Roost Selection and Mass Variation Patterns of Temperate Bats in Eastern Canada

by

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Author's Declaration

I hereby declare that I am the sole author of this thesis. This is a true copy of the thesis, including any required final revisions, as accepted by my examiners.

I understand that my thesis may be made electronically available to the public.

Abstract

Animals are expected to adjust their resource selection and behavioural patterns to improve fitness outcomes, such as fecundity or offspring survival. For long-lived hibernators, decisions made in each annual cycle may reflect considerations both for concurrent survival and reproduction, but also the pressure to maximize overwinter survival and future reproductive success. I examined how these elements manifest themselves in the roost selection and body mass variation patterns of temperate bats. First, I tested whether roost selection by little brown bats (*Myotis lucifugus*) on Prince Edward Island could be explained by landscape characteristics. Given a sample of roosts identified through radio telemetry and community reports and a randomly selected sample of comparison structures, I determined that a combination of proximity to forest and open wetland best explained roost selection. Second, I characterized the summer and fall mass variation patterns of both little brown myotis and northern myotis (*M. septentrionalis*) from a historic dataset. In summer, the estimated date of parturition was strongly associated with spring foraging conditions (low wind, low precipitation, warm temperatures), and mass gain associated with female reproduction conferred considerable differentiation between the mass variation patterns of females and males. In fall, differences were most apparent among species, although adults exhibited a greater capacity for rapid mass gain than juveniles. These results demonstrate how reproductive constraints and interannual survival have important influences on the behaviour of temperate bats. Roost selection appears to reflect the optimization of time and energy budgets, and the proportion of maternity roosts within the sample supports the contention that the effect of these constraints on roost selection may be more acute in reproductive females. Similarly, the relationship between foraging conditions and the timing of parturition provides further evidence that females facilitate early parturition through a combination of roost selection and capitalization on favourable foraging conditions. In fall however, the shared requirement of prehibernation mass gain among species, ages, and sexes yielded lower differentiation in mass variation than summer. Collectively, these outcomes provide evidence for the nuanced influence of life history characteristics on temperate bat behaviour. The disparate summer characteristics among sexes identified in my work suggest that management should provide nuanced supports for these endangered species, including the identification and preservation of important anthropogenic maternity roosts. Future work should seek to clarify the role of physical characteristics on roost structure selection and quantify the fitness benefits of patterns identified in this study, such as the rate of prehibernation mass gain.

Acknowledgements

Dedication

I dedicate this thesis to Mr. Kroeger, who got me started on nocturnal volant creatures.

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List of Abbreviations

1) PEI – Prince Edward Island

2) CWHC – Canadian Wildlife Health Cooperative

3) PEINP – Prince Edward Island National Park

4) RSF – Resource Selection Function

5) SD – Standard Deviation

6) SE – Standard Error

7) CI – Confidence Interval

8) LOESS – Locally Estimated Scatterplot Smoothing

9) DTW – Dynamic Time Warp

10) SSFC – Spring Suitable Foraging Condition

11) JSFC – Summer Suitable Foraging Condition

12) NB – New Brunswick

13) NS – Nova Scotia

14) NF – Newfoundland

15) ON – Ontario

16) PIT – Passive Integrated Transponder

List of Symbols

1) r – Pearson's correlation coefficient

2) ΔAIC_c – difference in Akaike Information Criterion adjusted for small sample size values

3) AIC_c – Akaike Information Criterion adjusted for small sample size

4) ω_i – Akaike weight

5) $\hat{\beta}$ – parameter estimate

6) R^2 – Nagelkerke's pseudo-R^2

7) K – number of parameters

8) $^{\circ}C$ – degrees Celsius

9) R^2 – coefficient of determination

10) n – sample size

Chapter 1
Introduction

Understanding how animals respond to seasonal and environmental change is fundamental to conservation and our understanding of natural history. However, anthropogenic activity has altered landscapes (Brooks et al. 2002, Hoekstra et al. 2005, Hansen et al. 2010, Powers and Jetz 2019) and climate change continues to shift the distribution and intensity of annual weather patterns (Badeck et al. 2004, IPCC 2014, Stott 2016). It is therefore important that we clarify the dynamic relationships between animal behaviour, environmental conditions, and landscape composition, so that we may conserve threatened populations and support the integrity of local ecosystems. The connection between behaviour and resource availability is referred to as resource selection (Manly et al. 2002), which can give insight to life history and phenological characteristics of species.

