AICc,delta AICc (ΔAICc) and AICc weight (ω) of generalized linear models with binomial family for each landscape features at each scale. In bold is the relevant scale chosen for this landscape to build the final multiscale model. (*) In case of equivalent models, the 2,000 m scale was chosen.

	South				**North**			
	Scale (m)	**AICc**	**ΔAICc**	**ω**	**Scale (m)**	**AICc**	**ΔAICc**	**ω**
%Annual Crop	5000	443.20	0.00	0.45	-	-	-	-
	2000*	443.66	0.45	0.36	-	-	-	-
	150	444.88	1.68	0.19	-	-	-	-
%Perennial Crop	**150**	442.48	0.00	0.61	-	-	-	-
	5000	444.63	2.15	0.21	-	-	-	-
	2000	444.88	2.40	0.18	-	-	-	-
%Coniferous forest	**2000**	435.70	0.00	0.66	5000	105.45	0.00	0.44
	150	438.07	2.37	0.20	**2000***	106.21	0.76	0.3
	5000	438.86	3.16	0.14	150	106.55	1.10	0.26
%Broadleaf forest	**5000**	439.41	0.00	0.58	5000	106.53	0.00	0.35
	150	441.42	2.01	0.21	150	106.63	0.10	0.33
	2000	441.52	2.11	0.20	**2000***	106.71	0.18	0.32
%Wetlands	**2000***	438.40	0.00	0.51	**150**	104.70	0.00	0.58
	150	439.67	1.26	0.27	5000	106.72	2.02	0.21
	5000	440.02	1.62	0.23	2000	106.74	2.04	0.21
%Water body	**2000**	437.73	0.00	0.75	**2000***	103.02	0.00	0.64
	5000	440.26	2.53	0.21	5000	105.10	1.99	0.24
	150	443.95	6.21	0.03	150	106.30	3.28	0.12
%Anthropogenic	**150**	408.12	0.00	1.00	5000	106.69	0.00	0.34
	2000	421.55	13.43	0.00	150	106.73	0.04	0.33
	5000	428.68	20.56	0.00	**2000***	106.75	0.06	0.33
%Harvested forest	**2000***	435.16	0.00	0.68	**2000***	106.52	0.00	0.35
	5000	436.82	1.66	0.30	150	106.66	0.14	0.33
	150	442.33	7.17	0.02	5000	106.71	0.19	0.32
Water edge	**2000**	430.08	0.00	0.99	**2000**	103.46	0.00	0.67
	5000	440.55	10.47	0.01	5,000	105.85	2.39	0.2
	150	444.39	14.31	0.00	150	106.75	3.29	0.13
Forest edge	**5000**	439.04	0.00	0.79	150	106.4	0.00	0.35
	2000	442.66	3.63	0.13	**2000***	106.49	0.09	0.33
	150	443.54	4.50	0.08	5000	106.53	0.14	0.32

Table S1.2. Selection tables of equivalent models (ΔAICc<2) from alternative models sets tested for maternity roosts selection in southern Quebec with generalized linear models with binomial family. AICc, delta (ΔAICc) and AICc weight (ω) for each equivalent model. In italic are the uncorrelated variable combination includes only in this model. Highlighted in grey, the most parsimonious model.

Models	**AICc**	**ΔAICc**	**ω**
Full model: *%Annual crop (2 km)* +%Harvested forest (2 km)+%Perennial crop (150 m) +%Conf. Forest (2 km) +%Wetlands (2 km) + %Anthropogenic (150 m)+ *Forest edge (5 km) + Water edge (2 km)* + Dist. Roads + Dist. Water			
%Anthropogenic (150 m) + Dist. Roads + Dist. Water + Water edge (2 km) + %Annual crop (2 km)	387.456	0.000	0.077
%Anthropogenic (150 m) + Dist. Roads + Dist. Water + Water edge (2 km)	388.425	0.969	0.048
%Anthropogenic (150 m) + Dist. Roads + Dist. Water + Water edge (2 km) +%Annual crop (2 km) + %Wetlands (2 km)	388.944	1.487	0.037
%Anthropogenic (150 m) + Dist. Roads + Dist. Water + Water edge (2 km) + Forest edge (5 km)	389.297	1.840	0.031
%Anthropogenic (150 m) + Dist. Roads + Dist. Water + Water edge (2 km) + %Annual crop (2 km) + Forest edge (5 km)	389.351	1.895	0.030
%Anthropogenic (150 m) + Dist. Roads + Dist. Water + Water edge (2 km) + %Annual crop (2 km) + %Harvested forest (2 km)	389.398	1.942	0.029
%Anthropogenic (150 m) + Dist. Roads + Dist. Water + Water edge (2 km) + %Wetlands (2 km)	389.406	1.950	0.029
Full model: %Harvested forest (2 km)+%Perennial crop (150 m) +%Conf. Forest (2 km) +%Wetlands (2 km) + %Anthropogenic (150 m)+ *%Blf. Forest (5 km) + Water edge (2 km)* + Dist. Roads + Dist. Water			
%Anthropogenic (150 m) + Dist. Roads + Dist. Water + Water edge (2 km)	388.425	0.000	0.109
%Anthropogenic (150 m) + Dist. Roads + Dist. Water + Water edge (2 km) + %Wetlands (2 km)	389.406	0.981	0.067
%Anthropogenic (150 m) + Dist. Roads + Dist. Water + Water edge (2 km) + %Harvested forest (2 km)	389.762	1.337	0.056
%Anthropogenic (150 m) + Dist. Roads + Dist. Water + Water edge (2 km) + %Blf. Forest (5 km)	390.062	1.636	0.048
%Anthropogenic (150 m) + Dist. Roads + Dist. Water + Water edge (2 km) + %Perennial crop (150 m)	390.133	1.707	0.047
%Anthropogenic (150 m) + Dist. Roads + Dist. Water + Water edge (2 km) + %Conf. Forest (2 km)	390.182	1.756	0.045
Full model: *%Annual crop (2 km)* + %Harvested forest (2 km)+%Perennial crop (150 m) +%Conf. Forest (2 km) +%Wetlands (2 km) + %Anthropogenic (150 m)+ *Forest edge (5 km) + %Water (2 km)* + Dist. Roads + Dist. Water			
%Anthropogenic (150 m) + Dist. Roads + Dist. Water	394.813	0.000	0.042
%Anthropogenic (150 m) + Dist. Roads + Dist. Water + %Water (2 km)	395.151	0.338	0.035
%Anthropogenic (150 m) + Dist. Roads + Dist. Water + %Water (2 km) + %Annual crop (2 km)	395.300	0.487	0.033
%Anthropogenic (150 m) + Dist. Roads + Dist. Water + %Wetlands (2 km)	395.425	0.611	0.031
%Anthropogenic (150 m) + Dist. Roads + Dist. Water + %Annual crop (2 km)	395.745	0.932	0.026
%Anthropogenic (150 m) + Dist. Roads + Dist. Water + %Water (2 km) + %Wetlands (2 km)	396.015	1.202	0.023
%Anthropogenic (150 m) + Dist. Roads + Dist. Water + %Harvested forest (2 km)	396.092	1.279	0.022
%Anthropogenic (150 m) + Dist. Roads + Dist. Water + Forest edge (5 km)	396.109	1.295	0.022
%Anthropogenic (150 m) + Dist. Roads + Dist. Water + %Conf. Forest (2 km)	396.414	1.600	0.019

%Anthropogenic (150 m) + Dist. Roads + Dist. Water + %Water (2 km) + Forest edge (5 km)	396.483	1.670	0.018
%Anthropogenic (150 m) + Dist. Roads + Dist. Water + %Water (2 km) + %Water (2 km) + %Wetlands (2 km) + %Annual crop (2 km)	396.591	1.777	0.017
%Anthropogenic (150 m) + Dist. Roads + Dist. Water + %Water (2 km) + %Harvested forest (2 km)	396.605	1.792	0.017
%Anthropogenic (150 m) + Dist. Roads + Dist. Water + %Water (2 km) + %Wetlands (2 km) + %Annual crop (2 km)	396.667	1.854	0.017
Full model: %Harvested forest (2 km)+%Perennial crop (150 m) +%Conf. Forest (2 km) +%Wetlands (2 km) + %Anthropogenic (150 m)+ *%Blf. Forest (5 km) + %Water (2 km)* + Dist. Roads + Dist. Water			
%Anthropogenic (150 m) + Dist. Roads + Dist. Water	394.813	0.000	0.073
%Anthropogenic (150 m) + Dist. Roads + Dist. Water + %Water (2 km)	395.151	0.338	0.061
%Anthropogenic (150 m) + Dist. Roads + Dist. Water + %Wetlands (2 km)	395.425	0.611	0.053
%Anthropogenic (150 m) + Dist. Roads + Dist. Water + %Water (2 km) + %Wetlands (2 km)	396.015	1.202	0.040
%Anthropogenic (150 m) + Dist. Roads + Dist. Water + %Harvested forest (2 km)	396.092	1.279	0.038
%Anthropogenic (150 m) + Dist. Roads + Dist. Water + %Conf. Forest (2 km)	396.414	1.600	0.033
%Anthropogenic (150 m) + Dist. Roads + Dist. Water + %Water (2 km) + %Harvested forest (2 km)	396.605	1.792	0.030
%Anthropogenic (150 m) + Dist. Roads + Dist. Water + %Blf. Forest (5 km)	396.756	1.942	0.027

Table S1.3. Selection tables of equivalent models (ΔAICc<2) from alternative models sets tested for maternity roosts selection in norther Québec with generalized linear models with binomial family. AICc, delta (ΔAICc) and AICc weight (ω) for each equivalent model. In italic are the uncorrelated variable combination includes only in this model. Highlighted in grey, the most parsimonious model.

Model	**AICc**	**ΔAICc**	**ω**
Full model: %Harvested forest (2 km)+ %Conf. Forest (2 km) +%Wetlands (2 km) + %Anthropogenic (2 km)+ *%Blf. Forest (2 km) + %Water (2 km)* + Dist. Roads + Dist. Water			
%Water (2 km)	103.019	0.000	0.059
%Water (2 km) + Dist. Roads	103.959	0.941	0.037
null	104.641	1.623	0.026
%Water (2 km) + %Blf. Forest (5 km)	104.695	1.676	0.026
%Water (2 km) + %Harvested forest (2 km)	104.772	1.753	0.025
%Water (2 km) + %Blf. Forest (5 km) + Dist. Roads	104.922	1.903	0.023
%Water (2 km) + %Conf. Forest (2 km)	104.945	1.926	0.023
Full model:%Harvested forest (2 km)+ %Conf. Forest (2 km) +%Wetlands (2 km) + %Anthropogenic (2 km)+ *Forest edge (2 km) + Water edge (2 km)* + Dist. Roads + Dist. Water			
Water edge (2 km)	103.464	0.000	0.060
null	104.641	1.177	0.033
Water edge (2 km) + %Conf. Forest (2 km)	104.682	1.218	0.033
Water edge (2 km) + Dist. Roads	104.745	1.281	0.032
Water edge (2 km) + %Harvested forest (2 km)	105.378	1.914	0.023
Full model: %Harvested forest (2 km) +%Conf. Forest (2 km) +%Wetlands (2 km) + %Anthropogenic (150 m)+ %*Blf. Forest (2 km) + Water edge (2 km)* + Dist. Roads + Dist. Water			
Water edge (2 km)	103.464	0.000	0.060
null	104.641	1.177	0.033
Water edge (2 km) + %Conf. Forest (2 km)	104.682	1.218	0.033
Water edge (2 km) + Dist. Roads	104.745	1.281	0.032
Water edge (2 km) + %Harvested forest (2 km)	105.378	1.914	0.023
Full model: %Harvested forest (2 km) +%Conf. Forest (2 km) +%Wetlands (2 km) + %Anthropogenic (150 m)+ *Forest edge (2 km) + %Water (2 km)* + Dist. Roads + Dist. Water			
%Water (2 km)	103.019	0.000	0.067
%Water (2 km) + Dist. Roads	103.959	0.941	0.042
null	104.641	1.623	0.030
%Water (2 km) + %Harvested forest (2 km)	104.772	1.753	0.028
%Water (2 km) + %Conf. Forest (2 km)	104.945	1.926	0.025
%Water (2 km) + Forest edge (2 km)	104.963	1.945	0.025

Table S1.4. Hibernacula population size pre-WNS in Québec based on landscape features at each scales in univariate models. AICc, delta AICc (ΔAICc) and AICc weight (ω) of each univariate linear model. In bold is the relevant scale chosen for this landscape to build the final multiscale model. (*) In case of equivalent models, the 10,000 m scales were chosen.

landscape features	**Scale (m)**	**AICc**	**ΔAICc**	**ω**
%Forest	5000	144.00	0.00	0.44
	10000*	144.65	0.65	0.32
	2000	145.81	1.81	0.18
	150	148.24	4.24	0.05
%Wetlands	**10000***	148.69	0.00	0.32
	5000	149.26	0.57	0.24
	150	149.43	0.74	0.22
	2000	149.45	0.76	0.22
%Water	2000	147.82	0.00	0.38
	10000*	148.51	0.69	0.27
	5000	149.17	1.35	0.19
	150	149.44	1.61	0.17
%Human modified	**2000***	145.50	0.00	0.57
	5000	147.58	2.08	0.20
	10000	148.26	2.76	0.14
	150	149.25	3.75	0.09
Forest edge	**10000***	147.73	0.00	0.38
	150	148.22	0.49	0.29
	5000	149.37	1.64	0.17
	2000	149.38	1.65	0.16
Water edge	2000	148.67	0.00	0.29
	5000	148.99	0.33	0.25
	150	149.14	0.48	0.23
	10000*	149.14	0.48	0.23

Table S1.5. Selection tables of equivalent models (ΔAICc<2) from alternative models sets tested for hibernacula population size pre-WNS in Québec with linear models. AICc, delta AICc (ΔAICc) and AICc weight (ω) for all equivalent models. In italic are the uncorrelated variable combination includes only in this model. Highlighted in grey, the most parsimonious model chosen as the best model.

Model	**AICc**	**ΔAICc**	**ω**
Full model: %Human modified (2 km) + %Wetlands (10 km) + Dist. Water + Dist. Roads + *Forest edge (10 km) + %Water (10 km)*			
%Human modified (2 km) + Forest edge (10 km)	143.456	0.000	0.145
%Human modified (2 km) + Forest edge (10 km) + Dist. Roads	143.532	0.076	0.139
Full model: %Human modified (2 km) + %Wetlands (10 km) + *Forest edge (10 km) + Water edge (10 km)*			
%Human modified (2 km) + Forest edge (10 km)	143.456	0.000	0.147
%Human modified (2 km) + Forest edge (10 km) + Dist. Roads	143.532	0.076	0.142
Full model: %Human modified (2 km) + %Wetlands (10 km) + Dist. Water + Dist. Roads + *%Forest (10 km) + %Water (10 km)*			
%Forest (10 km) + %Wetlands (10 km)	145.217	0.000	0.076
%Human modified (2 km)	145.499	0.282	0.066
%Human modified (2 km) + Dist. Water	145.757	0.540	0.058
%Forest (10 km)	145.810	0.593	0.057
%Forest (10 km) + %Wetlands (10 km) + %Human modified (2 km)	146.278	1.061	0.045
%Wetlands (10 km) + %Human modified (2 km)	146.636	1.419	0.037
%Forest (10 km) + %Human modified (2 km)	146.686	1.469	0.037
%Forest (10 km) + %Human modified (2 km) + %Wetlands + Dist. Roads	146.872	1.655	0.033
%Human modified (2 km) + Dist. Water + Dist. Roads	146.930	1.713	0.032
null	147.006	1.789	0.031
%Human modified (2 km) + Dist. Roads	147.194	1.977	0.028
Full model: %Human modified (2 km) + %Wetlands (10 km) + Dist. Water + Dist. Roads + *%Forest (10 km) + Water edge (10 km)*			
%Forest (10 km) + %Wetlands (10 km)	145.217	0.000	0.079
%Human modified (2 km)	145.499	0.282	0.069
%Human modified (2 km) + Dist. Water	145.757	0.540	0.060
%Forest (10 km)	145.810	0.593	0.059
%Forest (10 km) + %Wetlands (10 km) + %Human modified (2 km)	146.278	1.061	0.046
%Wetlands (10 km) + %Human modified (2 km)	146.636	1.419	0.039
%Forest (10 km) + %Human modified (2 km)	146.686	1.469	0.038
%Forest (10 km) + %Human modified (2 km) + %Wetlands + Dist. Roads	146.872	1.655	0.035
%Human modified (2 km) + Dist. Water + Dist. Roads	146.930	1.713	0.034
null	147.006	1.789	0.032
%Human modified (2 km) + Dist. Roads	147.194	1.977	0.029

CONNECTING STATEMENT

In Chapter One, I studied habitat selection at the colony level for three bat species in Québec by extracting landscape features around summer and winter roosts using different scales. Assuming that bats concentrated their home range around maternity roosts and hibernacula most of the year, we looked at 2nd order habitat selection (selection of a home range). Maternity roost selection was positively influenced by water features within their foraging range and anthropogenic landscape elements close to the roost, potentially because it offers more roosting opportunities. On the other hand, hibernacula hosted more bats when there was less human-modified landscape and more forest edges in the surrounding area. Those results can inform multi-species management plans on a large scale. In Chapter Two, I zoom in on 3rd order habitat selection (selection of habitat) and the behaviour of the endangered little brown bat (*Myotis lucifugus*) during different periods of the year. I used automated radiotelemetry to track movements surrounding a maternity roost in summer and surrounding a hibernaculum during the mating season in late summer. I evaluated the return rate to each site and how bats moved within the surroundings, hoping to understand how behaviour may constrain habitat selection. I also looked at activity level in different habitat types to target important habitat to protect seasonally.

NOTE ON CHAPTER 2

This chapter corresponds to a manuscript with the same title that should be submitted for publication in Journal of Mammalogy soon. The data in this chapter were collected in the field with the help of MELCCFP, particularly Valérie Simard, Anne-Marie Béland, Anouk Simard, and field assistants particularly Catriona Daley (McGill University). This chapter was conceptualized by me with ideas from MELCCFP and the help and supervision of Dr. Anouk Simard (MELCCFP), Dr. Liam P. McGuire (University of Waterloo) and Dr. Kyle H. Elliott (McGill University).

CHAPTER 2 : The Use of Seasonal Residences and Surrounding Habitats by *Myotis lucifugus*: From Central Place at the Maternity Roost to Focal Place at the Hibernaculum

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Abstract

Life history activities of many species are often segregated temporally and spatially. Habitat requirements are expected to vary according to environmental variation and constraints associated with activities like reproduction, hibernation, migration, or other important behaviours. Failure to meet habitat requirements during one period can create carryover effects affecting fitness over longer periods of time. The little brown bat (*Myotis lucifugus*) is an interesting species to explore variation in habitat requirements temporally, spatially and between sexes being a local migrant that complete their annual cycle at two seasonal residences. We tracked bats using automated radiotelemetry around a maternity roost in summer (lactation) and around a hibernaculum in late summer (mating season) prior to hibernation. Maternity roosts acted as a typical central place with females returning 83 ± 28% of the night they had their tag and with activity concentrated in a ~ 5 km radius of the roost, primarily along a riparian corridor. At the hibernaculum, both males and females returned only 22 ± 27% of the night they had their tag, although when they returned, males spent more time at the hibernaculum than females. Bats were detected foraging and roosting up to 13 km from the hibernaculum and males were detected substantially more than females in the surroundings. We suggest hibernacula act as "focal place" in the late summer before hibernation. At both sites, we found only weak evidence of habitat preferences, implying that foraging distance from the central place was more important than habitat, that most of the surrounding habitat was suitable, or that selection was on a finer scale than we could measure. Our study highlights variation in habitat uses behaviour around seasonal residences according to life history and sexes and add to a growing body of literature supporting the need for seasonal management practices.

Keywords

Maternity roost, Hibernaculum, Swarming, Little brown bat, Automated telemetry, Habitat Selection, Central Place, Focal Place

Introduction

Habitat selection and the availability of high-quality habitats are key determinants of survival and fitness, as animals seek to find food, shelter, safety from predators, and favourable microclimates (Garshelis, 2000; Johnson, 1980; Krausman, 1999). In the context of global habitat loss (Newbold et al., 2015; Venter et al., 2006), habitat selection has received considerable attention, especially for vulnerable species (Mathewson & Morrison, 2015; Mayor et al., 2009). However, animal habitat requirements are expected to vary temporally and spatially according to different environmental constraints, life stages, or periods of the annual cycle (e.g., Lamb et al., 2020; O'Neill et al., 2020; Stanley et al., 2021). For example, songbirds during migration tend to be more generalist in terms of habitat selection, contrary to breeding seasons when they may select certain habitats to fulfill needs to rear and protect young (e.g., Stanley et al., 2021). Environmental constraints linked to food availability or physical limitations can also modulate habitat requirements. For example, white-tailed deer (*Odocoileus virginianus*) in the northern part of the species range select closed habitats that limit snow cover and favour movement in winter, while selecting open habitats with greater foraging opportunities in the summer (Beier & McCullough, 1990). Failure to meet habitat requirements at one period has the potential of creating carryover effects over the full annual cycle (Harrison et al., 2011), thus the importance of understanding seasonal variations in habitat selection.

Further, habitat selection is also subject to spatial constraints, especially for species depending on a residence (roost, den, nest, etc.) or other focal sites (e.g., mating sites, water holes). In such cases, the benefit of visiting a habitat patch must outweigh the cost of commuting to and from the central point (Olsson et al., 2008; Orians & Pearson, 1979; Pyke, 2019). In a scenario where an animal often returns to its residence (e.g., chick-rearing birds), the relative value of closer habitat patches increases because of low commuting costs (Olsson & Bolin, 2014). As such, purple martin (*Progne subis*) foraging range from their central place is 100 times less during the breeding season when adults must provision chicks at the nest many times a day (Lalla et al., 2022). The flexibility of returning only once a day to the roost during the non-breeding period allows the selection of farther, but higher quality, habitat patches (Lalla et al., 2022). Dependence on a residence or focal site creates a spatial dependency that dictates the relative value and availability of habitat patches, and is crucial in the habitat selection process (Rainho & Palmeirim, 2011; Rosenberg & McKelvey, 1999).

The little brown bat (*Myotis lucifugus*) is one species where habitat selection likely varies at different spatial and temporal scales. Little brown bats are regional migrants that complete their annual cycle at two seasonal residences. In summer, females gather at maternity roosts for the period of pregnancy and lactation (Henry et al., 2002). In late summer, males and females gather at hibernacula which serve as swarming (mating) and hibernation sites (Gallant & Broders, 2015; McGuire et al., 2009). Little brown bat offers a great opportunity to study variation in behaviour at two ecologically relevant sites and how that could affect variation in habitat preferences. Moreover, this species is listed as endangered (IUCN red list 2018; Solari, 2021; COSEWIC, 2013) and could benefit from management plans adapted to the different period of their annual cycle.

We contrasted little brown bat behaviour and habitat prefered at a maternity roost and at a swarming site. We first aimed to characterize the return rate and visitation time at both sites to understand how bats are constrained to stay in the vicinity. Second, we aimed to characterize the distribution of bat activity in the surroundings and identify preferred habitat. Females need to nurse their pups on a nightly basis and consequently, we hypothesized that they would return every night to the maternity roost and that they would concentrate activity in habitats close to the roost. At the hibernaculum in late summer, bats must tradeoff time and effort invested in mating and foraging activities prior to hibernation. Consequently, we hypothesized that bats could either commute to the hibernaculum, that serves as swarming site, on some nights; alternatively they could commute to the hibernaculum every night to mate and forage near the hibernaculum. At both sites, we predicted that activity would be higher in high-quality habitat (see Table 2.1 for detailed prediction). Finally, as a promiscuous species (Thomas et al., 1979), we hypothesized sex-biased behaviour at the hibernaculum as males could invest more time in mating activity compared to females. Frequent return to the swarming site might benefit males more than females in terms of increased mating opportunities (Burns & Broders, 2015). Females may also favour foraging activity over frequent return to the mating site as they recover from the energetic demands of summer reproduction (pregnancy and lactation; Jonasson & Willis, 2012).

Methods

Study Sites

We selected one maternity roost in a house and one hibernaculum in a cave about 110 km apart in the Outaouais region of Québec, Canada. Both sites hosted mainly little brown bats based on capture data and acoustic monitoring. The maternity colony occupied the roof and walls of a house since 2011 according to the owner of the house (Montcerf-Lytton, Québec, approximate location [46.60, -76.00]; Figure 2.1). We counted the emergence of 147 bats the night before the capture (Figure 2.1). Our hibernaculum site, Laflèche Cave (Val-des-Monts, Québec [45.65, -75.79]), is a year round commercially operated tourist cave. In March 2021, 468 bats were counted in the cave, mostly identified as little brown bats or northern long-eared bats (*Myotis septentrionalis*). Following widespread population declines from white-nose syndrome, Laflèche Cave is among the few known hibernacula in the province with over 100 bats left. Bats fly into and out of the cave from one known entry next to a small lake (Figure 2.1).

Automated and Manual Radiotelemetry

We captured bats using harp traps and mist nests on 20 June 2021 at the maternity roost and 31 August 2021 at the hibernaculum. We noted body mass sex, reproductive status (pregnant, lactating, post-lactating, non-reproductive), age (adult or subadult), and forearm length. We attached digitally encoded radio transmitters (hereafter "tags"; Nanotag NTQB2-1, 0.26 g < 4% of body mass; Lotek Wireless, Newmarket, Ontario, Canada) with GLUture topical adhesive (Zoetis Inc, Kalamazoo, Michigan) after trimming the fur in the intrascapular dorsal region. All tags were encoded on the same frequency but had a unique digital signature allowing simultaneous monitoring. Radio tags had a pulse rate of 5.3 s for a total expected battery life of approximately one month. All research activities were conducted under a license from the Ministère de l'Environnement, de la Lutte contre les changements climatiques, de la Faune et des Parcs (MELCCFP) and approved by both the McGill University Animal Care Committee and the MELCCFP Animal Care Committee

(#21-16). In the context of COVID-19, Canadian Wildlife Health Cooperative guidelines were followed (Canadian Wildlife Health Cooperative, 2021).

We tracked bats using automated telemetry with fixed receiver towers (hereafter "towers"), complemented with manual mobile telemetry. Towers consisted of a data logger (SRX800 or SRX1200; Lotek Wireless) connected to four 5-element Yagi antennas (Lotek Wireless) mounted at a height of 4 m, with a switch box that cycled through each antenna every 8 s. We installed an array of towers (ten at the maternity roost or eight at the hibernaculum) that represented a radius of 4.5 km around the maternity roost and 6 km around the hibernaculum (Figure 2.1). During swarming, we installed two additional towers at the entry of known hibernacula in close vicinity of our study cave: Emerald Mine (24 km away) and High Rock Mine (20 km away; Figure 2.1). To monitor return activity, we installed one tower as close as possible to the entry of the maternity roost (<10 m; identified as M1 in Figure 2.1) and hibernaculum (<100 m; identified as H1 in Figure 2.1). We chose the location of other towers based on accessibility, the distribution in the landscape, and habitat type.

We also opportunistically tracked bats using mobile receivers and handheld 3-element Yagi antennas, and additionally searched for day roosts during the swarming period. Following roads inside and outside the detection range of towers, we randomly scanned the landscape for at least 5 min at fixed location where the habitat seems favourable. We achieved 44 manual scans within a 5.7 km radius of the maternity roost over a period of eight nights. For the hibernaculum, we increased to 278 telemetry manual scans within a 14.5 km radius of the hibernaculum during 12 nights and days. If a bat was detected during the day, we triangulated its position, when possible, but did not track the bats to its roost because of limited access to private properties. We used manual telemetry data to evaluate the approximate area used around both sites and to complement automated telemetry detections.

Figure 2.1. Study areas and receiver tower locations around the maternity roost (Montcerf-Lytton) and the hibernaculum (Val-des-Monts) in the Outaouais region, Québec, Canada.

Automated Telemetry Data Cleaning

We filtered all detections collected from towers following best practices (Crewe et al., 2018), considering only observations with three or more consecutive detections at one receiver (run length ≥3; Crewe et al., 2018). We considered consecutive detections as separated by < 40 s, accounting for the time required to cycle through all antennas of a tower and the tag pulse rate. We estimated the minimum number of nights tags remained attached to bats by assuming a tag fell off when we detected regular detection with consistent power at one tower, or when there were no further detections. Data cleaning and all subsequent analyses were performed in R (version 4.2.2 ; R Core Team, 2022).

Return Rate and Visitation Times

We calculated the nightly return rate based on detections from the closest tower to the maternity roost and the hibernaculum (M1 & H1; Figure 2.1). If we detected a bat at any antenna of the central tower (M1 & H1) for over two consecutive minutes, we assumed that it returned to the site that night. We selected a two minute threshold to ensure that bats were not just commuting past the tower and because our analyses revealed no differences between either a two, five or eight minute thresholds. We calculated the return rate as the proportion of nights a bat returned to the site on the number of night they kept their tag, excluding bats with only one night of tracking data. We used logistic regression to compare the return rate between sites and sexes (significance $\alpha<0.05$).

When bats returned, we evaluated the visitation time during the night at both sites using detections from towers closest to each site (M1 and H1; Figure 2.1). We defined a visit to the site by any batch of detections that was < 15 min apart for the maternity roost and < 30 min apart for the hibernaculum. We chose 15 min as preliminary observations revealed that bats at the maternity roost could leave and be detected by other towers for about 15 min before coming back to the roost. For the hibernaculum, we chose the 30 min threshold based on the swarming time of Gallant & Broders (2015) and our analyses revealed no differences between either a 15, 30 or 45 min threshold. We used generalized least square models to compare visitation time per night between site and sexes while allowing for different standard deviation by groups.

For both return rate and visitation time analyses, our telemetry configuration did not allow differentiating when bats were inside the cave or maternity roost. Rather, it confirmed whether bats were within 500 m of each site (see Appendix 1 for methods of estimation of detection range; Figure S2.1).

Distribution of Bat Activity

To understand bat behaviour away from the maternity roost and the swarming site, we examined the directionality of their activity. We calculated the bearing from the maternity roost/hibernaculum to each tower and used the number of detections per tower as a proxy of bat activity. We then examined the activity level in relation to the bearing from the maternity roost/hibernaculum. We used circular statistics from the *circular* package (Agostinelli & Lund, 2022), and performed a Rayleigh test to evaluate departure from uniformity (Landler et al., 2018). Rayleigh test measured data dispersion around a central point by looking at the mean resultant length, a value between 0 and 1 referring to the degree of concentration around a point (Cremers & Klugkist, 2018).

Habitat Preference

We evaluated habitat preferences by calculating the relationship between activity level (number of detections at each antenna by nights by bats) and habitat cover within the range of each antenna. We excluded towers M1 and H1 in this analysis, as their proximity to the maternity roost or hibernaculum (respectively) could bias activity at those towers. We defined the detection range of each antenna by dividing a 500 m circular buffer around towers in four quadrants centred on each antenna (Figure 2.1; see Appendix 1 and Figure S2.1 for methods of estimation of detection range). Although we acknowledge that antennas can detect at larger spectrum than 90º, the probability of detection decreases substantially from a 90º to 180º offset angle (Crewe et al., 2019; Lotek, 2022). We then characterized the habitat within the detection range of each antenna. We extracted 12 habitat features which are predicted to influence bat activity (Table 2.1). We used the 2019 Québec Land Use Classification to extract habitat cover and edges at each antenna (10 m resolution; Ministère de l'Environnement et de la Lutte contre les changements climatiques, 2022). We characterized forest structure from the 2015 Québec Forest Survey Data, documenting stand age including annually updated harvesting activity (Ministère des Forêts, de la Faune et des Parcs, 2022b, 2022a). Using QGIS software (QGIS.org, 2022), we classified forest stands by their dominant age: young growth (<80 years old) and old growth (>80 years old). We calculated the minimum Euclidian distance between towers and the maternity roost/hibernaculum to account for the spatial attraction to those sites. For the maternity roost, we also calculated the minimum Euclidian distance between towers and the Désert River, a major landscape feature in the study area (Figure 2.1).We acknowledge that this method does not accurately locate bats as towers may detect bats even from a considerable distance. Although, if the distribution of bat detections by a tower is proportional to the use of the area in the surroundings, then this approach can give an idea of the habitat composition in which bats are most likely to be found.

Table 2.1. Habitat features description, mechanisms, and their predicted effects on little brown bat activity level around a maternity roost (June-July 2021) and a hibernaculum (September 2021) in the Outaouais region, Québec, Canada.

Habitat features	**Predicted Effect**	**Description**	**Mechanism**	**References**
Distance to Maternity/ Hibernaculum	-	Minimum Euclidian distance to the maternity roost/ hibernaculum	Space use is constrained by the distance to the site.	(Orians & Pearson, 1979; Rosenberg & McKelvey, 1999)
Distance to River (maternity only)	-	Minimum Euclidian distance to the Désert River	Bats use linear features such as rivers to commute and forage.	(Furmankiewicz & Kucharska, 2009; Rainho & Palmeirim, 2011)
% Young forest	-	% forest stand <80 years old	Bats avoid young forest because it is too cluttered.	(Thomas et al., 2021)
% Old forest	+	% forest stand >80 years of	Bats prefer to commute and forage in old forest because it is less cluttered and potentially supports more insects.	(Crampton & Barclay, 1998; Law et al., 2016; Vasko et al., 2020)
% Water	+	% cover of water	Little brown bats forage over water.	(Bergeson et al., 2013; Clare et al., 2011; Gili et al., 2020; Kniowski & Gehrt, 2014)
% Wetlands	+	% cover of wetland	Wetlands provide high abundance and diversity of insects where bats can forage.	(Coleman et al., 2014; Lookingbill et al., 2010)
% Urban	-	% cover of human modified surface (including roads, urban and industrial cover)	Little brown bats avoid foraging in human-modified habitat.	(Fabianek et al., 2011; Krauel & LeBuhn, 2016)
% Harvested	-	% harvested forest in the last 15 years	Bat activity decreased in harvested forest patches.	(Grindal & Brigham, 1999; Law et al., 2016; Patriquin & Barclay, 2003)
% Agriculture	-	% cover of all types of agriculture	Little brown bats avoid open spaces like agriculture.	(Kniowski & Gehrt, 2014; Thomas et al., 2021)
Water edges	+	Density of water edges	Bats use water edges for commuting and foraging.	(Ford et al., 2005; Gorman et al., 2022; Holloway & Barclay, 2000; Kniowski & Gehrt, 2014)
Forest edges	+	Density of forest edges	Bats use forest edges for commuting and foraging.	(Crampton & Barclay, 1998; Grindal & Brigham, 1999; Krauel & LeBuhn, 2016; Law et al., 2016; Patriquin & Barclay, 2003)

We evaluated the influence of habitat on bat activity by developing seven candidate hypotheses (Table 2.2) with uncorrelated predictors (Pearson $r < 0.6$; Harrison et al., 2018). We used linear mixed effect models to account for repeated measures with random effect of bat ID using the *lmertest* package (Kuznetsova et al., 2017). We chose the best fit hypotheses based on the Akaike information criterion corrected for small sample size (AICc; Burnham et al., 2011) and considered all hypotheses with ΔAICc < 2 as equivalent (Burnham et al., 2011; Harrison et al., 2018). We quantified effect sizes with model coefficient estimates, evaluated significance with confidence intervals and assessed goodness of fit with pseudo-R^2 (Nakagawa et al., 2017). All variables were Z-standardized before analysis.

Table 2.2. Candidate hypotheses and mechanisms to explain little brown bat activity level around a maternity roost (June-July 2021) and a hibernaculum (September 2021) in the Outaouais region, Québec, Canada. Linear mixed effect model structures are presented for each hypothesis. See table 2.1. for predicted effect of each habitat features.

Hypotheses	**Mechanism**	**Model structure**
	Maternity roost	
Base model	Bat activity is concentrated close to the residence and the river (potential principal commuting and foraging area).	Dist. Maternity + Dist. River + (1|TagID)
Habitat cover	Bat activity is positevely influenced by the amount of foraging habitat.	%Young Forest + %Old Forest + %Water + %Wetlands + Dist. Maternity + Dist. River + (1|TagID)
Water edges	Bat activity is positively influenced by the amount of water edge.	Water edge density + Dist. Maternity + Dist. River + (1|TagID)
Forest edges	Bat activity is positively influenced by the amount of forest edge.	Forest edge density + Dist. Maternity + Dist. River + (1|TagID)
Anthropogenic	Bat activity is negatively influenced by the amount of anthropogenic habitat.	%Urban + %Agriculture + Dist. Maternity + Dist. River + (1|TagID)
Null model	Bat activity is not influenced by habitat features.	1 + (1|TagID)
	Hibernaculum	
Base model	Bat activity is concentrated close to the residence	Dist. Hibernaculum + (1|TagID)
Habitat cover	Bat activity is positively influenced by the amount of foraging habitat.	%Young Forest + %Old Forest+ %Water + %Wetlands +%Harvesting + Dist. Hibernaculum + (1|TagID)
Water edges	Bat activity is positively influenced by the amount of water edge.	Water edge density + Dist. Hibernaculum + (1|TagID)
Forest edges	Bat activity is positively influenced by the amount of forest edge.	Forest edge density + Dist. Hibernaculum + (1|TagID)
Anthropogenic	Bat activity is negatively influenced by the amount of anthropogenic habitat.	%Urban + %Agriculture + Dist. Hibernaculum + (1|TagID)
Null model	Bat activity is not influenced by habitat features.	1 + (1|TagID)

Results

At the maternity roost, we tagged 23 lactating females (body mass = 9.31 ± 1.38 g, forearm length 39.78 ± 1.65 mm) and collected 377 023 detections from the towers over 18 days and nights in June-July 2021. We estimated that bats kept their tags on average 5 nights (range 2 – 18 nights). Most tags fell in the roost, leading to constant detection power at tower M1. Most females spent their days in or near the maternity roost (tower M1), but we did detect three bats that each spent at least one day roosting at other locations near towers M2, M7 and M6. Using manual telemetry, we detected active females as far as 5 km from the maternity roost.

At the hibernaculum, we tagged 39 adults (24 males, body mass = 8.73 ± 1.22 g, forearm length 38.19 ± 2.02 mm ; 15 females, body mass = 8.00 ± 0.81 g, forearm length 39.08 ± 1.45 mm) and collected 260 582 detections from towers over 28 days and nights in September 2021. However, we excluded one atypical male that spent most of the day and night around tower H8 (away from the hibernaculum; Figure 2.1), representing > 39% of all detections. Of the 91 575 remaining detections, more were from males (85 392) than females (6 183; two sample test of proportion, $\chi^2 = 59.56$, $p< 0.0001$). We estimated that males kept their tags on average for a minimum 14 nights (range 1 – 27 nights) and females for a minimum of 6 nights (range 1 – 20 nights). No tags fell off in the detection range of a tower, and we identified the time the tag fell as the last detection for each bat, although we cannot exclude that bats left the study area. We detected six roosting males during the day by six different towers, three of which were at tower H1 close to the hibernaculum for at least a day. Using manual telemetry, we also detected a male and a female, day-roosting (~10 km & ~8.4 km away from the hibernaculum, respectively). For most bats during swarming, day roost locations remained unknown. The farthest detections we had at night using manual telemetry were two individuals detected over a lake almost 13 km east of the cave. No bats were detected at the two towers placed at other hibernacula.

Return Rate & Visitation Time

All but one female returned to the maternity roost at least once during the study period, and they returned on 83 ± 28% of nights (Figure 2.2A). Females at the maternity roost had a higher return rate than females at the swarming site (β = -3.26, SE = 1.03, p = 0.002; Figure 2.2A). There was no difference in proportion of males (76%) and females (70%) that returned to the swarming site (two sample test of proportion, $\chi^2 < 0.001$, p = 1.00; combined proportion 74%). Males returned 25 ± 30% of nights while females returned 16 ± 17% of nights at the swarming site (combined male and female = 22 ± 27%). There was no difference between male and female return rates at the swarming site (β = 0.56, SE = 1.00, p = 0.58; Figure 2.2A). However, we acknowledge that four males did return more than 12 nights (range 12 – 25 days) to the swarming site during the study periods, while the maximum number of nights with return for a female was three.

When they did return to the maternity roost at night, females stayed for 105 ± 84 min (Figure 2.2B) with an average of three visits per night (max = 8 visits). In comparison, females stayed only 19.7 ± 16.7 min at the swarming site at night and averaged two visits per night (max = 4 visits; mean difference with females at maternity roost = 85.5 ± 9.9 [SE] min, p < 0.001; Figure 2.2B). Males remained at the swarming site 98.4 ± 96.0 min with two visits per night (max = 5), a time that was significantly higher than females at the swarming site (mean difference = 78.7 minutes, SE= 10.4 minutes, p < 0.001; Table 5; Figure 2.2B). Bats inside the cave were not detectable, and two visits at the swarming site might represent only one (bats entering and bats going out the cave). Consequently, visitation time is likely underestimated.