One of the most intuitive ways to characterize resource selection is through an energy budget perspective, in which animals balance food intake against energy expenditure (Charnov 1976, Orians and Pearson 1979, Owen-Smith et al. 2010). Food items may vary both in terms of quality and quantity, and selection for certain food items reflects concurrent metabolic expenditures, such as thermoregulation or gestation (Brown 1988, Patenaude-Monette et al. 2014, but see Pierce and Ollason 1987). As expenditures increase, we expect animals to adjust their foraging behaviour to meet the increased demand (Schoener 1979). However, the composition of the landscape affects not only the distribution of food items, but also other important resources such as nests (e.g., Lambrechts et al. 2004), or movement corridors (e.g., James and Stuart-Smith 2000). Accordingly, heterogeneous landscape composition (Forman 1995) yields patches of relatively higher value than others (Sergio and Newton 2003, North and Ovaskainen 2007, Poniatowski et al. 2018) and the home range of an individual is therefore the product of a dynamic relationship between its needs and the distribution of resources within the landscape.

Another important influence on animal energetic budgets is weather, which varies both on short- and long-term scales. On the short term, daily temperature fluctuations may influence an individual's foraging behaviour (Grubb Jr 1977, Hilton et al. 1999, Aublet et al. 2009), dispersal (Bronikowski and Altmann 1996, Lea et al. 2009, Kuussaari et al. 2016) or interactions with conspecifics (Edelman and Koprowski 2007). In context with the energetic budget of an animal, factors like their metabolic response capacities (McNab 2012) or insulative and thermal conductance (Scholander et al. 1950) set thermal thresholds beyond which metabolic processes are detrimentally inefficient. In cases where the ambient temperature is too hot or cold, individuals may therefore alter their physiology (Geiser and Ruf 1995), social behaviour, or even relocate entirely (Terrien et al. 2011). These short-term variations in temperature are thus responsible for a wide variety of behavioural and morphological adaptations, but these adaptations must be placed in context with selective pressures that act on much broader temporal scales.

On the long term, annually predictable patterns of weather are associated with similarly predictable patterns of animal behaviour (e.g., Porter and Tschinkel 1987, Haest et al. 2019). This relationship is especially evident in seasonal northern environments, which are characterized by long cold winters that reduce or eliminate foraging opportunities (Humphries et al. 2003). Strategies like hibernation (Ultsch 1989, Buck and Barnes 1999, Robbins et al. 2012) and long-distance migration (Newton 2008, Avgar et al. 2014) allow individuals to mitigate the thermoregulatory costs and diminished foraging opportunities associated with long periods of adverse ambient temperatures. Despite the considerable reduction of recurring metabolic costs provided by both strategies, many species still require a period fat deposition prior to their onset in fall (Odum 1960, Bairlein and Simons 1995, Speakman and Rowland 1999, Sheriff et al. 2013). The annual behaviour of migrating and hibernating animals is thus divided into phases, including reproductive, fat deposition, and overwintering behaviour. Although some species (e.g., Robbins et al. 2012) undergo lactation during fasting periods, extended

periods of euthermia or reproductive behaviours are generally limited during this time and are instead confined to the end of the hibernation period (Michener 1998, Czenze and Willis 2015). Because of the lack of foraging opportunities in spring, an individual's reproductive behaviour post-emergence is largely dependent on its remaining energy stores after hibernation. For this reason, the positive association between early reproduction and reproductive success (Kunz et al. 1998, Michener 1998) places pressure on individuals to optimize their hibernation phenology and energetic expenditures throughout the hibernation period.