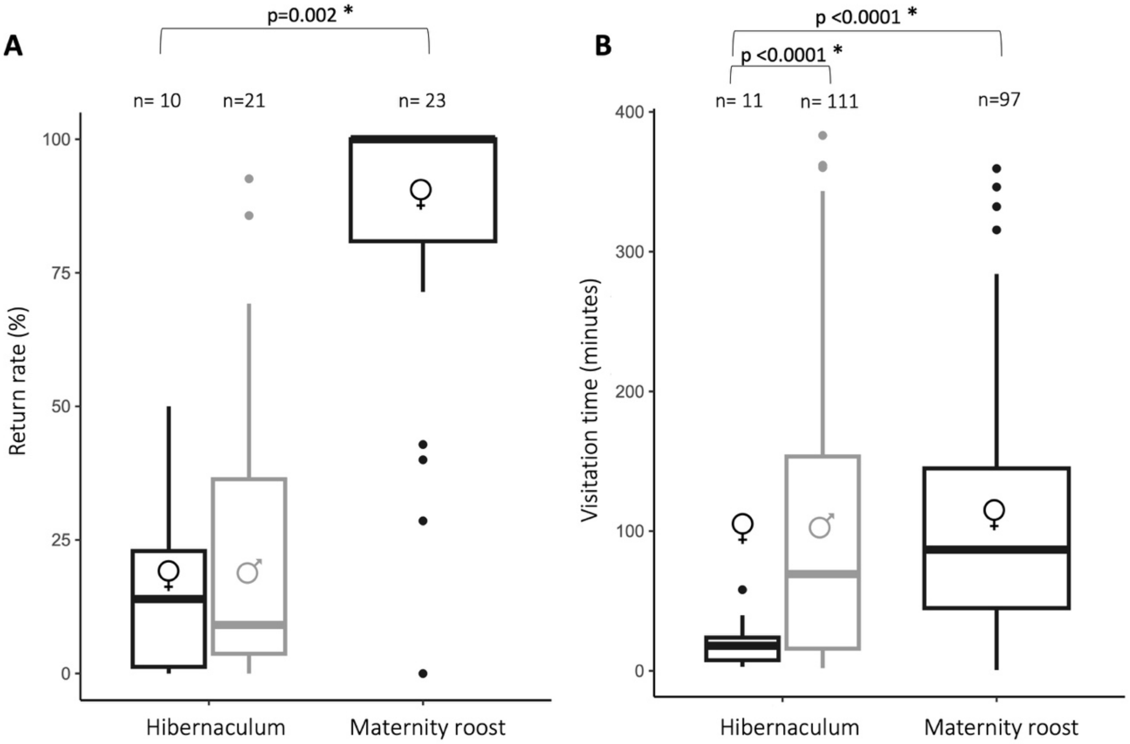

Figure 2.2. Little brown bat return rate and visitation behaviour by sexes at a maternity roost (June-July 2021) and a hibernaculum (September 2021) in the Outaouais region, Québec, Canada. A) Percent of nights with at least one return to the site and the number of bats considered as sample size (n). B) Nightly visitation time (minutes) at the site and the number of nights with at least one visit to the site by bats as sample size (n).

Directionality

Bat activity around both sites was not distributed uniformly. At the maternity roost, we observed a bimodal pattern with activity distributed to the south or north of the roost (mean resultant length [degree of concentration around a point]= 0.1515, $p < 0.0001$; Figure 2.3A). The mean vectors for individual bats were concentrated in two groups, showing that each bat appeared to consistently exploit habitats in one direction of the maternity roost (Figure 2.3C). At the hibernaculum, activity was concentrated to the south-east, for both males (mean resultant length = 0.201, < 0.0001; Figure 2.3B) and females (mean resultant length = 0.569, $p < 0.0001$; Figure 2.3B). When looking at individual mean vectors, we observed no clear pattern (Figure 2.3D), suggesting that some individuals with more detections might drive the overall directionality estimate.

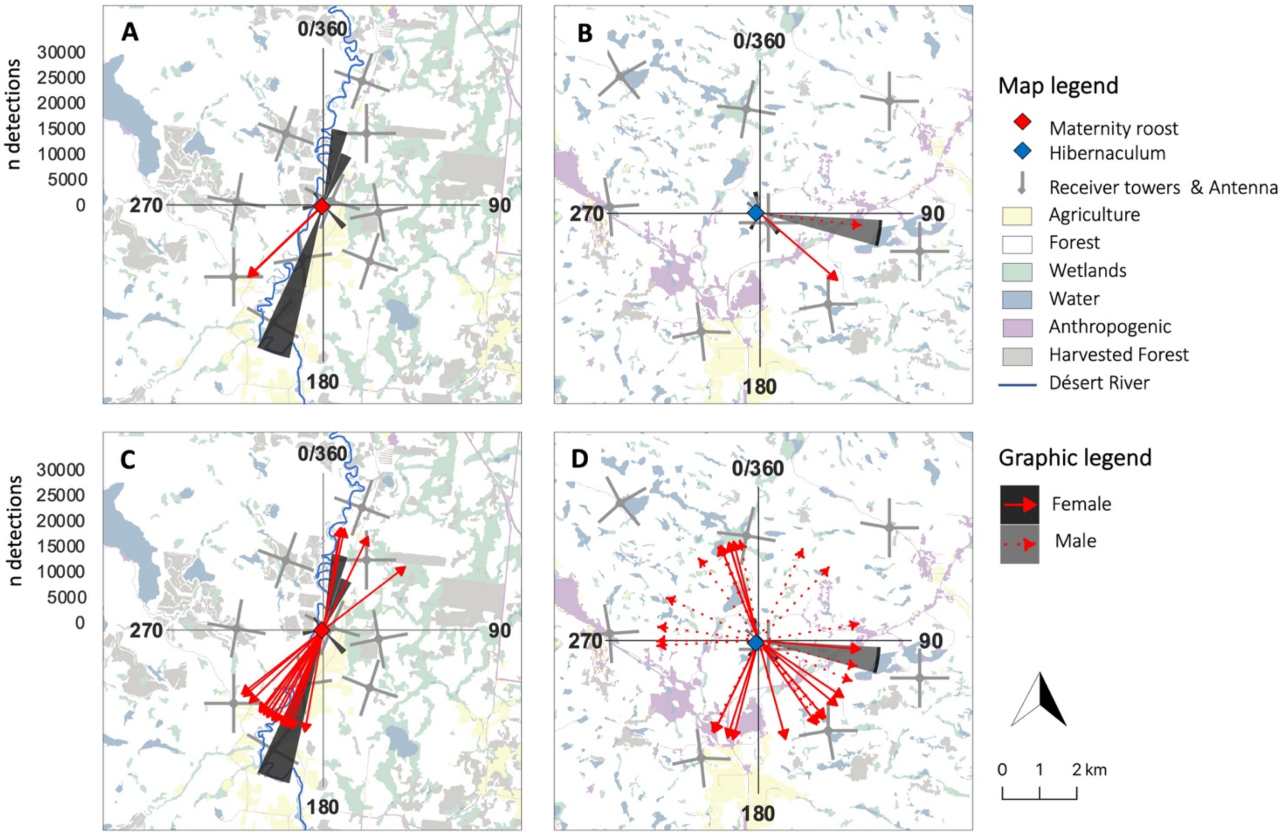

Figure 2.3. Distribution of little brown bat activity around a maternity roost (June – July 2021; A & C) and a hibernaculum (September 2021; B &D) in the Outaouais region, Québec, Canada. The center of each circular plot is the maternity roost / hibernaculum, the bars represents the number of bat detections by tower according to the bearing from the maternity roost / hibernaculum. The arrows are the mean vector for all bats grouped (A,B) and for individuals bats (C,D). Females are indicated by black bars and with solid line arrows while males are indicated with grey bars and dashed line arrows.

Habitat Preferences

Habitat features partially explained bat activity at both sites. Maternity roost data supported the *habitat cover* hypothesis (Marginal R^2= 0.081 ; Table 2.3). Bat activity decreased with distance from the river (ß = -0.290, SE = 0.064, t_{1653} = -4.50, 95% CI= [-0.417, -0.164]) and distance from the maternity roost (ß = -0.229, SE = 0.042, t_{1640} = -5.40, 95% CI= [-0.312, -0.146]; Figure 2.4A). Less activity occurred in areas with high harvested forest cover (ß = -0.178, SE = -0.046, t_{1626} = -3.87, 95% CI = [-0.269, -0.088]; Figure 2.5A). Hibernaculum data supported the *forest edge* hypothesis (Marginal R^2= 0.024 ; Table 2.3). Bat activity decreased with forest edge density (ß = -0.212, SE = 0.040, t_{1267} =-5.34, 95% CI= [-0.290, -0.134]; Figure 2.5B). However, contrary to the maternity roost, we found no effect of distance to the hibernaculum on bat activity (Figure 2.5B). We did not separate males and females for the habitat preference analysis at the hibernaculum because of the disproportionate number of detections between sexes. We also acknowledge that detections from males accounted for more than 92% of the detections from receiver towers (other than tower H1) and that our analysis is highly male biased at the hibernaculum.

Table 2.3. Candidate hypotheses explaining little brown bat activity around a maternity roost (June-July 2021) and a hibernaculum (September 2021) in the Outaouais region, Québec, Canada. Candidate hypotheses ranked by AICc, delta (ΔAICc), and AICc weight (ω). Pseudo-marginal and pseudo-conditional R^2 also presented for each hypothesis. Only hypotheses with ΔAICc < 2, highlighted in grey, were considered for subsequent analyses. Candidate model descriptions and linear mixed effect model structure are presented in Table 2.2.

Maternity roost						**Hibernaculum**					
Hypothesis	**AICc**	**ΔAICc**	**ω**	**Marginal R^2**	**Conditional R^2**	**Hypothesis**	**AICc**	**ΔAICc**	**ω**	**Marginal R^2**	**Conditional R^2**
Habitat cover	5770.69	0.00	0.95	0.081	0.115	Forest edges	4302.15	0.00	0.98	0.024	0.193
Anthropogenic	5776.70	6.01	0.05	0.074	0.113	Anthropogenic	4310.07	7.92	0.02	0.020	0.192
Forest edges	5785.46	14.77	0.00	0.068	0.108	Habitat cover	4324.07	21.92	0.00	0.014	0.180
Base	5787.79	17.09	0.00	0.065	0.104	Base	4328.27	26.12	0.00	0.003	0.187
Water edges	5788.02	17.33	0.00	0.066	0.106	Water edges	4328.73	26.58	0.00	0.004	0.186
Null	5898.60	127.90	0.00	0.000	0.038	Null	4330.28	28.12	0.00	0.000	0.181

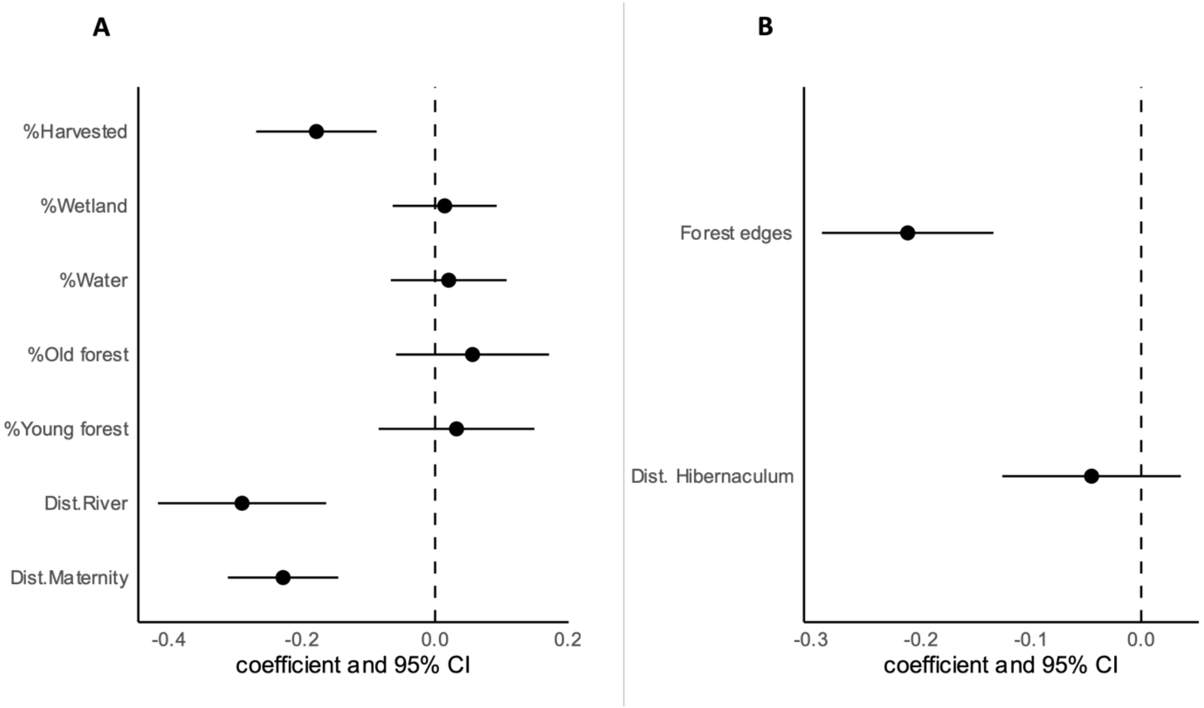

Figure 2.4. Habitat features influencing little brown bat activity in the Outaouais region, Québec, Canada. Linear mixed effect model coefficient estimates (points) and 95% confidence intervals on coefficient estimates (bars; 95% CI) for all habitat features included in the best supported hypotheses for A) female little brown bat activity around a maternity roost (June-July 2021) and B) combined male and female little brown bat activity around a hibernaculum (September 2021). Habitat features are considered significant if the 95% confidence intervals do not include zero.

Discussion

Habitat selection varies temporally and spatially because of constraints associated with different periods of the annual cycle. Understanding such variation is crucial to determine habitat requirements of a species and enhance management plans to avoid stress in one period that could influence the other (carryover effect). We contrasted little brown bat behaviour and habitat preferences around a maternity roost in summer during lactation and a hibernaculum in late summer during the swarming period. At the maternity roost, females returned to the roost most nights. When they left the roost, they remained in the vicinity, following the river but avoiding recently harvested forests. At the hibernaculum, bats did not return every night, and when they visited, the visitation time was longer for males than females. Individual bats seems to moved out in different direction from the hibernaculum and more activity were recorded in areas with low forest edge density. Our result supports the importance of seasonality in bat activity and habitat preferences, and could be transposed to management practices for improved conservation measures.

Maternity Roost

During lactation, female little brown bats must trade off nursing at the roost, foraging, and commuting activities (Henry et al., 2002; Kurta et al., 1989). Lactating females, compared to non-reproductive females, return to the roost once or more to feed pups (Fontaine, 2021; Henry et al., 2002), decrease travel distance to foraging areas (Henry et al., 2002), and increase food intake (Anthony & Kunz, 1977; Kurta et al., 1989). This shift in behaviour suggests a strong spatial dependence on the roost during this period, with bats going back and forth to foraging areas and resting while nursing in the maternity (Henry et al., 2002). The return pattern we observed is similar to other little brown bat maternity colonies (Anthony & Kunz, 1977; Fontaine, 2021; Henry et al., 2002). Our estimated visitation time to the roost (105.2 ± 84.0 minutes) was lower but relatively similar than observed inactivity time in the roost (142 ± 66 minutes) of lactating little brown bats by Henry et al. (2002) in Québec. This suggests that our visitation time encompasses mostly resting and nursing activity in the roost rather than foraging in the surroundings, although we cannot confirm such hypothesis with our telemetry system.

Maternity colonies in the province are usually located where potential foraging areas (e.g., water edges) to compensate for the need to return regularly to the roost (Chapter 1). Accordingly, bat activity was concentrated close to the maternity roost in our study, where there was an abundance of vegetated riparian habitat, considered of high quality for insectivorous bats (Ford et al., 2005; Fukui et al., 2006; Holloway & Barclay, 2000). Notably, individual bats travelled either north or south of the maternity roost, along the Désert River. Although we only tracked a small proportion of the colony (~16% of the total number of adult bats occupying the colony), we hypothesized that dividing into different groups north and south might be a strategy to avoid competition and prey depletion near the roost (Hillen et al., 2009). In our study, the Désert River might provide crucial food resources for lactating bats with low commuting costs. However, we recognize that in a situation where optimal roosts are not close to foraging areas, bats could change foraging strategy by reducing the number of nightly visits to the roost and increase commuting distance to reach high-quality habitat (e.g., Daniel et al., 2008).

Corroborating the idea that habitat preference is driven by habitat quality and not only by proximity to the roost, putatively lower-quality habitats in the vicinity, like harvested clear-cut forests, were avoided. Bat activity usually decreases within harvested patches (Deans et al., 2005; Dodd et al., 2012; Law et al., 2016; but see Law et al. 2016; Patriquin & Barclay, 2003), which supports the negative effect of harvested forest cover found in our study.

Swarming site

In late summer, bats must trade off mating (swarming) and foraging activity to deposit fat before hibernation (Gallant & Broders, 2015; McGuire et al., 2009). Moreover, bats do not necessarily roost in hibernacula during early swarming periods (Brack, 2006; Gallant & Broders, 2015; Parsons & Jones, 2003). Then, if hibernacula act mostly as mating sites for adults during this period, swarming activity is likely one of the main drivers of return to hibernacula (Furmankiewicz, 2008; but see Davis & Hitchcock, 1965; see Fenton, 1969 and Fraser & McGuire, 2023 for alternative hypotheses). To balance between mating and fat deposition, bats seem to commute to the hibernaculum only on some nights, as evidenced by the observed 22% nightly return rate in our study. As many bats were out of sight for days in between returns, we suggest their activity range extended farther than our study area, in a radius that could reach > 13 km from the hibernaculum as indicated by our farthest detection.

Male bias at the hibernaculum during swarming activity has been observed through several studies, but rarely quantified (Burns & Broders, 2015; Davis & Hitchcock, 1965; Dekeukeleire et al., 2016; Fenton, 1969; Furmankiewicz, 2008; Rivers et al., 2006). As a promiscuous species (Thomas et al., 1979), sex-biased behavioural patterns during mating is expected. Males should spend more time at the hibernaculum than females to maximize mating opportunities (Burns & Broders, 2015; Furmankiewicz, 2008). Sex-specific energetic constraints are also anticipated, females being usually more energy-depleted than males after rearing pups but also usually heavier than males right before hibernation (Burns & Broders, 2015; Jonasson & Willis, 2011, 2012). In our study, we did not observe sex difference in return rates at the swarming site, but males did have longer visitation time suggesting that when they return, males spend more time actively swarming than females. We acknowledge that our visitation time might include non-swarming activity, as the detection range of the H1 tower encompassed a lake and a marsh surrounded by deciduous forest. Still, if this was an advantageous foraging or roosting habitat, there is no reason why females would also not use it as well, such that the visitation time differences between sexes tend to point toward mating activity drivers. Moreover, the disproportionate number of detections around the swarming site and the absolute higher number of visits from males compared to females could suggest that males stayed closer to the swarming site in general and tend to revisit more frequently (e.g., Furmankiewicz, 2008). Further analyses should be done to explore sex-specific and individual variations at the swarming site.

Low return rates at the hibernaculum likely allow greater flexibility in habitat selection in the surroundings. Assuming that bats return at least once for hibernation (Van Schaik et al., 2015), we suggest that the hibernaculum imposes a flexible catchment area in which bats can disperse for roosting and foraging activity in late summer. Low return rate to the hibernaculum could allow bats to 1) mitigate competition around hibernacula which can attract thousands of bats (Brack, 2006; Fenton, 1969), at a time when food resources are usually decreasing (Wang et al., 2010), and 2) reach farther high-quality habitat patches to promote fat deposition before hibernation (Jonasson & Willis, 2011; McGuire et al., 2009), or 3) visit other swarming sites in the area (e.g., Brack, 2006; Fenton, 1969; Rivers et al., 2006). However, many species seem to be faithful to one swarming site (Burns & Broders, 2015; Parsons & Jones, 2003) and we did not detect our tagged bats at the two other major hibernacula in the area. We suggest those movements are rare events.

Individual bat activity seems uniformly distributed around the hibernaculum and we detected avoidance for areas with high forest edges density. Forest edges are usually good foraging and commuting habitat for bats (Crampton & Barclay, 1998; Patriquin & Barclay, 2003). However, forest edge density does not necessarily correlate with the presence of good forest edges (adjacent to other foraging habitats like water or wetlands). The negative effect of forest edge density could also illustrate a preference for forest interior, which may be good roosting habitat (Crampton & Barclay, 1998; Grindal & Brigham, 1999). Indeed, bats may use torpor to conserve energy in late summer (McGuire et al., 2016) and we suspect that we recorded some torpor bouts at night because of relatively constant and stable detections from some towers. Overall, we have relatively few detections at the hibernaculum and the surrounding, compared to the maternity roost and we detected bats farther than the area covered by our automated telemetry network (i.e., 13 km from the hibernaculum). This suggests that we did not cover all the movement and essential habitat that bats use surrounding the hibernaculum.

Laflèche Cave is one of the few hibernacula in Québec where bat population significantly increased following declines imposed by the white-nose syndrome (WNS). Hibernaculum population size pre-WNS in Québec correlated positively with forest edge density and negatively with anthropogenic habitat in the surroundings (Chapter 1). The area around Lafleche Cave is mostly composed of natural forest, lakes, wetlands and minimal human activity. Consequently, this hibernaculum might already provide a suitable habitat matrix for bats, a possible interpretation of the low goodness of fit of the habitat preference model. Future studies at other maternity roosts and hibernacula in different landscapes should be done to complement our findings.

Implications

The use of maternity roosts embodies the typical consideration of a central place, namely, a high degree of spatial dependence on the residence, and bats commuting back and forth from the roost to habitat patches within ~ 5 km radius (Orians & Pearson, 1979; Rosenberg & McKelvey, 1999). This necessary behaviour during lactation might be facilitated by higher insect density, offering high-quality food sources and the mitigation of competition near the central place in summer (Henry et al., 2002). As for hibernacula, we suggest they act more as a "focal place" in late summer during swarming period, attracting bats for mating and ultimately hibernation. However, during the swarming period, bats have the flexibility to travel throughout a catchment area, ~13 km according to our findings but that could exceed 20 km (Dekeukeleire et al., 2016; Parsons & Jones, 2003).

The behaviour of little brown bats varied according to different periods of the year, highlighting the importance of seasonally explicit management plans. Movement patterns at the maternity roost were strongly influenced by the river that runs through our study site, with individual bat activity directed along the river, and distance to the river as an important predictor of activity. Therefore, we highlight the importance of protecting key habitats such as riparian corridors surrounding maternity roosts, also supported by many studies (chapter 1, Holloway & Barclay, 2000). On the other hand, bats dispersed around hibernacula in a ~13 km radius. In that sense, the protection of a matrix of suitable, connected natural habitats within the catchment area might allow bats to target multiple foraging patches. We still suggest that natural habitat close to the hibernaculum could minimize commuting between foraging and mating site which could help bats to accumulate fat stores before hibernation and enhance winter survival (chapter 1; Cheng et al., 2019; Frick et al., 2023). To date, there’s still little information on little brown bats habitat preferences and behaviour away from hibernaculum during swarming periods (Fraser & McGuire, 2023; Frick et al., 2023). Further studies should focus on identifying foraging habitat during this period to complement our study.

References

Agostinelli, C., & Lund, U. (2022). *R package "circular": Circular Statistics* (0.4-95). https://r-forge.r-project.org/projects/circular/

Anthony, E. L. P., & Kunz, T. H. (1977). Feeding Strategies of the Little Brown Bat, Myotis Lucifugus, in Southern New Hampshire. *Ecology*, *58*(4), 775–786. https://doi.org/10.2307/1936213

Avila-Flores, R., & Fenton, M. B. (2005). Use of spatial features by foraging insectivorous bats in a large urban landscape. *Journal of Mammalogy*, *86*(6), 1193–1204. https://doi.org/10.1644/04-MAMM-A-085R1.1

Beier, P., & McCullough, D. R. (1990). Factors Influencing White-Tailed Deer Activity Patterns and Habitat Use. *Wildlife Monographs*, *109*, 3–51.

Bergeson, S. M., Carter, T. C., & Whitby, M. D. (2013). Partitioning of foraging resources between sympatric Indiana and little brown bats. *Journal of Mammalogy*, *94*(6), 1311–1320. https://doi.org/10.1644/12-MAMM-A-311

Brack, V. (2006). Autumn Activity of Myotis sodalis (Indiana Bat) in Bland County, Virginia. *Northeastern Naturalist*, *13*(3), 421–434. https://doi.org/10.1656/1092-6194(2006)13[421:AAOMSI]2.0.CO;2

Burnham, K. P., Anderson, D. R., & Huyvaert, K. P. (2011). AIC model selection and multimodel inference in behavioral ecology: Some background, observations, and comparisons. *Behavioral Ecology and Sociobiology*, *65*(1), 23–35. https://doi.org/10.1007/s00265-010-1029-6

Burns, L. E., & Broders, H. G. (2015). Maximizing mating opportunities: Higher autumn swarming activity in male versus female myotis bats. *Journal of Mammalogy*, *96*(6), 1326–1336. https://doi.org/10.1093/jmammal/gyv141

Canadian Wildlife Health Cooperative. (2021). *Wildlife health and SARS-CoV-2 in Canada: Bats* (1.2).

Cheng, T. L., Gerson, A., Moore, M. S., Reichard, J. D., DeSimone, J., Willis, C. K. R., Frick, W. F., & Kilpatrick, A. M. (2019). Higher fat stores contribute to persistence of little brown bat populations with white-nose syndrome. Journal of Animal Ecology, 88(4), 591–600. https://doi.org/10.1111/1365-2656.12954

Clare, E. L., Barber, B. R., Sweeney, B. W., Hebert, P. D. N., & Fenton, M. B. (2011). Eating local: Influences of habitat on the diet of little brown bats (Myotis lucifugus). *Molecular Ecology*, *20*(8), 1772–1780. https://doi.org/10.1111/j.1365-294X.2011.05040.x

Coleman, L. S., Ford, W. M., Dobony, C. A., & Britzke, E. R. (2014). Comparison of Radio-Telemetric Home-Range Analysis and Acoustic Detection for Little Brown Bat Habitat Evaluation. *Northeastern Naturalist*, *21*(3), 431–445. https://doi.org/10.1656/045.021.0309

Committee on the Status of Endangered Wildlife in Canada (COSEWIC). 2013. COSEWIC assessment and status report on the Little Brown Myotis Myotis lucifugus, Northern

Myotis Myotis septentrionalis and Tri-colored Bat Perimyotis subflavus in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. xxiv + 93 pp.

Crampton, L. H., & Barclay, R. M. R. (1998). Selection of Roosting and Foraging Habitat by Bats in Different-Aged Aspen Mixedwood Stands. *Conservation Biology*, *12*(6), 1347–1358. https://doi.org/10.1111/j.1523-1739.1998.97209.x

Cremers, J., & Klugkist, I. (2018). One Direction? A Tutorial for Circular Data Analysis Using R With Examples in Cognitive Psychology. *Frontiers in Psychology*, *9*, 2040. https://doi.org/10.3389/fpsyg.2018.02040

Crewe, T. L., Crysler, Z., & Taylor, P. (2018). *Motus R Book*.

Crewe, T. L., Deakin, J. E., Beauchamp, A. T., & Morbey, Y. E. (2019). Detection range of songbirds using a stopover site by automated radio-telemetry. *Journal of Field Ornithology*, *90*(2), 176–189. https://doi.org/10.1111/jofo.12291

Daniel, S., Korine, C., & Pinshow, B. (2008). Central-place foraging in nursing, arthropod-gleaning bats. *Canadian Journal of Zoology*, *86*(7), 623–626. https://doi.org/10.1139/Z08-041

Davis, W. H., & Hitchcock, H. (1965). Biology and migration of the bat, Myotis lucifugus , in New England. *Journal of Mammalogy*, *46*(2), 296–313.

Deans, A. M., Malcolm, J. R., Smith, S. M., & Bellocq, M. I. (2005). Edge effects and the responses of aerial insect assemblages to structural-retention harvesting in Canadian boreal peatland forests. *Forest Ecology and Management*, *204*(2–3), 249–266. https://doi.org/10.1016/j.foreco.2004.09.015

Dekeukeleire, D., Janssen, R., Haarsma, A. J., Bosch, T., & Van Schaik, J. (2016). Swarming Behaviour, Catchment Area and Seasonal Movement Patterns of the Bechstein's Bats: Implications for Conservation. *Acta Chiropterologica*, *18*(2), 349–358. https://doi.org/10.3161/15081109ACC2016.18.2.004

Dodd, L. E., Lacki, M. J., Britzke, E. R., Buehler, D. A., Keyser, P. D., Larkin, J. L., Rodewald, A. D., Wigley, T. B., Wood, P. B., & Rieske, L. K. (2012). Forest structure affects trophic linkages: How silvicultural disturbance impacts bats and their insect prey. *Forest Ecology and Management*, *267*, 262–270. https://doi.org/10.1016/j.foreco.2011.12.016

Fabianek, F., Gagnon, D., & Delorme, M. (2011). Bat distribution and activity in Montrél Island green spaces: Responses to multi-scale habitat effects in a densely urbanized area. *Ecoscience*, *18*(1), 9–17. https://doi.org/10.2980/18-1-3373

Fenton, M. B. (1969). Summer activity of M. lucifugus at hibernacula in Ontario and Quebec. *Canadian Journal of Zoology*, *47*, 597–602.

Fenton, M. B. (1997). Science and the conservation of bats. *Journal of Mammalogy*, *78*(12), 2059–2060. https://doi.org/10.1139/cjz-78-12-2059

Fontaine, A. (2021). *Citizen science and development of innovative tools to improve conservation of threatened bats*. McGill University.

Ford, W. M., Menzel, M. A., Rodrigue, J. L., Menzel, J. M., & Johnson, J. B. (2005). Relating bat species presence to simple habitat measures in a central Appalachian forest. *Biological Conservation*, *126*(4), 528–539. https://doi.org/10.1016/j.biocon.2005.07.003

Fraser, E. E., & McGuire, L. P. (2023). Prehibernation swarming in temperate bats: A critical transition between summer activity and hibernation. Canadian Journal of Zoology, cjz-2022-0129. https://doi.org/10.1139/cjz-2022-0129

Frick, W. F., Dzal, Y. A., Jonasson, K. A., Whitby, M. D., Adams, A. M., Long, C., Depue, J. E., Newman, C. M., Willis, C. K. R., & Cheng, T. L. (2023). Bats increased foraging activity at experimental prey patches near hibernacula. Ecological Solutions and Evidence, 4(1), 2688-8319.12217. https://doi.org/10.1002/2688-8319.12217

Fukui, D., Murakami, M., Nakano, S., & Aoi, T. (2006). Effect of emergent aquatic insects on bat foraging in a riparian forest. Journal of Animal Ecology, 75(6), 1252–1258. https://doi.org/10.1111/j.1365-2656.2006.01146.x

Furmankiewicz, J. (2008). Population size, catchment area, and sex-influenced differences in autumn and spring swarming of the brown long-eared bat (Plecotus auritus). *Canadian Journal of Zoology*, *86*(3), 207–216. https://doi.org/10.1139/Z07-134

Furmankiewicz, J., & Kucharska, M. (2009). Migration of Bats along a Large River Valley in Southwestern Poland. *Journal of Mammalogy*, *90*(6), 1310–1317. https://doi.org/10.1644/09-MAMM-S-099R1.1

Gallant, A. J., & Broders, H. G. (2015). Body condition explains little of the interindividual variation in the swarming behaviour of adult male little brown myotis (*Myotis lucifugus*) in Nova Scotia, Canada. *Canadian Journal of Zoology*, *93*(6), 469–476. https://doi.org/10.1139/cjz-2014-0249

Garshelis, D. L. (2000). Delusions in Habitat Evaluation: Measuring Use, Selection, and Importance. In *Research tech-niques in animal ecology: Controversies and consequences* (L. Boitani&T. K. Fuller, pp. 111–157). Columbia University Press.

Gili, F., Newson, S. E., Gillings, S., Chamberlain, D. E., & Border, J. A. (2020). Bats in urbanising landscapes: Habitat selection and recommendations for a sustainable future. *Biological Conservation*, *241*, 108343. https://doi.org/10.1016/j.biocon.2019.108343

Gorman, K., Deeley, S., Barr, E., Freeze, S., Kalen, N., Muthersbaugh, M., & Ford, W. (2022). Broad-scale geographic and temporal assessment of northern long-eared bat (Myotis septentrionalis) maternity colony-landscape association. *Endangered Species Research*, *47*, 119–130. https://doi.org/10.3354/esr01170

Grindal, S. D., & Brigham, R. M. (1999). Impacts of forest harvesting on habitat use by foraging insectivorous bats at different spatial scales. *Écoscience*, *6*(1), 25–34.

Harrison, X. A., Blount, J. D., Inger, R., Norris, D. R., & Bearhop, S. (2011). Carry-over effects as drivers of fitness differences in animals: Carry-over effects in animal populations. *Journal of Animal Ecology*, *80*(1), 4–18. https://doi.org/10.1111/j.1365-2656.2010.01740.x

Harrison, X. A., Donaldson, L., Correa-Cano, M. E., Evans, J., Fisher, D. N., Goodwin, C. E. D., Robinson, B. S., Hodgson, D. J., & Inger, R. (2018). A brief introduction to mixed effects modelling and multi-model inference in ecology. *PeerJ*, *6*, e4794. https://doi.org/10.7717/peerj.4794

Henry, M., Thomas, D. W., Vaudry, R., & Carrier, M. (2002). Foraging distances and home range of pregnant and lactating little brown bats (Myotis lucifugus). *Journal of Mammalogy*, *83*(3), 767–774. https://doi.org/10.1644/1545-1542(2002)083<0767:FDAHRO>2.0.CO;2

Hillen, J., Kiefer, A., & Veith, M. (2009). Foraging site fidelity shapes the spatial organisation of a population of female western barbastelle bats. *Biological Conservation*, *142*(4), 817–823. https://doi.org/10.1016/j.biocon.2008.12.017

Holloway, G. L., & Barclay, R. M. (2000). Importance of prairie riparian zones to bats in southeastern Alberta. *Écoscience*, *7*(2), 115–122. https://doi.org/10.1080/11956860.2000.11682579

Johnson, D. H. (1980). The Comparison of Usage and Availability Measurements for Evaluating Resource Preference. *Ecology*, *61*(1), 65–71. https://doi.org/10.2307/1937156

Jonasson, K. A., & Willis, C. K. R. (2011). Changes in Body Condition of Hibernating Bats Support the Thrifty Female Hypothesis and Predict Consequences for Populations with White-Nose Syndrome. *PLoS ONE*, *6*(6), e21061. https://doi.org/10.1371/journal.pone.0021061

Jonasson, K. A., & Willis, C. K. R. (2012). Hibernation energetics of free-ranging little brown bats. *Journal of Experimental Biology*, *215*(12), 2141–2149. https://doi.org/10.1242/jeb.066514

Kniowski, A. B., & Gehrt, S. D. (2014). Home range and habitat selection of the Indiana bat in an agricultural landscape. *Journal of Wildlife Management*, *78*(3), 503–512. https://doi.org/10.1002/jwmg.677

Krauel, J. J., & LeBuhn, G. (2016). Patterns of bat distribution and foraging activity in a highly urbanized temperate environment. *PLoS ONE*, *11*(12), 1–18. https://doi.org/10.1371/journal.pone.0168927

Krausman, P. R. (1999). Some Basic Principles of Habitat Use. In *Grazing Behavior of Livestock and Wildlife* (K.L. Launchbaugh, K.D. Sanders, J.C. Mosley., p. 6). Idaho Forest, Wildlife & Range Exp.

Kurta, A., Bell, G. P., Nagy, K. A., & Kunz, T. H. (1989). Energetics of pregnancy and lactation in free-ranging little brown bats (Myotis lucifugus). *Physiological Zoology*, *62*(3), 804–818. https://doi.org/10.1086/physzool.62.3.30157928

Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). lmerTest Package: Tests in Linear Mixed Effects Models. *Journal of Statistical Software*, *82*(13). https://doi.org/10.18637/jss.v082.i13

Lalla, K. M., Fraser, K. C., Frei, B., Fischer, J. D., Siegrist, J., Ray, J. D., Cohn-Haft, M., & Elliott, K. H. (2022). Central-place foraging poses variable constraints year-round in a neotropical migrant. *Movement Ecology*, *10*(1). https://doi.org/10.1186/s40462-022-00337-2

Lamb, J. S., Paton, P. W. C., Osenkowski, J. E., Badzinski, S. S., Berlin, A. M., Bowman, T., Dwyer, C., Fara, L. J., Gilliland, S. G., Kenow, K., Lepage, C., Mallory, M. L., Olsen, G. H., Perry, M. C., Petrie, S. A., Savard, J.-P. L., Savoy, L., Schummer, M., Spiegel, C. S., & McWilliams, S. R. (2020). Assessing year-round habitat use by migratory sea ducks in a multi-species context reveals seasonal variation in habitat selection and partitioning. *Ecography*, *43*(12), 1842–1858. https://doi.org/10.1111/ecog.05003

Landler, L., Ruxton, G. D., & Malkemper, E. P. (2018). Circular data in biology: Advice for effectively implementing statistical procedures. *Behavioral Ecology and Sociobiology*, *72*(8), 128. https://doi.org/10.1007/s00265-018-2538-y

Law, B., Park, K. J., & Lacki, M. J. (2016). Insectivorous Bats and Silviculture: Balancing Timber Production and Bat Conservation. In C. C. Voigt & T. Kingston (Eds.), *Bats in the Anthropocene: Conservation of Bats in a Changing World* (pp. 105–150). Springer International Publishing. https://doi.org/10.1007/978-3-319-25220-9_5

Lookingbill, T. R., Elmore, A. J., Engelhardt, K. A. M., Churchill, J. B., Edward Gates, J., & Johnson, J. B. (2010). Influence of wetland networks on bat activity in mixed-use landscapes. *Biological Conservation*, *143*(4), 974–983. https://doi.org/10.1016/j.biocon.2010.01.011

Lowe, A. J. (2012). *Swarming behaviour and fall roost-use of little brown (Myotis lucifugus), and northern long-eared bats (Myotis septentrionalis) in Nova Scotia, Canada*. St. Mary's University.

Mathewson, H. A., & Morrison, M. L. (2015). *Wildlife Habitat Conservation*. Johns Hopkins University Press. https://doi.org/10.1353/book.39709

Mayor, S. J., Schneider, D. C., Schaefer, J. A., & Mahoney, S. P. (2009). Habitat selection at multiple scales. *Ecoscience*, *16*(2), 238–247. https://doi.org/10.2980/16-2-3238

McGuire, L. P., Fenton, M. B., & Guglielmo, C. G. (2009). Effect of age on energy storage during prehibernation swarming in little brown bats (Myotis lucifugus). *Canadian Journal of Zoology*, *87*(6), 515–519. https://doi.org/10.1139/Z09-041

McGuire, L. P., Muise, K. A., Shrivastav, A., & Willis, C. K. R. (2016). No evidence of hyperphagia during prehibernation in a northern population of little brown bats (*Myotis lucifugus*). *Canadian Journal of Zoology*, *94*(12), 821–827. https://doi.org/10.1139/cjz-2016-0110

ministère de l'Environnement et de la Lutte contre les changements climatiques. (2022). *Utilisation du territoire*. https://www.donneesquebec.ca/recherche/dataset/utilisation-du-territoire

ministère des Forêts, de la Faune et des Parcs. (2022a). *Carte écoforestière originale et résultats d'inventaire*. https://www.donneesquebec.ca/recherche/dataset/resultats-d-inventaire-et-carte-ecoforestiere

ministère des Forêts, de la Faune et des Parcs. (2022b). *Récolte et autres interventions sylvicoles*. https://www.donneesquebec.ca/recherche/dataset/resultats-d-inventaire-et-carte-ecoforestiere

Nakagawa, S., Johnson, P. C. D., & Schielzeth, H. (2017). The coefficient of determination R2 and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. *Journal of Royal Society Interface*, *14*(20170213), 11.

Nelson, J. J., & Gillam, E. H. (2017). Selection of foraging habitat by female little brown bats (Myotis lucifugus). *Journal of Mammalogy*, *98*(1), 222–231. https://doi.org/10.1093/jmammal/gyw181

Newbold, T., Hudson, L. N., Hill, S. L. L., Contu, S., Lysenko, I., Senior, R. A., Börger, L., Bennett, D. J., Choimes, A., Collen, B., Day, J., De Palma, A., Díaz, S., Echeverria-Londoño, S., Edgar, M. J., Feldman, A., Garon, M., Harrison, M. L. K., Alhusseini, T., … Purvis, A. (2015). Global effects of land use on local terrestrial biodiversity. *Nature*, *520*(7545), 45–50. https://doi.org/10.1038/nature14324

Olsson, O., Brown, J. S., & Helf, K. L. (2008). A guide to central place effects in foraging. *Theoretical Population Biology*, *74*(1), 22–33. https://doi.org/10.1016/j.tpb.2008.04.005

O'Neill, H. M. K., Durant, S. M., & Woodroffe, R. (2020). What wild dogs want: Habitat selection differs across life stages and orders of selection in a wide-ranging carnivore. *BMC Zoology*, *5*(1), 1. https://doi.org/10.1186/s40850-019-0050-0

Orians & Pearson. (1979). On the theory of central place foraging. In J. Horn, R. Srairs, & R. D. Mitchell (Eds.), *Analysis of Ecological Systems* (pp. 155–177). Ohio State Press.