Just as the influence of environmental conditions on an animal's energetic budget varies, so too do the expenditures of individuals within populations. In mammals, reproductive investments differ markedly in form or cost among males and females (Trivers 1972, Smith 1977, Clutton-Brock 2007). Chief among these differences is the disparate energetic requirements of gestation and lactation in females and spermatogenesis in males. Lactation and gestation represent enormous investments by reproductive females (Gittleman and Thompson 1988, Clutton-Brock et al. 1989) and are generally greater than those of males (Dewsbury 1982, but see Key and Ross 1999). Parents may also make energetic investments in addition to those associated with reproduction, including teaching, protection, or transport of young (Gittleman and Thompson 1988), but these roles are not always shared equally among parents (Kleiman and Malcolm 1981, Winkler 1987). Parental roles are made even more explicit in species with sexual dimorphism, in which sexual selection or intraspecific niche partitioning confer not only behavioural differences, but morphometric ones as well (Shine 1989, Isaac 2005). Increased female size is generally associated with fecundity, but sexual competition is associated with morphological and behavioural divergence in males, including strategies like fighting or sneaking (Gadgil 1972, Gross 1996). Collectively, the disparate selective pressures present in mammalian species often lead to greater energy expenditures among males during periods of copulation, and a temporal decoupling with the female investments of gestation and lactation.

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In addition to the disparate reproductive expenditures of adults, constraints imposed by reproductive behaviours or development (Marchetti and Price 1989) differentially affect how adults and juveniles balance their energetic budgets. In species with relatively long lifespans or low fecundity, juveniles tend to reach sexual maturity more slowly, and often necessitate greater parental investment (Stearns 1976, Promislow and Harvey 1990, Sibly and Brown 2007, Klug and Bonsall 2010). It follows then that species with 'slow' life histories have periods in which parental energetic budgets must account for the foraging inefficiency and early learning periods of offspring (e.g., birds: Weathers and Sullivan 1989, Wheelwright and Templeton 2003).

Given how important it is to understand the connection between life history characteristics and resource selection, wildlife biologists have developed several tools to monitor the behaviour of individuals over time. One common tool is radio telemetry, in which small transmitting devices are implanted in or affixed to captured animals and tracked via radio signals (Obbard and Brooks 1981, Aldridge and Brigham 1988, Garcia-Sanchez et al. 2010, Sokolov 2011, Thorstad et al. 2013). This technique allows researchers to remotely characterize not only dispersal and migratory patterns (Fuller and Snow 1988, Gerlier and Roche 1998), but also to characterize geographic features associated with the space-use of tracked animals (Boyce et al. 2003, King et al. 2006). Despite the value of this technique, the cost, size, and functionality limitations associated with telemetry can detract from its efficacy in wildlife monitoring (Samuel and Kenow 1992, Rettie and McLoughlin 1999, Daniel Kissling et al. 2014). An alternate strategy is to collate and examine long-term capture data. In this strategy, morphometric and reproductive conditions can be measured over time to detect population level trends spanning many years (e.g., Gardner et al. 2011). Although such data inherently lack behavioural characteristics of observed individuals, their format facilitates large sample sizes (Rioux Paquette et al. 2014) and can be coupled with tagging techniques (e.g., bands: Norquay et al. 2013) to characterize site fidelity and survival

patterns. Collectively, these techniques can overcome sampling limitations to provide insight into resource selection and life history characteristics not easily observed in a laboratory setting.

One group of species for whom these techniques have proved especially useful is in temperate bats, whose small size, nocturnal behaviour, and movement patterns (Fenton and Barclay 1980, Caceres and Barclay 2000, Fleming 2019) confer considerable monitoring challenges. In North America, some bat species have also recently undergone drastic recent population declines due to white-nose syndrome and habitat loss (Blehert et al. 2009, Frick et al. 2010*a*, COSEWIC 2013), which makes population monitoring especially important. In Canada, three species are listed as endangered, including the little brown myotis (*Myotis lucifugus*) and northern myotis (*M. septentrionalis*)(Environment and Climate Change Canada 2018). An ongoing concern for these species is the identification and conservation of their critical habitat, including important foraging and roosting areas (Environment and Climate Change Canada 2018).

Patterns of resource selection and energy allocation in temperate bats are of particular note not only because of their conservation implications, but also because of temperate bats' unique life history. Unlike mammals such as ground squirrels (e.g., Williams et al. 2014) or bears (e.g., Steyaert et al. 2012) which mate near the beginning of the active season, little brown myotis and northern myotis mate prior to hibernation (Fenton 1969, Thomas et al. 1979, Whitaker and Rissler 1992). This timing posits a trade-off between reproductive opportunities and prehibernation fat deposition for males, and places the primary female reproductive investment immediately after hibernation. Given these characteristics, little brown myotis and northern myotis are uniquely situated for investigation into how long-lived hibernators respond to reproductive and survival selective pressures in light of geographic and environmental constraints.