Parsons, K. N., & Jones, G. (2003). Dispersion and habitat use by Myotis daubentonii and Myotis nattereri during the swarming season: Implications for conservation. *Animal Conservation*, *6*(4), 283–290. https://doi.org/10.1017/S1367943003003342

Patriquin, K. J., & Barclay, R. M. R. (2003). Foraging by bats in cleared, thinned and unharvested boreal forest. *Journal of Applied Ecology*, *40*(4), 646–657. https://doi.org/10.1046/j.1365-2664.2003.00831.x

Pyke, G. H. (2019). Optimal Foraging Theory: An Introduction. In *Encyclopedia of Animal Behavior* (pp. 111–117). Elsevier. https://doi.org/10.1016/B978-0-12-809633-8.01156-0

QGIS.org. (2022). *QGIS Geographic Information System*. QGIS Association. http://www.qgis.org

R Studio Team. (2022). *RStudio: Integrated Development Environment for R*. http://www.rstudio.com/

Rainho, A., & Palmeirim, J. M. (2011). The importance of distance to resources in the spatial modelling of bat foraging habitat. *PLoS ONE*, *6*(4). https://doi.org/10.1371/journal.pone.0019227

Rivers, N. M., Butlin, R. K., & Altringham, J. D. (2006). Autumn swarming behaviour of Natterer's bats in the UK: Population size, catchment area and dispersal. *Biological Conservation*, *127*(2), 215–226. https://doi.org/10.1016/j.biocon.2005.08.010

Rosenberg, D. K., & McKelvey, K. S. (1999). Estimation of Habitat Selection for Central-Place Foraging Animals. *The Journal of Wildlife Management*, *63*(3), 1028–1038. https://doi.org/10.2307/3802818

Schooley, R. L. (1994). Annual Variation in Habitat Selection: Patterns Concealed by Pooled Data. *The Journal of Wildlife Management*, *58*(2), 367–374. https://doi.org/10.2307/3809404

Solari, S. (2021). *Myotis lucifugus (amended version of 2018 assessment)*. The IUCN Red List of Threatened Species 2021: E.T14176A208031565. https://dx.doi.org/10.2305/IUCN.UK.2021-3.RLTS.T14176A208031565.en

Stanley, C. Q., Dudash, M. R., Ryder, T. B., Shriver, W. G., Serno, K., Adalsteinsson, S., & Marra, P. P. (2021). Seasonal variation in habitat selection for a Neotropical migratory songbird using high-resolution GPS tracking. *Ecosphere*, *12*(3). https://doi.org/10.1002/ecs2.3421

Taylor, P. D., Crewe, T. L., Mackenzie, S. A., Lepage, D., Aubry, Y., Crysler, Z., Finney, G., Francis, C. M., Guglielmo, C. G., Hamilton, D. J., Holberton, R. L., Loring, P. H., Mitchell, G. W., Norris, D. R., Paquet, J., Ronconi, R. A., Smetzer, J. R., Smith, P. A., Welch, L. J., & Woodworth, B. K. (2017). The motus wildlife tracking system: A collaborative research network to enhance the understanding of wildlife movement. *Avian Conservation and Ecology*, *12*(1). https://doi.org/10.5751/ACE-00953-120108

Thomas, D. W., Fenton, M. B., & Barclay, R. M. R. (1979). Social Behavior of the Little Brown Bat, Myotis lucifugus: I. Mating Behavior. *Behavioral Ecology and Sociobiology*, *6*(2), 129–136.

Thomas, J. P., Kukka, P. M., Benjamin, J. E., Barclay, R. M. R., Johnson, C. J., Schmiegelow, F. K. A., & Jung, T. S. (2021). Foraging habitat drives the distribution of an endangered bat in an urbanizing boreal landscape. *Ecosphere*, *12*(3). https://doi.org/10.1002/ecs2.3457

Van Schaik, J., Janssen, R., Bosch, T., Haarsma, A. J., Dekker, J. J. A., & Kranstauber, B. (2015). Bats swarm where they hibernate: Compositional similarity between autumn swarming and winter hibernation assemblages at five underground sites. *PLoS ONE*, *10*(7), 1–12. https://doi.org/10.1371/journal.pone.0130850

Vasko, V., Blomberg, A. S., Vesterinen, E. J., Suominen, K. M., Ruokolainen, L., Brommer, J. E., Norrdahl, K., Niemelä, P., Laine, V. N., Selonen, V., & Lilley, T. M. (2020). Within-season changes in habitat use of forest-dwelling boreal bats. *Ecology and Evolution*, *10*(9), 4164–4174. https://doi.org/10.1002/ece3.6253

Venter, O., Brodeur, N. N., Nemiroff, L., Belland, B., Dolinsek, I. J., & Grant, J. W. A. (2006). Threats to Endangered Species in Canada. *BioScience*, *56*(11), 903. https://doi.org/10.1641/0006-3568(2006)56[903:TTESIC]2.0.CO;2

Wang, J., Gao, W., Wang, L., Metzner, W., Ma, J., & Feng, J. (2010). Seasonal variation in prey abundance influences habitat use by greater horseshoe bats (Rhinolophus ferrumequinum) in a temperate deciduous forest. *Canadian Journal of Zoology*, *88*(3), 315–323. https://doi.org/10.1139/Z10-005

CHAPTER 2 : SUPPLEMENTARY MATERIALS

Appendix 1: Methods of Estimation of the detection Range of the Receiver Towers

We evaluated the detection range of the towers in the study areas using different methods. We waved a test tag for three minutes at known locations around towers (every ~250 m till about 1500 m from the tower) using one of the following methods: tag mounted on a wooden stick (~5 m into the air); tag attached to a 50 ml saltwater tube mounted on a wooden stick (~5 m into the air) and tag attached to a 50 ml saltwater tube hanged to a drone (DJI Phantom 4, TS2 Space, Poland) with 100 cm rope (fly with constant rotation at five meters, 15 m and 30 m into the air). We used a saltwater tube to mimic the body of the animal. We did not find any major differences in detection range evaluated with the different methods and height. Depending on accessibility, we tested the detection range of at least one antenna for each tower. We tested the towers at 182 locations at the maternity roost and at 108 locations at the hibernaculum. Towers detected test tag up to 3060 m away, but generally much closer with a median detection range of 335.4 m and a means of 462.7 m (Figure S2.1). We acknowledge that it is impossible to accurately mimic the effect of the animals with a tag, and that those tests can only give an approximation of the detection range of our towers.

We also estimated the detection range of towers using simultaneous detections of bats between towers. When simultaneous detections occurred, it was from towers separated on average by 2072 m (median= 1916 m, max= 6096 m), which suggest a detection range of about 1036 m by towers. However, simultaneous detections represented 1.06% of total detections, suggesting that they were rare events. We estimated that the effective detection range of our towers was between 500 m and 1000 m, and consider 500 m as a conservative detection range (Crewe et al., 2019). We acknowledge that detection range might vary among towers depending on the landscape and line of sight (Crewe et al., 2019; Taylor et al., 2017).

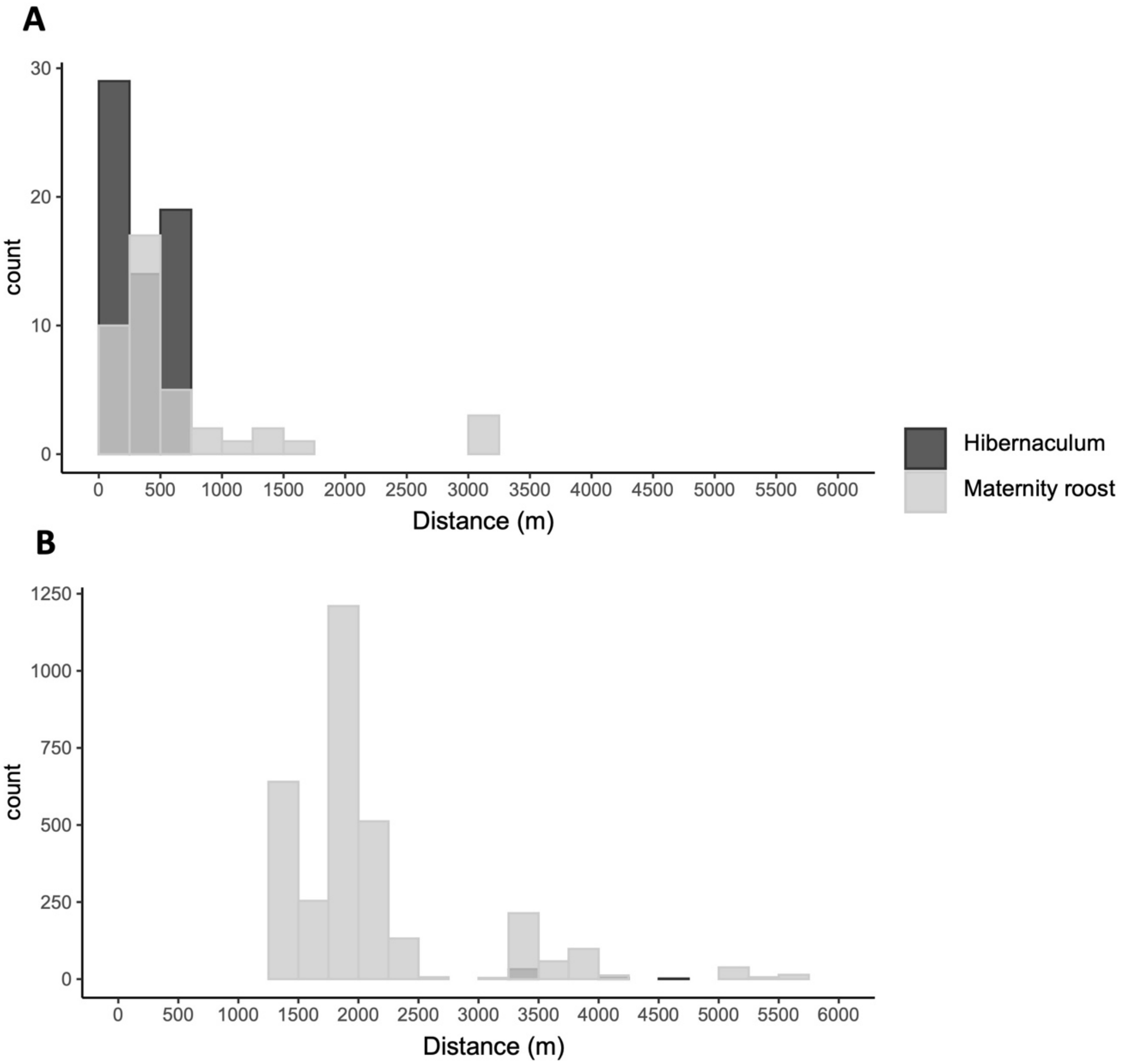

Figure S2.1. Evaluation of the detection ranges of the automated receiver towers at the maternity roost and hibernaculum A) Distance between towers and location of test tags detected ; B) Distance between towers when simultaneous detection of a bat happened.

GENERAL DISCUSSION

Temperate bats are affected by many threats like wildlife diseases (e.g., WNS; Frick et al., 2010), land use changes (Frick et al., 2019) and human disturbances (mining and electrical; Arnett et al., 2016; Frick et al., 2019). Understanding their habitat requirements is one of the key steps to enhance management programs, but many aspects must be considered. Temperate bats are highly mobile mammals that travel relatively long distances within nights and across seasons (Best & Geluso, 2003; Norquay et al., 2013; Roby et al., 2019). Habitat selection must thus span large spatial (e.g., Gallo et al., 2018) and temporal scales (e.g., Smeraldo et al., 2018). This thesis examined habitat selection and various aspects of temperate bat ecology considering temporal and spatial variation (Figure 3).

Chapter Summaries

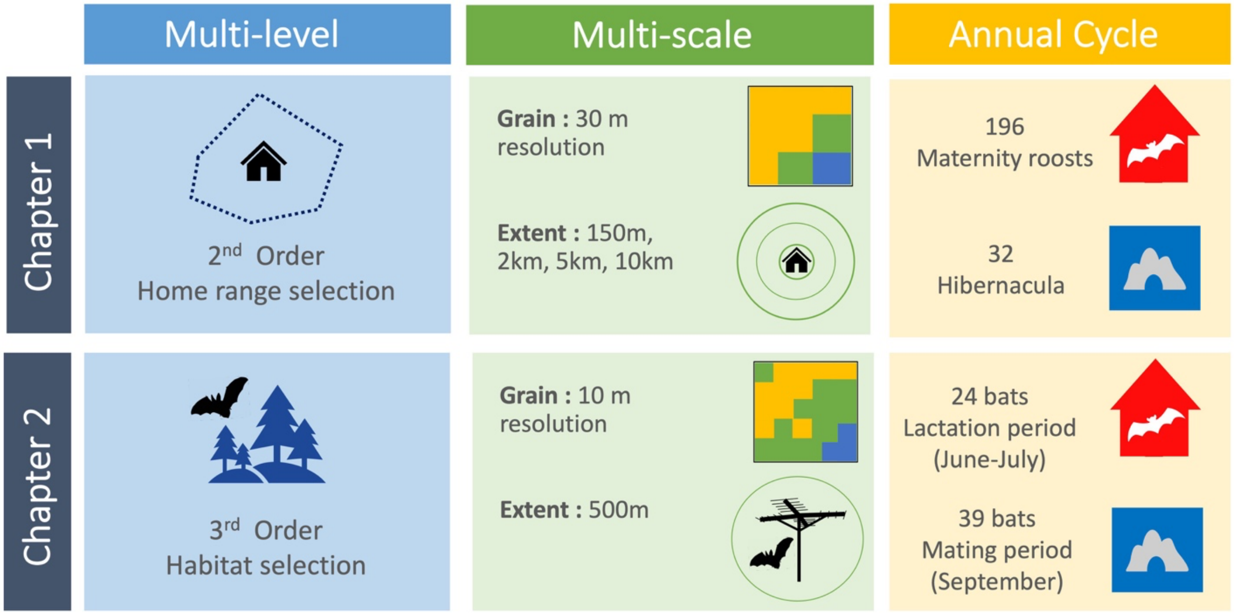

Figure 3. Summary of the framework used in both chapter of this thesis.

In Chapter 1, I studied large-scale roost selection of temperate bats using citizen science, a governmental database and land use data. I examined landscape patterns around summer maternity roosts used by females and around hibernacula used for mating and hibernation from late summer to spring. Both anthropogenic landscape and waterbodies positively influenced maternity roost selection. Hibernacula surrounded by less anthropogenically modified landscapes and more densely forested edges hosted more bats before WNS declines. Following WNS, hibernacula that had the lowest declines in bat population had more water features (area and edges density) in their surroundings, although future study should investigate this relation.

In Chapter 2, I focused on the little brown bat behaviour and habitat preferences at two periods of their annual cycle using automated telemetry. I looked at the behaviour of little brown bats at a maternity roost during summer lactation and at a hibernaculum during mating periods in late summer. Females at the maternity roost returned regularly and used a common feature (a river) in the vicinity. In fall, males and females did not return nightly to the hibernaculum and dispersed in a large home range in the surroundings.

Both chapters are related because roost selection can influence habitat preference or behaviour in the surroundings and vice versa (Daniel et al., 2008; Rosenberg & McKelvey, 1999). I demonstrated the importance of water features for maternity roost selection and for little brown bat activity during lactation which corroborates other studies on temperate bats (e.g., Balzer et al., 2022; Bergeson et al., 2013; Gorman et al., 2022). However, some discontinuity arises when looking at hibernacula. Forest edge density positively influenced hibernacula selection but negatively influenced bat activity levels in the surroundings. Bats commonly use forest edges to commute and forage (e.g., Grindal & Brigham, 1999; Kalcounis-Rueppell et al., 2013; Patriquin & Barclay, 2003), which complicated the interpretation of my results. Greater forest edge density around populated hibernacula could suggest that bats prefer more heterogeneous habitats with forest patches interwoven with other habitats like waterbodies and wetlands. Also, with the second chapter design, I cannot confirm that bat avoid using forest edges, I can only infer that bats activity level was higher in areas that cover little forest edges density. I recognize that the second chapter explored bat activity levels in relation to habitat at only one maternity roost and one hibernaculum. The habitat available around those sites could have influenced bat behaviour and habitat preferences (Geggie & Fenton, 1985; Laforge et al., 2021), which could explain the discontinuity between chapters. Future studies at different sites could help to contrast those findings.

In both chapters, habitat had a weak effect on roost selection and bat activity level. Chapter 1, the weak effect of habitat could reflect the selection pressure for the roost and hibernacula itself (e.g.,Neubaum et al., 2010; Randall & Broders, 2014). Furthermore, maternity roost and hibernacula in our study were concentrated in relatively high anthropogenic landscape which might have limited the variance in surrounding habitats. Similarly, in chapter 2 we may not have enough variation in habitat covered by the receiver towers to derive inference on habitat selection. The weak effect of habitat in our study could also suggest that 1) Bats can exploit microhabitats like single trees (Gehrt & Chelsvig, 2003; Moretto et al., 2019), that may not be detected by the grain of our habitat data; 2) the species I studied are generalists and can thrive in various habitat matrices (Agosta, 2002; Clare et al., 2014; Shively et al., 2018).

Limitations, Methods and Recommendations

Bat habitat requirements and behaviour are expected to vary according to their annual cycle (Smeraldo et al., 2018). Events during one period can create carry-over effects influencing the success of an animal in other periods (e.g., Davy et al., 2017; Harrison et al., 2011). Therefore, understanding the ecology and habitat requirements over the full annual cycle is crucial to develop comprehensive management plans. In my thesis I focused on roost selection and habitat preference during lactation period at the maternity roost and the mating period at the hibernaculum (Figure 4). I acknowledge that many variations can occur within those periods and that Chapter 2, for example, focused only on a few days during those periods. Indeed, as pups become volant visitation pattern at the maternity roost is expected to change (Anthony et al., 1981; Henry et al., 2002) and swarming is divided in different phases that could influence activity at the hibernaculum and its vicinity (e.g., Fenton, 1997). I must also acknowledge the importance of spring and autumn migration in the annual cycle of temperate bats (Roby, 2019). During migration, bats can cover hundreds of kilometers in a few days, sometimes stopping on the way to exploit foraging and roosting habitats (Norquay et al., 2013; Roby, 2019; Samoray et al., 2019). Studying bats during migration periods is very challenging (Roby, 2019) and miniaturization of GPS devices with remote download capability and/or the advancement of satellite tracking systems (e.g., ICARUS, https://www.icarus.mpg.de/en) might eventually allow enhancing such understanding.

Using technologies and innovative ways to locate and track bats is necessary due to their cryptic and nocturnal nature (Meyer, 2015; O’Mara et al., 2014). Citizen science is one method that encourages gathering data on rare and cryptic species and that can contribute significantly to their management (Fontaine et al., 2022). Inevitably, citizen science often produces “presence only” data that are spatially biased towards inhabited areas, which can be challenging for habitat selection studies (Johnston et al., 2022). In my thesis, I used a “used vs. available” framework suited to presence only data (Johnson et al., 2006; Manly et al., 2002; Warton & Aarts, 2013) and I controlled for the potential spatial bias of citizen science data (e.g., by generating available roosts with similar bias as used roosts; Phillips et al., 2009) to the extent that is possible. I am confident that my roost selection analyses derived from citizen science are robust and reliable. Other studies have successfully used citizen science to study diverse aspects of bat research (e.g., Barlow et al., 2015; Gili et al., 2020; Shively & Barboza, 2017). As locating bats is a major challenge for studying them, citizen science can be a decisive tool to find bats over large scales (Barlow et al., 2015; Fontaine et al., 2022).

Once located, collecting data on bat movement and selected habitats remain challenging because of their small size and speed (Aldridge & Brigham, 1988; O'Mara et al., 2014). To date, small bat research relies on banding or passive integrated transponder (PIT) systems which inform on the start and the end point of a trip, such as entry and return to a central place (Fontaine, 2021) or movement among sites (Norquay et al., 2013). In habitat preference studies, bat activity levels according to habitat types had traditionally been quantified by acoustic detectors (e.g., Thomas et al., 2021). Yet, acoustic data are limited to inform on a species occurrence and cannot give insight on abundance nor individual variation (Gannon et al., 2003). To date, radiotracking is one of the only methods permitting small bats monitoring from roosts to foraging areas with precise individual level information (O'Mara et al., 2014). However, traditional frequency encoded radiotelemetry usually involves a lot of human effort for a small number of locations (Martin et al., 2009; O'Mara et al., 2014; Taylor et al., 2017).

Automated telemetry can provide new opportunities for research on small, cryptic, and fast-moving animals allowing almost continuous and simultaneous monitoring of many individuals. Automated telemetry has already proven to be relevant in studying various aspects of bat movement ecology and behaviour (e.g., Krauel et al., 2018; McGuire et al., 2012). So far, researchers have used automated tower networks to study habitat selection and movement patterns at large scales (Taylor et al., 2017). I showed that this technology is also promising on a small scale, especially for animals, like bats, that concentrate their movements around residences where receiver towers can be dispersed (also see Lenske & Nocera, 2018; McGuire et al., 2012; Nelson & Gillam, 2017). I acknowledge that while automated telemetry comes with high temporal coverage, it trades offs with spatial precision. Indeed, I could not estimate the exact position of bats on the landscape nor the exact detection range of our receiver towers. For these reasons, automated telemetry, although feasible, has limits in regards to its use in small-scale habitat selection studies (also see methods developed by Nelson & Gillam, 2017). Following our study, here are some recommendations for further studies using an automated telemetry design to study animals on small scales:

1) In studies where habitat components are important, the only habitat that can be considered in further analyses are the one within the detection range of receiver towers. Thus, positioning each receiver tower in different habitat matrices can ease to highlight habitat selection patterns.

2) In studies that rather focus on movement or activity where habitat components are not a priority, I suggest installing receiver towers in preferred habitats of the study species to maximize detection likelihood.

3) A spatial analysis of the study site should be done prior to the receiver towers installation to ensure topography allows reasonable line of sight to maximize detection ranges. Although already a good practice (Crewe et al., 2019; Taylor et al., 2017), this analysis should be done prior to the selection of the study sites as some areas are not suited to an automated telemetry design.

4) Detection range should be carefully studied, to understand how it varies with flight altitude, landscape features and antenna configuration.

5) Automated telemetry produced presence only data that are sometimes unbalanced among individuals. Automated telemetry can also produce thousands of data point and animals behaviours can be hard to differentiate (resting or moving). Further studies should focus on developing robust analytical methods to deal with these challenges.

THESIS CONCLUSION

Habitat selection is one of the most studied themes in ecology, perhaps because it remains a challenge to understand multi-scale mechanisms and because of the challenge to track animals movement (Mayor et al., 2009; McGarigal et al., 2016). As habitat modification and destruction are expected to remain one of the major drivers of biodiversity loss (Powers & Jetz, 2019), comprehensively understanding habitat requirements of vulnerable species becomes crucial. In my thesis, I developed an approach to study habitat selection and behaviour of small and cryptic mammals at different temporal and spatial scales using citizen science and innovative tracking technologies. I demonstrated the importance of natural habitat on the selection and on summer and winter roosts by temperate bats. Mainly, I demonstrated the importance of riparian habitat and rivers in at least a 2-5km radius of maternity roost as those features influenced positively both roost selection and bats activity in their surroundings. As for hibernacula, I demonstrated the importance of preserving a matrix of natural habitat in a radius of at least 13 km as bats roost and forage variably in that extend during mating periods. I recommend complementing the finding of this thesis by studying bat behaviour and habitat preference at different roosts and in different landscape matrices. Future research should also focus on habitat selection during other periods, such as migration and maternity colony breakup, to fulfill knowledge gaps in the full annual cycle.

REFERENCES

Adams, R. A., & Hayes, M. A. (2008). Water Availability and Successful Lactation by Bats as Related to Climate Change in Arid Regions of Western North America. *Journal of Animal Ecology*, *77*(6), 1115–1121.

Agosta, S. J. (2002). Habitat use, diet and roost selection by the big brown bat (Eptesicus fuscus) in North America: A case for conserving an abundant species. *Mammal Review*, *32*(3), 179–198. https://doi.org/10.1046/j.1365-2907.2002.00103.x

Alcalde, J. T., Jiménez, M., Brila, I., Vintulis, V., Voigt, C. C., & Pētersons, G. (2021). Transcontinental 2200 km migration of a Nathusius' pipistrelle (*Pipistrellus nathusii*) across Europe. *Mammalia*, *85*(2), 161–163. https://doi.org/10.1515/mammalia-2020-0069

Aldridge, H. D. J. N., & Brigham, R. M. (1988). Load Carrying and Maneuverability in an Insectivorous Bat: A Test of the 5% "Rule" of Radio-Telemetry. *Journal of Mammalogy*, *69*(2), 379–382. https://doi.org/10.2307/1381393

Andersen, B. R., McGuire, L. P., Wigley, T. B., Miller, D. A., & Stevens, R. D. (2022). Habitat Associations of Overwintering Bats in Managed Pine Forest Landscapes. *Forests*, *13*(5), 803. https://doi.org/10.3390/f13050803

Anthony, E. L. P., Stack, M. H., & Kunz, T. H. (1981). Night roosting and the nocturnal time budget of the little brown bat, Myotis lucifugus: Effects of reproductive status, prey density, and environmental conditions. *Oecologia*, *51*(2), 151–156. https://doi.org/10.1007/BF00540593

Arnett, E. B., Baerwald, E. F., Mathews, F., Rodrigues, L., Rodríguez-Durán, A., Rydell, J., Villegas-Patraca, R., & Voigt, C. C. (2016). Impacts of Wind Energy Development on Bats: A Global Perspective. In C. C. Voigt & T. Kingston (Eds.), *Bats in the Anthropocene: Conservation of Bats in a Changing World* (pp. 295–323). Springer International Publishing. https://doi.org/10.1007/978-3-319-25220-9_11

Avila-Flores, R., & Fenton, M. B. (2005). Use of spatial features by foraging insectivorous bats in a large urban landscape. *Journal of Mammalogy*, *86*(6), 1193–1204. https://doi.org/10.1644/04-MAMM-A-085R1.1

Balzer, E. W., McBurney, T. S., & Broders, H. G. (2022). Little brown Myotis roosts are spatially associated with foraging resources on Prince Edward Island. *Wildlife Society Bulletin*. https://doi.org/10.1002/wsb.1405

Barlow, K. E., Briggs, P. A., Haysom, K. A., Hutson, A. M., Lechiara, N. L., Racey, P. A., Walsh, A. L., & Langton, S. D. (2015). Citizen science reveals trends in bat populations: The National Bat Monitoring Programme in Great Britain. *Biological Conservation*, *182*, 14–26. https://doi.org/10.1016/j.biocon.2014.11.022

Beier, P., & McCullough, D. R. (1990). Factors Influencing White-Tailed Deer Activity Patterns and Habitat Use. *Wildlife Monographs*, *109*, 3–51.

Bellamy, C., & Altringham, J. (2015). Predicting species distributions using record centre data: Multi-scale modelling of habitat suitability for bat roosts. *PLoS ONE*, *10*(6). https://doi.org/10.1371/journal.pone.0128440

Bergeson, S. M., Carter, T. C., & Whitby, M. D. (2013). Partitioning of foraging resources between sympatric Indiana and little brown bats. *Journal of Mammalogy*, *94*(6), 1311–1320. https://doi.org/10.1644/12-MAMM-A-311

Best, T. L., & Geluso, K. N. (2003). SUMMER FORAGING RANGE OF MEXICAN FREE-TAILED BATS (TADARIDA BRASILIENSIS MEXICANA) FROM CARLSBAD CAVERN, NEW MEXICO. *The Southwestern Naturalist*, *48*(4), 590–596. https://doi.org/10.1894/0038-4909(2003)048<0590:SFROMF>2.0.CO;2

Bjørneraas, K., Herfindal, I., Solberg, E. J., Sæther, B.-E., van Moorter, B., & Rolandsen, C. M. (2012). Habitat quality influences population distribution, individual space use and functional responses in habitat selection by a large herbivore. *Oecologia*, *168*(1), 231–243. https://doi.org/10.1007/s00442-011-2072-3

Bohn, K. M., & Gillam, E. H. (2018). In-flight social calls: A primer for biologists and managers studying echolocation. *Canadian Journal of Zoology*, *96*(8), 787–800. https://doi.org/10.1139/cjz-2017-0188

Boughey, K. L., Lake, I. R., Haysom, K. A., & Dolman, P. M. (2011). Effects of landscape-scale broadleaved woodland configuration and extent on roost location for six bat species across the UK. *Biological Conservation*, *144*(9), 2300–2310. https://doi.org/10.1016/j.biocon.2011.06.008

Boyles, J. G., Dunbar, M. B., & Whitaker Jr, J. O. (2006). Activity following arousal in winter in North American vespertilionid bats. *Mammal Review*, *36*(4), 267–280. https://doi.org/10.1111/j.1365-2907.2006.00095.x

Brack, V. (2006). Autumn Activity of Myotis sodalis (Indiana Bat) in Bland County, Virginia. *Northeastern Naturalist*, *13*(3), 421–434. https://doi.org/10.1656/1092-6194(2006)13[421:AAOMSI]2.0.CO;2

Bridge, E. S., Kelly, J. F., Contina, A., Gabrielson, R. M., MacCurdy, R. B., & Winkler, D. W. (2013). Advances in tracking small migratory birds: A technical review of light-level geolocation: Light-Level Geolocation Dataloggers. *Journal of Field Ornithology*, *84*(2), 121–137. https://doi.org/10.1111/jofo.12011

Broders, H. G., & Forbes, G. J. (2004). Interspecific and Intersexual Variation in Roost-Site Selection of Northern Long-Eared and Little Brown Bats in the Greater Fundy National Park Ecosystem. *The Journal of Wildlife Management*, *68*(3), 602–610.

Broders, H. G., Forbes, G. J., Woodley, S., & Thompson, I. D. (2006). Range Extent and Stand Selection for Roosting and Foraging in Forest-Dwelling Northern Long-Eared Bats and Little Brown Bats in the Greater Fundy Ecosystem, New Brunswick. *Journal of Wildlife Management*, *70*(5), 1174–1184. https://doi.org/10.2193/0022-541x(2006)70[1174:reassf]2.0.co;2

Brooks, R. T., & Ford, W. M. (2005). Bat Activity in a Forest Landscape of Central Massachusetts. *Northeastern Naturalist*, *12*(4), 447–462.

Burns, L. E., & Broders, H. G. (2015). Maximizing mating opportunities: Higher autumn swarming activity in male versus female myotis bats. *Journal of Mammalogy*, *96*(6), 1326–1336. https://doi.org/10.1093/jmammal/gyv141

Cagnacci, F., Boitani, L., Powell, R. A., & Boyce, M. S. (2010). Animal ecology meets GPS-based radiotelemetry: A perfect storm of opportunities and challenges. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1550), 2157–2162. https://doi.org/10.1098/rstb.2010.0107

Canadian Council on Animal Care. (2023). *CCAC guidelines: Wildlife*. https://ccac.ca/Documents/Standards/Guidelines/CCAC_Guidelines-Wildlife.pdf

Chandler, M., See, L., Copas, K., Bonde, A. M. Z., López, B. C., Danielsen, F., Legind, J. K., Masinde, S., Miller-Rushing, A. J., Newman, G., Rosemartin, A., & Turak, E. (2017). Contribution of citizen science towards international biodiversity monitoring. *Biological Conservation*, *213*, 280–294. https://doi.org/10.1016/j.biocon.2016.09.004

Cheng, T. L., Gerson, A., Moore, M. S., Reichard, J. D., DeSimone, J., Willis, C. K. R., Frick, W. F., & Kilpatrick, A. M. (2019). Higher fat stores contribute to persistence of little brown bat populations with white-nose syndrome. *Journal of Animal Ecology*, *88*(4), 591–600. https://doi.org/10.1111/1365-2656.12954

Cheng, T. L., Reichard, J. D., Coleman, J. T. H., & Weller, T. J. (2021). The scope and severity of white-nose syndrome on hibernating bats in North America. *Conservation Biology*, *35*, 1586–1597. https://doi.org/DOI: 10.1111/cobi.13739

Clare, E. L., Symondson, W. O. C., & Fenton, M. B. (2014). An inordinate fondness for beetles? Variation in seasonal dietary preferences of night-roosting big brown bats (Eptesicus fuscus). *Molecular Ecology*, *23*(15), 3633–3647. https://doi.org/10.1111/mec.12519

Cooper, C. B., Hawn, C. L., Larson, L. R., Parrish, J. K., Bowser, G., Cavalier, D., Dunn, R. R., Haklay, M. (Muki), Gupta, K. K., Jelks, N. O., Johnson, V. A., Katti, M., Leggett, Z., Wilson, O. R., & Wilson, S. (2021). Inclusion in citizen science: The conundrum of rebranding. *Science*, *372*(6549), 1386–1388. https://doi.org/10.1126/science.abi6487

Crawford, R. D., & O'Keefe, J. M. (2021). Avoiding a conservation pitfall: Considering the risks of unsuitably hot bat boxes. *Conservation Science and Practice*, *3*(6). https://doi.org/10.1111/csp2.412

Crewe, T. L., Deakin, J. E., Beauchamp, A. T., & Morbey, Y. E. (2019). Detection range of songbirds using a stopover site by automated radio-telemetry. *Journal of Field Ornithology*, *90*(2), 176–189. https://doi.org/10.1111/jofo.12291

Daniel, S., Korine, C., & Pinshow, B. (2008). Central-place foraging in nursing, arthropod-gleaning bats. *Canadian Journal of Zoology*, *86*(7), 623–626. https://doi.org/10.1139/Z08-041

Davis, W. H., & Hitchcock, H. (1965). Biology and migration of the bat, Myotis lucifugus , in New England. *Journal of Mammalogy*, *46*(2), 296–313.

Davy, C. M., Mastromonaco, G. F., Riley, J. L., Baxter-Gilbert, J. H., Mayberry, H., & Willis, C. K. R. (2017). Conservation implications of physiological carry-over effects in bats recovering from white-nose syndrome: Carry-Over Effects of Pathogen Exposure. *Conservation Biology*, *31*(3), 615–624. https://doi.org/10.1111/cobi.12841 de Boer, W. F., de Koppel, S. van, de Knegt, H. J., & Dekker, J. J. A. (2013). Hibernation site requirements of bats in man-made hibernacula in a spatial context. *Ecological Applications*, *23*(2), 502–514. https://doi.org/10.1890/1051-0761-23.2.502

Dekeukeleire, D., Janssen, R., Haarsma, A. J., Bosch, T., & Van Schaik, J. (2016). Swarming Behaviour, Catchment Area and Seasonal Movement Patterns of the Bechstein's Bats: Implications for Conservation. *Acta Chiropterologica*, *18*(2), 349–358. https://doi.org/10.3161/15081109ACC2016.18.2.004

Dickinson, J. L., Zuckerberg, B., & Bonter, D. N. (2010). Citizen Science as an Ecological Research Tool: Challenges and Benefits. *Annual Review of Ecology, Evolution, and Systematics*, *41*(1), 149–172. https://doi.org/10.1146/annurev-ecolsys-102209-144636

Dietz, M., Bögelsack, K., Krannich, A., & Simon, O. (2020). Woodland fragments in urban landscapes are important bat areas: An example of the endangered Bechstein's bat Myotis bechsteinii. *Urban Ecosystems*, *23*(6), 1359–1370. https://doi.org/10.1007/s11252-020-01008-z

Dodd, L. E., Lacki, M. J., Britzke, E. R., Buehler, D. A., Keyser, P. D., Larkin, J. L., Rodewald, A. D., Wigley, T. B., Wood, P. B., & Rieske, L. K. (2012). Forest structure affects trophic linkages: How silvicultural disturbance impacts bats and their insect prey. *Forest Ecology and Management*, *267*, 262–270. https://doi.org/10.1016/j.foreco.2011.12.016

Domashinski, G. (2022). *The physiological ecology of preparing for and recovering from hibernation in temperate insectivorous bats*. University of Waterloo.

Elliott, K. H., Woo, K. J., Gaston, A. J., Benvenuti, S., Dall'Antonia, L., & Davoren, G. K. (2009). Central-place Foraging in an Arctic Seabird Provides Evidence for Storer-Ashmole's Halo. *The Auk*, *126*(3), 613–625. https://doi.org/10.1525/auk.2009.08245

Fabianek, F., Gagnon, D., & Delorme, M. (2011). Bat distribution and activity in Montrél Island green spaces: Responses to multi-scale habitat effects in a densely urbanized area. *Ecoscience*, *18*(1), 9–17. https://doi.org/10.2980/18-1-3373

Farhadinia, M. S., Moll, R. J., Montgomery, R. A., Ashrafi, S., Johnson, P. J., Hunter, L. T. B., & Macdonald, D. W. (2018). Citizen science data facilitate monitoring of rare large carnivores in remote montane landscapes. *Ecological Indicators*, *94*, 283–291. https://doi.org/10.1016/j.ecolind.2018.06.064

Fattebert, J., Michel, V., Scherler, P., Naef-Daenzer, B., Milanesi, P., & Grüebler, M. U. (2018). Little owls in big landscapes: Informing conservation using multi-level resource selection functions. *Biological Conservation*, *228*, 1–9. https://doi.org/10.1016/j.biocon.2018.09.032

Fenton, M. B. (1969). Summer activity of M. lucifugus at hibernacula in Ontario and Quebec. *Canadian Journal of Zoology*, *47*, 597–602.

Fenton, M. B. (1997). Science and the conservation of bats. *Journal of Mammalogy*, *78*(12), 2059–2060. https://doi.org/10.1139/cjz-78-12-2059

Festa, F., Ancillotto, L., Santini, L., Pacifici, M., Rocha, R., Toshkova, N., Amorim, F., Benítez-López, A., Domer, A., Hamidović, D., Kramer-Schadt, S., Mathews, F., Radchuk, V., Rebelo, H., Ruczynski, I., Solem, E., Tsoar, A., Russo, D., & Razgour, O. (2023). Bat responses to climate change: A systematic review. *Biological Reviews*, *98*(1), 19–33. https://doi.org/10.1111/brv.12893

Finch, D., Schofield, H., & Mathews, F. (2020). Traffic noise playback reduces the activity and feeding behaviour of free-living bats. *Environmental Pollution*, *263*. https://doi.org/10.1016/j.envpol.2020.114405

Fisher, K. E., Adelman, J. S., & Bradbury, S. P. (2020). Employing Very High Frequency (VHF) Radio Telemetry to Recreate Monarch Butterfly Flight Paths. *Environmental Entomology*, *49*(2), 312–323. https://doi.org/10.1093/ee/nvaa019

Fontaine, A. (2021). *Citizen science and development of innovative tools to improve conservation of threatened bats*. McGill University.

Fontaine, A., Simard, A., Brunet, N., & Elliott, K. H. (2022). The scientific contributions of citizen science applied to rare or threatened animals. *Conservation Biology*, cobi.13976. https://doi.org/10.1111/cobi.13976

Fontaine, A., Simard, A., Dubois, B., Dutel, J., & Elliott, K. H. (2021). Using mounting , orientation , and design to improve bat box thermodynamics in a northern temperate environment. *Scientific Reports*, 1–15. https://doi.org/10.1038/s41598-021-87327-3

Ford, W. M., Menzel, M. A., Rodrigue, J. L., Menzel, J. M., & Johnson, J. B. (2005). Relating bat species presence to simple habitat measures in a central Appalachian forest. *Biological Conservation*, *126*(4), 528–539. https://doi.org/10.1016/j.biocon.2005.07.003

Fraser, E. E., & McGuire, L. P. (2023). Prehibernation swarming in temperate bats: A critical transition between summer activity and hibernation. *Canadian Journal of Zoology*, cjz-2022-0129. https://doi.org/10.1139/cjz-2022-0129

Frick, W. F., Dzal, Y. A., Jonasson, K. A., Whitby, M. D., Adams, A. M., Long, C., Depue, J. E., Newman, C. M., Willis, C. K. R., & Cheng, T. L. (2023). Bats increased foraging activity at experimental prey patches near hibernacula. *Ecological Solutions and Evidence*, *4*(1), 2688-8319.12217. https://doi.org/10.1002/2688-8319.12217

Frick, W. F., Kingston, T., & Flanders, J. (2019). A review of the major threats and challenges to global bat conservation. *Annals of the New York Academy of Sciences*. https://doi.org/10.1111/nyas.14045 CITATIONS

Frick, W. F., Pollock, J. F., Hicks, A. C., Langwig, K. E., Reynolds, D. S., Turner, G. G., Butchkoski, C. M., & Kunz, T. H. (2010). An emerging disease causes regional population collapse of a common North American bat species. *Science*, *329*(5992), 679–682. https://doi.org/10.1126/science.1188594

Fukui, D., Murakami, M., Nakano, S., & Aoi, T. (2006). Effect of emergent aquatic insects on bat foraging in a riparian forest. *Journal of Animal Ecology*, *75*(6), 1252–1258. https://doi.org/10.1111/j.1365-2656.2006.01146.x

Furmankiewicz, J. (2008). Population size, catchment area, and sex-influenced differences in autumn and spring swarming of the brown long-eared bat (Plecotus auritus). *Canadian Journal of Zoology*, *86*(3), 207–216. https://doi.org/10.1139/Z07-134

Furmankiewicz, J., & Altringham, J. (2007). Genetic structure in a swarming brown long-eared bat (Plecotus auritus) population: Evidence for mating at swarming sites. *Conservation Genetics*, *8*(4), 913–923. https://doi.org/10.1007/s10592-006-9246-2

Furmankiewicz, J., & Kucharska, M. (2009). Migration of Bats along a Large River Valley in Southwestern Poland. *Journal of Mammalogy*, *90*(6), 1310–1317. https://doi.org/10.1644/09-MAMM-S-099R1.1

Gallant, A. J., & Broders, H. G. (2015). Body condition explains little of the interindividual variation in the swarming behaviour of adult male little brown myotis (*Myotis lucifugus*) in Nova Scotia, Canada. *Canadian Journal of Zoology*, *93*(6), 469–476. https://doi.org/10.1139/cjz-2014-0249

Gallo, T., Lehrer, E. W., Fidino, M., Kilgour, R. J., Wolff, P. J., & Magle, S. B. (2018). Need for multiscale planning for conservation of urban bats. *Conservation Biology*, *32*(3), 638–647. https://doi.org/10.1111/cobi.13047

Gannon, W. L., Sherwin, R. E., & Haymond, S. (2003). On the Importance of Articulating Assumptions When Conducting Acoustic Studies of Habitat Use. *Wildlife Society Bulletin*, *31*(1), 45–61.

Garbino, G. S. T., Feijó, A., Beltrão-Mendes, R., & Da Rocha, P. A. (2021). Evolution of litter size in bats and its influence on longevity and roosting ecology. *Biological Journal of the Linnean Society*, *132*(3), 676–684. https://doi.org/10.1093/biolinnean/blaa203

Garshelis, D. L. (2000). Delusions in Habitat Evaluation: Measuring Use, Selection, and Importance. In *Research tech-niques in animal ecology: Controversies and consequences* (L. Boitani&T. K. Fuller, pp. 111–157). Columbia University Press.