I will address the resource selection and energy allocation patterns of little brown myotis and northern myotis through a combination of radio telemetry and historical body mass data analysis. In

Chapter 2, I examined whether the distribution or quantity of landscape variables influence roost selection in little brown myotis. In Chapter 3, I characterized and compared the summer and fall body mass variation patterns of little brown myotis and northern myotis, and tested whether these patterns were associated with weather conditions. I have presented each chapter as a manuscript in publication format, and concluded with a summary, Chapter 4, which discusses the preceding manuscript chapters.

Chapter 2

Proximity to Forest and Open Wetland Explain Roost Selection of Little Brown Myotis on Prince Edward Island

2.1 Introduction

Animal fitness is a measure of an individual lifetime reproductive success. One contributing factor to fitness is the suite of behaviours exhibited by an individual, including those that affect predation risk, offspring success, or physiological costs (e.g., Campagna and Le Boeuf 1988; Spoon et al. 2006; Pruitt and Riechert 2009). Given the finite amount of energy that can be allocated to maintenance, growth, and reproduction (Gittleman and Thompson 1988, Perrigo 1990, Lika and Kooijman 2003), energy allocation strategies are subject to selection. We therefore expect animals to behave in such a way that minimizes energetic expenditures (e.g., thermoregulation) to maximizes fitness (Pyke 1984, Parker and Smith 1990, Olsson et al. 2008, Patenaude-Monette et al. 2014). Within the suite of factors that influence an individual's energetic budget is the quality of accessible foraging, nesting, or commuting resources (Komdeur 1992, Sergio and Newton 2003, Owen-Smith et al. 2010, Poniatowski et al. 2018). As habitat loss (Kerr and Deguise 2004, Swift and Hannon 2010, Mantyka-Pringle et al. 2012, Russo and Ancillotto 2015, Krauel and LeBuhn 2016) and fragmentation (Fahrig 2003, Cushman 2006, Ethier and Fahrig 2011, Harms et al. 2017) continue to alter landscapes, it is increasingly important to identify how animal behaviour is linked to the availability and distribution of landscape features.

Central place foraging theory describes a strategy in which individuals make return trips between foraging areas and a central location such as a nest (Orians and Pearson 1979, Andersson 1981, Kotler et al. 1999, Daniel et al. 2008). Central place foraging theory is commonly used to examine predictions about foraging behaviour in landscapes with heterogeneous resource distribution (e.g., Patenaude-Monette et al. 2014), but it also provides a useful conceptual framework to consider other resource

selection patterns. For example, fidelity to a central place over time can confer advantages associated with familiarity, such as knowledge of local foraging resources or predator escape routes (Clarke et al. 1993, Dall et al. 2005, Brown et al. 2008, Forrester et al. 2015). We can examine how individuals address their energetic budgets through trade-offs associated with selecting a particular central place and its associated foraging areas (Daniel et al. 2008, Patenaude-Monette et al. 2014).

Many temperate bats are central place foragers during the active summer period. These bats rest during the day at diurnal roosts (i.e., the central place) and forage at nearby forests or open water (Anthony and Kunz 1977, Fenton and Barclay 1980, Caceres and Barclay 2000, Nelson and Gillam 2017). Bats roost in a variety of spaces, including trees, cliff overhangs, and anthropogenic structures (Henry et al. 2002, Broders et al. 2006, Olson and Barclay 2013, Randall et al. 2014). These landscape elements or roosts differ in quality, therefore roost selection for particular attributes can confer appreciable benefits to individuals (Kunz 1982, Williams and Brittingham 1997, Willis and Brigham 2005). Accordingly, the characteristics of bat summer habitat selection can be explained by various factors, including roost availability (Broders and Forbes 2004), flight characteristics (Adams 1997), and energetic costs (i.e., thermoregulation and spatial-temporal variation in foraging success). Collectively, we expect bats to select high quality roosts near high quality foraging areas, but measures of quality for each element are multi-faceted.