Geggie, J. F., & Fenton, M. B. (1985). A comparison of foraging by *Eptesicus fuscus* (Chiroptera: Vespertilionidae) in urban and rural environments. *Canadian Journal of Zoology*, *63*(2), 263–266. https://doi.org/10.1139/z85-040

Gehrt, S. D., & Chelsvig, J. E. (2003). Bat Activity in an Urban Landscape: Patterns at the Landscape and Microhabitat Scale A. *Ecological Applications*, *13*(4), 939–950.

Gili, F., Newson, S. E., Gillings, S., Chamberlain, D. E., & Border, J. A. (2020). Bats in urbanising landscapes: Habitat selection and recommendations for a sustainable future. *Biological Conservation*, *241*, 108343. https://doi.org/10.1016/j.biocon.2019.108343

Glover, A. M., & Altringham, J. D. (2008). Cave selection and use by swarming bat species. *Biological Conservation*, *141*(6), 1493–1504. https://doi.org/10.1016/j.biocon.2008.03.012

Gorman, K., Deeley, S., Barr, E., Freeze, S., Kalen, N., Muthersbaugh, M., & Ford, W. (2022). Broad-scale geographic and temporal assessment of northern long-eared bat (Myotis septentrionalis) maternity colony-landscape association. *Endangered Species Research*, *47*, 119–130. https://doi.org/10.3354/esr01170

Gray, C. L., Hill, S. L. L., Newbold, T., Hudson, L. N., Börger, L., Contu, S., Hoskins, A. J., Ferrier, S., Purvis, A., & Scharlemann, J. P. W. (2016). Local biodiversity is higher inside than outside terrestrial protected areas worldwide. *Nature Communications*, *7*(1), 12306. https://doi.org/10.1038/ncomms12306

Grindal, S. D., & Brigham, R. M. (1999). Impacts of forest harvesting on habitat use by foraging insectivorous bats at different spatial scales. *Écoscience*, *6*(1), 25–34.

Hammerson, G. A., Kling, M., Harkness, M., Ormes, M., & Young, B. E. (2017). Strong geographic and temporal patterns in conservation status of North American bats. *Biological Conservation*, *212*(February), 144–152. https://doi.org/10.1016/j.biocon.2017.05.025

Harrison, X. A., Blount, J. D., Inger, R., Norris, D. R., & Bearhop, S. (2011). Carry-over effects as drivers of fitness differences in animals: Carry-over effects in animal populations. *Journal of Animal Ecology*, *80*(1), 4–18. https://doi.org/10.1111/j.1365-2656.2010.01740.x

Henry, M. (2001). *Étude de l'écologie d'une population de petites chauves-souris brunes (Myotis Lucifugus Leconte) en vue d'un programme de conservation*. Sherbrooke University.

Henry, M., Thomas, D. W., Vaudry, R., & Carrier, M. (2002). Foraging distances and home range of pregnant and lactating little brown bats (Myotis lucifugus). *Journal of Mammalogy*, *83*(3), 767–774. https://doi.org/10.1644/1545-1542(2002)083<0767:FDAHRO>2.0.CO;2

Holloway, G. L., & Barclay, R. M. (2000). Importance of prairie riparian zones to bats in southeastern Alberta. *Écoscience*, *7*(2), 115–122. https://doi.org/10.1080/11956860.2000.11682579

Hoyt, J. R., Kilpatrick, A. M., & Langwig, K. E. (2021). Ecology and impacts of white-nose syndrome on bats. *Nature Reviews Microbiology*, *19*(3), 196–210. https://doi.org/10.1038/s41579-020-00493-5

Johnson, C. J., Nielsen, E., Merrill, E. H., Mcdonald, T. L., & Boyce, M. S. (2006). Resource Selection Functions Based on Use–Availability Data: Theoretical Motivation and Evaluation Methods. *Journal of Wildlife Management*, *70*(2), 347–357. https://doi.org/10.2193/0022-541x(2006)70[347:rsfbou]2.0.co;2

Johnson, D. H. (1980). The Comparison of Usage and Availability Measurements for Evaluating Resource Preference. *Ecology*, *61*(1), 65–71. https://doi.org/10.2307/1937156

Johnston, A., Matechou, E., & Dennis, E. B. (2022). Outstanding challenges and future directions for biodiversity monitoring using citizen science data. *Methods in Ecology and Evolution*, 2041-210X.13834. https://doi.org/10.1111/2041-210X.13834

Jonasson, K. A., & Willis, C. K. R. (2011). Changes in Body Condition of Hibernating Bats Support the Thrifty Female Hypothesis and Predict Consequences for Populations with White-Nose Syndrome. *PLoS ONE*, *6*(6), e21061. https://doi.org/10.1371/journal.pone.0021061

Jonasson, K. A., & Willis, C. K. R. (2012). Hibernation energetics of free-ranging little brown bats. *Journal of Experimental Biology*, *215*(12), 2141–2149. https://doi.org/10.1242/jeb.066514

Jordan, G. W. (2020). Status of an Anomalous Population of Northern Long-Eared Bats in Coastal North Carolina. *Journal of Fish and Wildlife Management*, *11*(2), 665–678. https://doi.org/10.3996/JFWM-20-018

Jung, K., Kaiser, S., Böhm, S., Nieschulze, J., & Kalko, E. K. V. (2012). Moving in three dimensions: Effects of structural complexity on occurrence and activity of insectivorous bats in managed forest stands. *Journal of Applied Ecology*, *49*(2), 523–531. https://doi.org/10.1111/j.1365-2664.2012.02116.x

Jung, K., & Threlfall, C. G. (2018). Trait-dependent tolerance of bats to urbanization: A global meta-analysis. *Proceedings of the Royal Society B: Biological Sciences*, *285*(1885), 20181222. https://doi.org/10.1098/rspb.2018.1222

Kalcounis-Rueppell, M. C., Briones, K. M., Homyack, J. A., Petric, R., Marshall, M. M., & Miller, D. A. (2013). Hard forest edges act as conduits, not filters, for bats. *Wildlife Society Bulletin*, *37*(3), 571–576. https://doi.org/10.1002/wsb.289

Katzner, T. E., & Arlettaz, R. (2020). Evaluating Contributions of Recent Tracking-Based Animal Movement Ecology to Conservation Management. *Frontiers in Ecology and Evolution*, *7*, 519. https://doi.org/10.3389/fevo.2019.00519

Kays, R., Crofoot, M. C., Jetz, W., & Wikelski, M. (2015). Terrestrial animal tracking as an eye on life and planet. *Science*, *348*(6240), aaa2478. https://doi.org/10.1126/science.aaa2478

Kerth, G. (2008). Causes and consequences of sociality in bats. *BioScience*, *58*(8), 737–746. https://doi.org/10.1641/B580810

Kerth, G., Weissmann, K., & König, B. (2001). Day Roost Selection in Female Bechstein's Bats (Myotis bechsteinii): A Field Experiment to Determine the Influence of Roost Temperature. *Oecologia*, *126*(1), 1–9.

King, D. I., Degraaf, R. M., Smith, M. -L., & Buonaccorsi, J. P. (2006). Habitat selection and habitat-specific survival of fledgling ovenbirds (*Seiurus aurocapilla*). *Journal of Zoology*, *269*(4), 414–421. https://doi.org/10.1111/j.1469-7998.2006.00158.x

Kissling, D. W., Pattemore, D. E., & Hagen, M. (2014). Challenges and prospects in the telemetry of insects: Insect telemetry. *Biological Reviews*, *89*(3), 511–530. https://doi.org/10.1111/brv.12065

Klüg-Baerwald, B. J., Lausen, C. L., Willis, C. K. R., & Brigham, R. M. (2017). Home is where you hang your bat: Winter roost selection by prairie-living big brown bats. *Journal of Mammalogy*, *98*(3), 752–760. https://doi.org/10.1093/jmammal/gyx039

Kniowski, A. B., & Gehrt, S. D. (2014). Home range and habitat selection of the Indiana bat in an agricultural landscape. *Journal of Wildlife Management*, *78*(3), 503–512. https://doi.org/10.1002/jwmg.677

Krauel, J. J., McGuire, L. P., & Boyles, J. G. (2018). Testing traditional assumptions about regional migration in bats. *Mammal Research*, *63*(2), 115–123. https://doi.org/10.1007/s13364-017-0346-9

Krausman, P. R. (1999). Some Basic Principles of Habitat Use. In *Grazing Behavior of Livestock and Wildlife* (K.L. Launchbaugh, K.D. Sanders, J.C. Mosley., p. 6). Idaho Forest, Wildlife & Range Exp.

Kunz, T. H., de Torrez, E. B., Bauer, D., Lobova, T., & Fleming, T. H. (2011). Ecosystem services provided by bats. *Annals of the New York Academy of Sciences*, *1223*(1), 1–38. https://doi.org/10.1111/j.1749-6632.2011.06004.x

Kunz, T. H., Whitaker, J. O., & Wadanoli, M. D. (1995). Dietary energetics of the insectivorous Mexican free-tailed bat (Tadarida brasiliensis) during pregnancy and lactation. *Oecologia*, *101*(4), 407–415. https://doi.org/10.1007/BF00329419

Kunz, T. H., Wrazen, J. A., & Burnett, C. D. (1998). Changes in body mass and fat reserves in prehibernating little brown bats (Myotis lucifugus). *Ecoscience*, *5*(1), 8–17.

Kurta, A., Bell, G. P., Nagy, K. A., & Kunz, T. H. (1989). Energetics of pregnancy and lactation in free-ranging little brown bats (Myotis lucifugus). *Physiological Zoology*, *62*(3), 804–818. https://doi.org/10.1086/physzool.62.3.30157928

Kurta, A., Kunz, T. H., & Nagy, K. A. (1990). Energetics and Water Flux of Free-Ranging Big Brown Bats (Eptesicus fuscus) during Pregnancy and Lactation. *Journal of Mammalogy*, *71*(1), 59–65. https://doi.org/10.2307/1381316

Laforge, A., Archaux, F., Coulon, A., Sirami, C., Froidevaux, J., Gouix, N., Ladet, S., Martin, H., Barré, K., Roemer, C., Claireau, F., Kerbiriou, C., Barbaro, L., & Algar, A. (2021). Landscape composition and life-history traits influence bat movement and space use: Analysis of 30 years of published telemetry data. *Global Ecology and Biogeography*, *30*(12), 2442–2454. https://doi.org/10.1111/geb.13397

Lalla, K. M., Fraser, K. C., Frei, B., Fischer, J. D., Siegrist, J., Ray, J. D., Cohn-Haft, M., & Elliott, K. H. (2022). Central-place foraging poses variable constraints year-round in a neotropical migrant. *Movement Ecology*, *10*(1). https://doi.org/10.1186/s40462-022-00337-2

Lamb, J. S., Paton, P. W. C., Osenkowski, J. E., Badzinski, S. S., Berlin, A. M., Bowman, T., Dwyer, C., Fara, L. J., Gilliland, S. G., Kenow, K., Lepage, C., Mallory, M. L., Olsen, G. H., Perry, M. C., Petrie, S. A., Savard, J.-P. L., Savoy, L., Schummer, M., Spiegel, C. S., & McWilliams, S. R. (2020). Assessing year-round habitat use by migratory sea ducks in a multi-species context reveals seasonal variation in habitat selection and partitioning. *Ecography*, *43*(12), 1842–1858. https://doi.org/10.1111/ecog.05003

Langwig, K. E., Frick, W. F., Bried, J. T., Hicks, A. C., Kunz, T. H., & Marm Kilpatrick, A. (2012). Sociality, density-dependence and microclimates determine the persistence of populations suffering from a novel fungal disease, white-nose syndrome. *Ecology Letters*, *15*(9), 1050–1057. https://doi.org/10.1111/j.1461-0248.2012.01829.x

Langwig, K. E., Frick, W. F., Reynolds, R., Parise, K. L., Drees, K. P., Hoyt, J. R., Cheng, T. L., Kunz, T. H., Foster, J. T., & Marm Kilpatrick, A. (2015). Host and pathogen ecology drive the seasonal dynamics of a fungal disease, white-nose syndrome. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1799), 10–12. https://doi.org/10.1098/rspb.2014.2335

Lausen, C. L., & Barclay, R. M. R. (2006). Benefits of living in a building: Big brown bats (Eptesicus fuscus) in rocks versus buildings. *Journal of Mammalogy*, *87*(2), 362–370. https://doi.org/10.1644/05-MAMM-A-127R1.1

Law, B., Park, K. J., & Lacki, M. J. (2016). Insectivorous Bats and Silviculture: Balancing Timber Production and Bat Conservation. In C. C. Voigt & T. Kingston (Eds.), *Bats in the Anthropocene: Conservation of Bats in a Changing World* (pp. 105–150). Springer International Publishing. https://doi.org/10.1007/978-3-319-25220-9_5

Lehrer, E. W., Gallo, T., Fidino, M., Kilgour, R. J., Wolff, P. J., & Magle, B. (2021). Landscape and Urban Planning Urban bat occupancy is highly influenced by noise and the location of water: Considerations for nature-based urban planning. *Landscape and Urban Planning*, *210*. https://doi.org/10.1016/j.landurbplan.2021.104063

Lele, S. R., Merrill, E. H., Keim, J., & Boyce, M. S. (2013). Selection, use, choice and occupancy: Clarifying concepts in resource selection studies. *Journal of Animal Ecology*, *82*(6), 1183–1191. https://doi.org/10.1111/1365-2656.12141

Lenske, A. K., & Nocera, J. J. (2018). Field test of an automated radio-telemetry system: Tracking local space use of aerial insectivores. *Journal of Field Ornithology*, *89*(2), 173–187. https://doi.org/10.1111/jofo.12254

Lewis, S. E. (1995). *Roost Fidelity of bats: A Review*. *76*(2), 481–496.

Long, R. A., Bowyer, R. T., Porter, W. P., Mathewson, P., Monteith, K. L., Findholt, S. L., Dick, B. L., & Kie, J. G. (2016). Linking habitat selection to fitness-related traits in herbivores: The role of the energy landscape. *Oecologia*, *181*(3), 709–720. https://doi.org/10.1007/s00442-016-3604-7

Lookingbill, T. R., Elmore, A. J., Engelhardt, K. A. M., Churchill, J. B., Edward Gates, J., & Johnson, J. B. (2010). Influence of wetland networks on bat activity in mixed-use landscapes. *Biological Conservation*, *143*(4), 974–983. https://doi.org/10.1016/j.biocon.2010.01.011

Lorch, J. M., Palmer, J. M., Lindner, D. L., Ballmann, A. E., George, K. G., Griffin, K., Knowles, S., Huckabee, J. R., Haman, K. H., Anderson, C. D., Becker, P. A., Buchanan, J. B., Foster, J. T., & Blehert, D. S. (2016). First Detection of Bat White-Nose Syndrome in Western North America. *MSphere*, *1*(4), e00148-16. https://doi.org/10.1128/mSphere.00148-16

Lowe, A. J. (2012). *Swarming behaviour and fall roost-use of little brown (Myotis lucifugus), and northern long-eared bats (Myotis septentrionalis) in Nova Scotia, Canada*. St. Mary's University.

Luszcz, T. M. J., & Barclay, R. M. R. (2016). Influence of forest composition and age on habitat use by bats in southwestern British Columbia. *Canadian Journal of Zoology*, *94*(2), 145–153. https://doi.org/10.1139/cjz-2015-0167

MacArthur, R. H., & Pianka, E. R. (1966). On Optimal Use of a Patchy Environment. *The American Naturalist*, *100*(916), 603–609. https://doi.org/10.1086/282454

Mackie, I. J., & Racey, P. A. (2007). Habitat use varies with reproductive state in noctule bats (Nyctalus noctula): Implications for conservation. *Biological Conservation*, *140*(1–2), 70–77. https://doi.org/10.1016/j.biocon.2007.07.031

Mainwaring, M. C., Hartley, I. R., Lambrechts, M. M., & Deeming, D. C. (2014). The design and function of birds' nests. *Ecology and Evolution*, *4*(20), 3909–3928. https://doi.org/10.1002/ece3.1054

Manly, McDonald, L. L., Thomas, Dana L., McDonald, T. L., & Erickson, W. P. (2002). *Resource Selection by Animals, Statistical Desing and Analysis for Field Studies* (Second Edition). Kluwer Academic Publisher.

Marra, P. P., Cohen, E. B., Loss, S. R., Rutter, J. E., & Tonra, C. M. (2015). A call for full annual cycle research in animal ecology. *Biology Letters*, *11*(8). https://doi.org/10.1098/rsbl.2015.0552

Martin, J., Modie, V., Tolon, Vincentorter, B., Basille, M., Calenge, C., & Moorter, B. V. (2009). On the use of telemetry in habitat selection studies. *...) Habitat Selection ...*, *November 2015*, 1–19.

Martin, T. G., Kehoe, L., Mantyka-Pringle, C., Chades, I., Wilson, S., Bloom, R. G., Davis, S. K., Fisher, R., Keith, J., Mehl, K., Diaz, B. P., Wayland, M. E., Wellicome, T. I., Zimmer, K. P., & Smith, P. A. (2018). Prioritizing recovery funding to maximize conservation of endangered species. *Conservation Letters*, *11*(6), e12604. https://doi.org/10.1111/conl.12604

Maslo, B., Valent, M., Gumbs, J. F., & Frick, W. F. (2015). Conservation implications of ameliorating survival of little brown bats with white-nose syndrome. *Ecological Applications*, *25*(7), 1832–1840. https://doi.org/10.1890/14-2472.1

Mathewson, H. A., & Morrison, M. L. (2015). *Wildlife Habitat Conservation*. Johns Hopkins University Press. https://doi.org/10.1353/book.39709

Mayor, S. J., Schneider, D. C., Schaefer, J. A., & Mahoney, S. P. (2009). Habitat selection at multiple scales. *Ecoscience*, *16*(2), 238–247. https://doi.org/10.2980/16-2-3238

McClure, M. L., Crowley, D., Haase, C. G., McGuire, L. P., Fuller, N. W., Hayman, D. T. S., Lausen, C. L., Plowright, R. K., Dickson, B. G., & Olson, S. H. (2020). Linking surface and subterranean climate: Implications for the study of hibernating bats and other cave dwellers. *Ecosphere*, *11*(10). https://doi.org/10.1002/ecs2.3274

McCracken, G. F., & Gustin, M. K. (1991). Nursing Behavior in Mexican Free-tailed Bat Maternity Colonies. *Ethology*, *89*(4), 305–321. https://doi.org/10.1111/j.1439-0310.1991.tb00376.x

McGarigal, K., Wan, H. Y., Zeller, K. A., Timm, B. C., & Cushman, S. A. (2016). Multi-scale habitat selection modeling: A review and outlook. *Landscape Ecology*, *31*(6), 1161–1175. https://doi.org/10.1007/s10980-016-0374-x

McGuire, L. P., Fenton, M. B., & Guglielmo, C. G. (2009). Effect of age on energy storage during prehibernation swarming in little brown bats (Myotis lucifugus). *Canadian Journal of Zoology*, *87*(6), 515–519. https://doi.org/10.1139/Z09-041

McGuire, L. P., Guglielmo, C. G., Mackenzie, S. A., & Taylor, P. D. (2012). Migratory stopover in the long-distance migrant silver-haired bat, Lasionycteris noctivagans. *Journal of Animal Ecology*, *81*(2), 377–385. https://doi.org/10.1111/j.1365-2656.2011.01912.x

McGuire, L. P., Muise, K. A., Shrivastav, A., & Willis, C. K. R. (2016). No evidence of hyperphagia during prehibernation in a northern population of little brown bats (*Myotis lucifugus*). *Canadian Journal of Zoology*, *94*(12), 821–827. https://doi.org/10.1139/cjz-2016-0110

Meyer, C. F. J. (2015). Methodological challenges in monitoring bat population- and assemblage-level changes for anthropogenic impact assessment. *Mammalian Biology*, *80*(3), 159–169. https://doi.org/10.1016/j.mambio.2014.11.002

Monck-Whipp, L., Martin, A. E., Francis, C. M., & Fahrig, L. (2018). Farmland heterogeneity benefits bats in agricultural landscapes. *Agriculture, Ecosystems and Environment*, *253*(November 2017), 131–139. https://doi.org/10.1016/j.agee.2017.11.001

Moretto, L., Fahrig, L., Smith, A. C., & Francis, C. M. (2019). A small-scale response of urban bat activity to tree cover. *Urban Ecosystems*, *22*(5), 795–805. https://doi.org/10.1007/s11252-019-00846-w

Morningstar, D., & Sandilands, A. (2019). Summer movements of a radio-tagged Hoary Bat (*Lasiurus cinereus*) captured in southwestern Ontario. *The Canadian Field-Naturalist*, *133*(2), 125. https://doi.org/10.22621/cfn.v133i2.2148

Motus Wildlife Tracking. (2022). *Explore data*. https://motus.org/explore/

Nelson, J. J., & Gillam, E. H. (2017). Selection of foraging habitat by female little brown bats (Myotis lucifugus). *Journal of Mammalogy*, *98*(1), 222–231. https://doi.org/10.1093/jmammal/gyw181

Neubaum, D. J. (2018). Unsuspected retreats: Autumn transitional roosts and presumed winter hibernacula of little brown myotis in Colorado. *Journal of Mammalogy*. https://doi.org/10.1093/jmammal/gyy120

Neubaum, D. J., Wilson, K. R., & O'Shea, T. J. (2010). Urban Maternity-Roost Selection by Big Brown Bats in Colorado. *The Journal of Wildlife Management*, *71*(3), 728–736.

Newbold, T., Hudson, L. N., Hill, S. L. L., Contu, S., Lysenko, I., Senior, R. A., Börger, L., Bennett, D. J., Choimes, A., Collen, B., Day, J., De Palma, A., Díaz, S., Echeverria-Londoño, S., Edgar, M. J., Feldman, A., Garon, M., Harrison, M. L. K., Alhusseini, T., … Purvis, A. (2015). Global effects of land use on local terrestrial biodiversity. *Nature*, *520*(7545), 45–50. https://doi.org/10.1038/nature14324

Nilsson, L., Persson, J., Bunnefeld, N., & Månsson, J. (2020). Central place foraging in a human-dominated landscape: How do common cranes select feeding sites? *Journal of Avian Biology*, *51*(6), jav.02487. https://doi.org/10.1111/jav.02487

Norquay, K. J. O., Martinez-Nuñez, F., Dubois, J. E., Monson, K. M., & Willis, C. K. R. (2013). Long-distance movements of little brown bats (Myotis lucifugus). *Journal of Mammalogy*, *94*(2), 506–515. https://doi.org/10.1644/12-MAMM-A-065.1

Norquay, K. J. O., & Willis, C. K. R. (2014). Hibernation phenology of Myotis lucifugus. *Journal of Zoology*, *294*(2), 85–92. https://doi.org/10.1111/jzo.12155

Ober, H. K., & Hayes, J. P. (2008). Influence of forest riparian vegetation on abundance and biomass of nocturnal flying insects. *Forest Ecology and Management*, *256*(5), 1124–1132. https://doi.org/10.1016/j.foreco.2008.06.010

Olsson, O., & Bolin, A. (2014). A model for habitat selection and species distribution derived from central place foraging theory. *Oecologia*, *175*(2), 537–548. https://doi.org/10.1007/s00442-014-2931-9

Olsson, O., Brown, J. S., & Helf, K. L. (2008). A guide to central place effects in foraging. *Theoretical Population Biology*, *74*(1), 22–33. https://doi.org/10.1016/j.tpb.2008.04.005

O'Mara, T., Wikelski, M., & Dechmann, D. K. N. (2014). 50 years of bat tracking: Device attachment and future directions. *Methods in Ecology and Evolution*, *5*(4), 311–319. https://doi.org/10.1111/2041-210X.12172

Orians & Pearson. (1979). On the theory of central place foraging. In J. Horn, R. Srairs, & R. D. Mitchell (Eds.), *Analysis of Ecological Systems* (pp. 155–177). Ohio State Press.

O'Shea, T. J., Ellison, L. E., Neubaum, D. J., Neubaum, M. A., Reynolds, C. A., & Bowen, R. A. (2010). Recruitment in a Colorado population of big brown bats: Breeding probabilities, litter size, and first-year survival. *Journal of Mammalogy*, *91*(2), 418–428. https://doi.org/10.1644/08-MAMM-A-295.1

Oxberry, B. A. (1979). Female reproductive patterns in hibernating bats. *Reproduction*, *56*(1), 359–367. https://doi.org/10.1530/jrf.0.0560359

Parsons, K. N., & Jones, G. (2003). Dispersion and habitat use by Myotis daubentonii and Myotis nattereri during the swarming season: Implications for conservation. *Animal Conservation*, *6*(4), 283–290. https://doi.org/10.1017/S1367943003003342

Patriquin, K. J., & Barclay, R. M. R. (2003). Foraging by bats in cleared, thinned and unharvested boreal forest. *Journal of Applied Ecology*, *40*(4), 646–657. https://doi.org/10.1046/j.1365-2664.2003.00831.x

Patriquin, K. J., Leonard, M. L., Broders, H. G., Ford, W. M., Britzke, E. R., & Silvis, A. (2016). Weather as a proximate explanation for fission–fusion dynamics in female northern long-eared bats. *Animal Behaviour*, *122*, 47–57. https://doi.org/10.1016/j.anbehav.2016.09.022

Pauli, B. P., Badin, H. A., Haulton, G. S., Zollner, P. A., & Carter, T. C. (2015). Landscape features associated with the roosting habitat of Indiana bats and northern long-eared bats. *Landscape Ecology*, *30*(10), 2015–2029. https://doi.org/10.1007/s10980-015-0228-y

Perry, R. W. (2013). A review of factors affecting cave climates for hibernating bats in temperate North America. *Environmental Reviews*, *21*(1), 28–39. https://doi.org/10.1139/er-2012-0042

Pettorelli, N., Laurance, W. F., O'Brien, T. G., Wegmann, M., Nagendra, H., & Turner, W. (2014). Satellite remote sensing for applied ecologists: Opportunities and challenges. *Journal of Applied Ecology*, *51*(4), 839–848. https://doi.org/10.1111/1365-2664.12261

Phillips, S. J., Dudík, M., Elith, J., Graham, C. H., Lehmann, A., Leathwick, J., & Ferrier, S. (2009). Sample selection bias and presence-only distribution models: Implications for background and pseudo-absence data. *Ecological Applications*, *19*(1), 181–197. https://doi.org/10.1890/07-2153.1

Powers, R. P., & Jetz, W. (2019). Global habitat loss and extinction risk of terrestrial vertebrates under future land-use-change scenarios. *Nature Climate Change*, *9*(4), 323–329. https://doi.org/10.1038/s41558-019-0406-z

Put, J. E., Mitchell, G. W., & Fahrig, L. (2018). Higher bat and prey abundance at organic than conventional soybean fields. *Biological Conservation*, *226*(February), 177–185. https://doi.org/10.1016/j.biocon.2018.06.021

Pyke, G. H. (2019). Optimal Foraging Theory: An Introduction. In *Encyclopedia of Animal Behavior* (pp. 111–117). Elsevier. https://doi.org/10.1016/B978-0-12-809633-8.01156-0

R Core Team. (2022). *R: A language and environment for statistical computing. R Foundation for Statistical Computing* [Computer software]. https://www.R-project.org/

Racey, P. a, & Swift, S. M. (1981). Variations in gestation length in a colony of pipistrelle bats (Pipistrellus pipistrellus) from year to year. *Journal of Reproduction and Fertility*, *61*(1), 123–129.

Rainho, A., & Palmeirim, J. M. (2011). The importance of distance to resources in the spatial modelling of bat foraging habitat. *PLoS ONE*, *6*(4). https://doi.org/10.1371/journal.pone.0019227

Randall, J., & Broders, H. G. (2014). Identification and Characterization of Swarming Sites used by Bats in Nova Scotia, Canada. *Acta Chiropterologica*, *16*(1), 109–116. https://doi.org/10.3161/150811014X683327

Reeder, D. A. M., Frank, C. L., Turner, G. G., Meteyer, C. U., Kurta, A., Britzke, E. R., Vodzak, M. E., Darling, S. R., Stihler, C. W., Hicks, A. C., Jacob, R., Grieneisen, L. E., Brownlee, S. A., Muller, L. K., & Blehert, D. S. (2012). Frequent arousal from hibernation linked to severity of infection and mortality in bats with white-nose syndrome. *PLoS ONE*, *7*(6). https://doi.org/10.1371/journal.pone.0038920

Rivers, N. M., Butlin, R. K., & Altringham, J. D. (2006). Autumn swarming behaviour of Natterer's bats in the UK: Population size, catchment area and dispersal. *Biological Conservation*, *127*(2), 215–226. https://doi.org/10.1016/j.biocon.2005.08.010

Roby, P. L. (2019). *The Ecology and Behavior of Spring Migrating Indiana Bats (Myotis sodalis)* [University of Kentucky Libraries]. https://doi.org/10.13023/ETD.2019.410

Roby, P. L., Gumbert, M. W., & Lacki, M. J. (2019). Nine years of Indiana bat (Myotis sodalis) spring migration behavior. *Journal of Mammalogy*, *100*(5), 1501–1511. https://doi.org/10.1093/jmammal/gyz104

Rockey, C. D., Stumpf, J. P., & Kurta, A. (2013). Additional Winter Recoveries of Indiana Bats (*Myotis sodalis*) Banded During Summer in Michigan. *Northeastern Naturalist*, *20*(3), N8–N13. https://doi.org/10.1656/045.020.0306

Rosenberg, D. K., & McKelvey, K. S. (1999). Estimation of Habitat Selection for Central-Place Foraging Animals. *The Journal of Wildlife Management*, *63*(3), 1028–1038. https://doi.org/10.2307/3802818

Ruczyński, I., & Bartoń, K. A. (2020). Seasonal changes and the influence of tree species and ambient temperature on the fission-fusion dynamics of tree-roosting bats. *Behavioral Ecology and Sociobiology*, *74*(5), 63. https://doi.org/10.1007/s00265-020-02840-1

Russo, D., & Ancillotto, L. (2014). Sensitivity of bats to urbanization: A review. *Mammalian Biology*, *80*(3), 205–212. https://doi.org/10.1016/j.mambio.2014.10.003

Rydell, J. (1992). Exploitation of Insects around Streetlamps by Bats in Sweden. *Functional Ecology*, *6*(6), 744–750.

Salinas-Ramos, V. B., Ancillotto, L., Cistrone, L., Nastasi, C., Bosso, L., Smeraldo, S., Sánchez Cordero, V., & Russo, D. (2021). Artificial illumination influences niche segregation in bats. *Environmental Pollution*, *284*. https://doi.org/10.1016/j.envpol.2021.117187

Samoray, S. T., Cotham, S. N., & Gumbert, M. W. (2019). Spring Migration Behavior of a Perimyotis subflavus (Tri-Colored Bat) from Tennessee. *Southeastern Naturalist*, *18*(3). https://doi.org/10.1656/058.018.0302

Schroder, E. S., Ekanayake, D. B., & Romano, S. P. (2017). Indiana bat maternity roost habitat preference within Midwestern United States upland Oak-Hickory (Quercus-Carya) forests. *Forest Ecology and Management*, *404*, 65–74. https://doi.org/10.1016/j.foreco.2017.08.032

Schweiger, B. R., Frey, J. K., & Cain, J. W. (2021). A case for multiscale habitat selection studies of small mammals. *Journal of Mammalogy*, *102*(5), 1249–1265. https://doi.org/10.1093/jmammal/gyab071

Senior, P., Butlin, R. K., & Altringham, J. D. (2005). Sex and segregation in temperate bats. *Proceedings of the Royal Society B: Biological Sciences*, *272*(1580), 2467–2473. https://doi.org/10.1098/rspb.2005.3237

Shively, R., & Barboza, P. (2017). Range And Roosting Ecology of the Little Brown Bat, *Myotis lucifugus* , In Interior and Northern Alaska. *Northwestern Naturalist*, *98*(2), 122–131. https://doi.org/10.1898/NWN16-16.1

Shively, R., Barboza, P., Doak, P., & Jung, T. S. (2018). Increased diet breadth of little brown bats (*Myotis lucifugus*) at their northern range limit: A multimethod approach. *Canadian Journal of Zoology*, *96*(1), 31–38. https://doi.org/10.1139/cjz-2017-0017

Shumba, T., Montgomery, R. A., Rasmussen, G. S. A., & Macdonald, D. W. (2018). African Wild Dog Habitat Use Modelling Using Telemetry Data and Citizen Scientist Sightings: Are the Results Comparable? *African Journal of Wildlife Research*, *48*(1), 013002. https://doi.org/10.3957/056.048.013002

Smeraldo, S., Di Febbraro, M., Bosso, L., Flaquer, C., Guixé, D., Lisón, F., Meschede, A., Juste, J., Prüger, J., Puig-Montserrat, X., & Russo, D. (2018). Ignoring seasonal changes in the ecological niche of non-migratory species may lead to biases in potential distribution models: Lessons from bats. *Biodiversity and Conservation*, *27*(9), 2425–2441. https://doi.org/10.1007/s10531-018-1545-7

Speakman, J. R., & Rowland, A. (1999). Preparing for inactivity: How insectivorous bats deposit a fat store for hibernation. *Proceedings of the Nutrition Society*, *58*(1), 123–131. https://doi.org/10.1079/PNS19990017

Stanley, C. Q., Dudash, M. R., Ryder, T. B., Shriver, W. G., Serno, K., Adalsteinsson, S., & Marra, P. P. (2021). Seasonal variation in habitat selection for a Neotropical migratory songbird using high-resolution GPS tracking. *Ecosphere*, *12*(3). https://doi.org/10.1002/ecs2.3421

Sullivan, B. L., Aycrigg, J. L., Barry, J. H., Bonney, R. E., Bruns, N., Cooper, C. B., Damoulas, T., Dhondt, A. A., Dietterich, T., Farnsworth, A., Fink, D., Fitzpatrick, J. W., Fredericks, T., Gerbracht, J., Gomes, C., Hochachka, W. M., Iliff, M. J., Lagoze, C., La Sorte, F. A., … Kelling, S. (2014). The eBird enterprise: An integrated approach to development and application of citizen science. *Biological Conservation*, *169*, 31–40. https://doi.org/10.1016/j.biocon.2013.11.003

Taylor, P. D., Crewe, T. L., Mackenzie, S. A., Lepage, D., Aubry, Y., Crysler, Z., Finney, G., Francis, C. M., Guglielmo, C. G., Hamilton, D. J., Holberton, R. L., Loring, P. H., Mitchell, G. W., Norris, D. R., Paquet, J., Ronconi, R. A., Smetzer, J. R., Smith, P. A., Welch, L. J., & Woodworth, B. K. (2017). The motus wildlife tracking system: A collaborative research network to enhance the understanding of wildlife movement. *Avian Conservation and Ecology*, *12*(1). https://doi.org/10.5751/ACE-00953-120108

Thomas, D. W., Dorais, M., & Bergeron, J.-M. (1990). Winter Energy Budgets and Cost of Arousals for Hibernating Little Brown Bats, Myotis lucifugus. *Journal of Mammalogy*, *71*(3), 475–479. https://doi.org/10.2307/1381967

Thomas, D. W., Fenton, M. B., & Barclay, R. M. R. (1979). Social Behavior of the Little Brown Bat, Myotis lucifugus: I. Mating Behavior. *Behavioral Ecology and Sociobiology*, *6*(2), 129–136.

Thomas, J. P., Kukka, P. M., Benjamin, J. E., Barclay, R. M. R., Johnson, C. J., Schmiegelow, F. K. A., & Jung, T. S. (2021). Foraging habitat drives the distribution of an endangered bat in an urbanizing boreal landscape. *Ecosphere*, *12*(3). https://doi.org/10.1002/ecs2.3457

Thompson, C. M., & McGarigal, K. (2002). The influence of research scale on bald eagle habitat selection along the lower Hudson River, New York (USA). *Landscape Ecology*, *17*(6), 569–586. https://doi.org/10.1023/A:1021501231182

Thorne, T. J., Matczak, E., Donnelly, M., Franke, M. C., & Kerr, K. C. R. (2021). Occurrence of a forest-dwelling bat , northern myotis (Myotis septentrionalis), within Canada ' s largest conurbation. *Journal of Urban Ecology*, 1–9. https://doi.org/10.1093/jue/juab029

Uhrin, M., Benda, P., & Kaňuch, P. (2017). Different responses of attic-dwelling bat species to landscape naturalness. *Mammalian Biology*, *82*, 48–56. https://doi.org/10.1016/j.mambio.2016.10.001

Van Schaik, J., Janssen, R., Bosch, T., Haarsma, A. J., Dekker, J. J. A., & Kranstauber, B. (2015). Bats swarm where they hibernate: Compositional similarity between autumn swarming and winter hibernation assemblages at five underground sites. *PLoS ONE*, *10*(7), 1–12. https://doi.org/10.1371/journal.pone.0130850

Venter, O., Brodeur, N. N., Nemiroff, L., Belland, B., Dolinsek, I. J., & Grant, J. W. A. (2006). Threats to Endangered Species in Canada. *BioScience*, *56*(11), 903. https://doi.org/10.1641/0006-3568(2006)56[903:TTESIC]2.0.CO;2

Verant, M. L., Boyles, J. G., Waldrep, W., Wibbelt, G., & Blehert, D. S. (2012). Temperature-Dependent Growth of Geomyces destructans, the Fungus That Causes Bat White-Nose Syndrome. *PLoS ONE*, *7*(9), e46280. https://doi.org/10.1371/journal.pone.0046280

Verant, M. L., Meteyer, C. U., Speakman, J. R., Cryan, P. M., Lorch, J. M., & Blehert, D. S. (2014). White-nose syndrome initiates a cascade of physiologic disturbances in the hibernating bat host. *BMC Physiology*, *14*(1). https://doi.org/10.1186/s12899-014-0010-4

Voigt, C. C., Phelps, K. L., Aguirre, L. F., Corrie Schoeman, M., Vanitharani, J., & Zubaid, A. (2016). Bats and Buildings: The Conservation of Synanthropic Bats. In C. C. Voigt & T. Kingston (Eds.), *Bats in the Anthropocene: Conservation of Bats in a Changing World* (pp. 427–462). Springer International Publishing. https://doi.org/10.1007/978-3-319-25220-9_14

Voigt, C. C., Scholl, J. M., Bauer, J., Teige, T., Yovel, Y., Kramer-Schadt, S., & Gras, P. (2020). Movement responses of common noctule bats to the illuminated urban landscape. *Landscape Ecology*, *35*(1), 189–201. https://doi.org/10.1007/s10980-019-00942-4

Walsh, A. L., & Harris, S. (1996). Foraging Habitat Preferences of Vespertilionid Bats in Britain. *British Ecological Society*, *33*(3), 508–518.

Warton, D., & Aarts, G. (2013). Advancing our thinking in presence-only and used-available analysis. *Journal of Animal Ecology*, *82*(6), 1125–1134. https://doi.org/10.1111/1365-2656.12071

Wethington, T. A., Leslie, D. M., Gregory, M. S., & Wethington, M. K. (1997). Vegetative structure and land use relative to cave selection by endangered Ozark big-eared bats (Corynorhinus townsendii ingens). *Southwestern Naturalist*, *42*(2), 177–181.

Whitaker, J. O., & Gummer, S. L. (2000). Population Structure and Dynamics of Big Brown Bats (Eptesicus fuscus) Hibernating in Buildings in Indiana. *The American Midland Naturalist*, *143*(2), 389–396. https://doi.org/10.1674/0003-0031(2000)143[0389:PSADOB]2.0.CO;2

White-Nose Syndrome response team. (2022). *Where is WNS Now?* https://www.whitenosesyndrome.org/where-is-wns

Wilkinson, G. S., & Adams, D. M. (2019). Recurrent evolution of extreme longevity in bats. *Biology Letters*, *15*(4), 20180860. https://doi.org/10.1098/rsbl.2018.0860

Williams, H. J., Taylor, L. A., Benhamou, S., Bijleveld, A. I., Clay, T. A., Grissac, S., Demšar, U., English, H. M., Franconi, N., Gómez-Laich, A., Griffiths, R. C., Kay, W. P., Morales, J. M., Potts, J. R., Rogerson, K. F., Rutz, C., Spelt, A., Trevail, A. M., Wilson, R. P., & Börger, L. (2020). Optimizing the use of biologgers for movement ecology research. *Journal of Animal Ecology*, *89*(1), 186–206. https://doi.org/10.1111/1365-2656.13094

Williams-Guillén, K., Olimpi, E., Maas, B., Taylor, P. J., & Arlettaz, R. (2016). Bats in the Anthropogenic Matrix: Challenges and Opportunities for the Conservation of Chiroptera and Their Ecosystem Services in Agricultural Landscapes. In C. C. Voigt & T. Kingston (Eds.), *Bats in the Anthropocene: Conservation of Bats in a Changing World* (pp. 151–186). Springer International Publishing. https://doi.org/10.1007/978-3-319-25220-9_6

Willis, C. K. R., Brigham, R. M., & Geiser, F. (2006). Deep, prolonged torpor by pregnant, free-ranging bats. *Naturwissenschaften*, *93*(2), 80–83. https://doi.org/10.1007/s00114-005-0063-0

Wilmers, C. C., Nickel, B., Bryce, C. M., Smith, J. A., Wheat, R. E., Yovovich, V., & Hebblewhite, M. (2015). The golden age of bio-logging: How animal-borne sensors are advancing the frontiers of ecology. *Ecology*, *96*(7), 1741–1753. https://doi.org/10.1890/14-1401.1

Wojciechowski, M. S., Jefimow, M., & Tęgowska, E. (2007). Environmental conditions, rather than season, determine torpor use and temperature selection in large mouse-eared bats (Myotis myotis). *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, *147*(4), 828–840. https://doi.org/10.1016/j.cbpa.2006.06.039

Zeller, K. A., Vickers, T. W., Ernest, H. B., & Boyce, W. M. (2017). Multi-level, multi-scale resource selection functions and resistance surfaces for conservation planning: Pumas as a case study. *PLoS ONE*, *12*(6), 1–20. https://doi.org/10.1371/journal.pone.0179570