Thermoregulation is an important aspect of endotherm energy budgets. As small-bodied heterothermic endotherms, bats must make a daily decision to either maintain energetically expensive euthermia or enter torpor, which can detrimentally delay offspring development (Studier and O'Farrell 1972, Lausen and Barclay 2003, Dzal and Brigham 2013) suppress immunity (Field et al. 2018), and may inhibit predator avoidance. In lieu of torpor, individuals can alleviate the cost of euthermia with social thermoregulation (Fenton and Barclay 1980, Kurta et al. 1989) and the selection of a roost with a favourable microclimate (Licht and Leitner 1967, Kurta 1985, Thomas et al. 1990, Willis and Brigham

2007, Mcguire et al. 2009, Wilcox and Willis 2016). For these reasons, structures whose size is sufficiently large to provide both a variable microclimate and accommodate numerous individuals may be best suited as roosts because they could facilitate euthermia across a variety of environmental conditions (Brittingham and Williams 2000, Hoeh et al. 2018).

Additionally, roost selection may be influenced by proximity to foraging resources, which have been important predictors of home range selection for many species (Kalcounis-Rüppell et al. 2005, Rainho and Palmeirim 2011). One species for whom this effect may be prevalent is little brown myotis (*Myotis lucifugus*), an insectivore (Belwood and Fenton 1976, Burles et al. 2009), whose prey is reflected in their foraging habitat use. Foraging little brown myotis demonstrate an affinity for lakes and streams, where they capture prey both in the air and at the water's surface (Anthony and Kunz 1977, Fenton and Bell 1979). In analyses of foraging within landscape mosaics, bats selected riparian areas (Broders et al. 2003, Bergeson et al. 2013, Coleman et al. 2014, Nelson and Gillam 2017) while avoiding open grasslands. Although some studies indicate the importance of forest edges for commuting or foraging (Patriquin and Barclay 2003, Jantzen and Fenton 2013), the wing-loading (Kalcounis and Brigham 1995) and echolocation characteristics (Ratcliffe and Dawson 2003, Broders et al. 2004) of little brown myotis make them especially well-adapted to foraging at open aquatic sites. Because reduced commute times confer reduced energetic expenditures and afford females greater access to offspring for care, roost selection disparity (Randall et al. 2014) among sexes suggests that proximity to landscape features is likely an important factor in little brown myotis roost selection.

The aim of this study is to use little brown myotis on Prince Edward Island (PEI), Canada as a case study to examine the roost selection of temperate bats with respect the landscape composition. I hypothesized that the accessibility and quantity of forest, linear features, and freshwater influence roost selection by this species, and predicted that roost sites would be more closely associated with these features than random comparison structures. Specifically, I predicted that due to the energetic benefits of

proximity, roosts would be closer to forest and open wetlands than random structures and similarly that

roosts would also have a greater area of forest and fresh water nearby.

2.2 Methods

I identified roosts through a combination of roost surveys, community reports, and targeted

trapping. Surveys were conducted by community members and Canadian Wildlife Health Cooperative

(CWHC) personnel at sites reported between 2018 and 2021 through the Bat Hotline program on PEI. To

ensure confidence in the use of a structure as a roost, I included surveyed structures with more ≥ 5 bats

observed at emergence. For structures with < 5 observed bats, or those that had not been surveyed, I

assessed homeowner reports for the longevity of use and anecdotal perspectives on the roosting

population size. I retained such sites when they had several noted years of recurrent roosting and strong

evidence for use by more than one individual (e.g., large guano deposits). I made the assumption that all

community-identified roosts were occupied by little brown myotis, because records of other

anthropogenic-roosting species (e.g. Big Brown Bats; *Eptesicus fuscus*) are exceedingly rare on PEI

(Henderson et al. 2009, Segers et al. 2016).

I captured bats between June 5 and August 13, 2019 at forested and freshwater pond sites in

Prince Edward National Park (PEINP). Mist nets were checked every 10 min, and I recorded standard

morphometric measurements (mass, sex, forearm length, reproductive status, age class) and collected

standard samples (wing tissue, hair, ectoparasites) on all bats. A subset of bats were affixed with LB-2X

radio transmitters (Holohil Systems Ltd, Carp, ON, Canada) at the interscapular region using medical

glue (Osto-bond; Montreal Ostomy, Vaudreuil, QC, Canada) and all were released at the point of capture.

Early in the season, I prioritized tagging females to find maternity roosts, but as I captured more

individuals and identified more roosts, I gradually began tracking males and finally juveniles. Beginning

the day following release, I searched daily for radio-tagged bats, until they were either located or the

transmitter had fallen off. I recorded the location of each identified roost, and time and weather permitting, subsequently conducted emergence counts.

For comparison, 'available' structures were randomly selected at a 3:1 ratio from within the study area, defined as an ellipse drawn around the furthest extent of the roost points and subsequently buffered by 5 km. This 5 km buffer was chosen based on observed female little brown myotis foraging ranges (2.6 ± 0.6 km; Henry et al. 2002, 5.2 ± 0.2 km; Randall et al. 2014). The dataset was thus comprised of 22 roost structures and 66 comparison structures. All structures were characterized according to their distance to each of the nearest open wetland, forest patch, river or stream, and the forest area, open wetland area, and river and stream length within 5 km of the structure. To exclude saltwater from my analyses, I did not include any wetlands categorized as inlets or open saltwater. These data were generated in ArcMap 10.8.1, (Environmental Systems Research Institute, Redlands, California, USA) with land cover data provided by the Province of Prince Edward Island, Department of Environment, Water and Climate Change. Forest area included stands classified as old, mature or young, with crown coverage equal to or greater than 25%, and minimum height of 5 m (Hansen et al. 2010). Open wetland included permanent or deep transient bodies of water with vegetation either confined to peripheral bands, dense patches, or diffuse stands, to a collective cover of no more than 75%. Little cover data was available for rivers and streams, so they were assessed according to length alone. Edge density was the sum of forest edge and linear treed feature length divided by the area of each 5 km buffer (78.54 km^2).

Given these potential parameters, I developed Design I resource selection functions (RSF)(Manly et al. 2002) of bat roost selection with logistic regression models in R (Version 3.6.3, R Core Team 2019). Candidate parameters were assessed for correlation (Pearson's $r \geq 0.65$) and multicollinearity (Variance Inflation Factor > 5)(Sheather 2009), and river and stream length was subsequently excluded from modelling due to high correlation with the forest area parameter (Pearson's $r = 0.73$). Because of limited sample size (22 roosts), I addressed assumptions regarding overdispersion, logit linearity, and influential

points across three two-parameter models which collectively represented all parameters, rather than through a global model. I inspected the performance of all models with 5-fold cross-validation, the Hosmer-Lemeshow test for goodness-of-fit (Hosmer and Lemeshow 2000), and Nagelkerke's pseudo-R^2 (Nagelkerke 1991, Harrell 2021). I finally assessed model support with Akaike's Information Criteria for small sample sizes (ΔAIC_c)(Burnham and Anderson 2002) with the MuMIn and AICcmodavg packages (Barton 2020, Mazerolle 2020) in R.

Logistic regression models were constructed according to a use-availability paradigm under the assumption that unknown-use contamination within the 'available' samples was low (<20%; Johnson et al. 2006). Because logistic regression requires outcomes to be considered either as a success (roost) or failure (availability), there needed to be confidence that the sample of structures classified as failure did not in truth contain a detrimental proportion of roosts. This contention is supported by a low capture rate (0.26 captures/net hour) and observed low degree of roost switching (1.24 unique roosts/individual, tracking days range: 3 - 23). For these reasons, logistic regression models are suitable estimates of the true RSF (Johnson et al. 2006). Given the sample size, I constructed a parsimonious and balanced set of candidate models, including a null model, based on *a priori* knowledge of bat foraging and roosting behaviour. Considering the available data (proximity and area measures), I chose models that reflected hypotheses regarding the relative influence of resource availability relative to resource proximity. I subsequently assessed parameter importance with their AIC_c weights ω_i (Burnham and Anderson 2002), odds ratios (Hosmer and Lemeshow 2000) and through the construction of a 95% confidence set (Symonds and Moussalli 2011).

2.3 Results

I captured 105 little brown myotis (31 male, 74 female), deployed 25 radio transmitters, and tracked 18 bats to 13 unique day roosts, including 11 houses (Fig. 2.1), one tree, and one shed adjacent to

a roost house. Although none were located within the PEINP boundary, all were within 5 km of its boundary. Community monitoring between 2018 and 2021 yielded several hundred reports of bat sightings and suspected roosts, 11 of which could be confidently classified as roosts in anthropogenic structures.
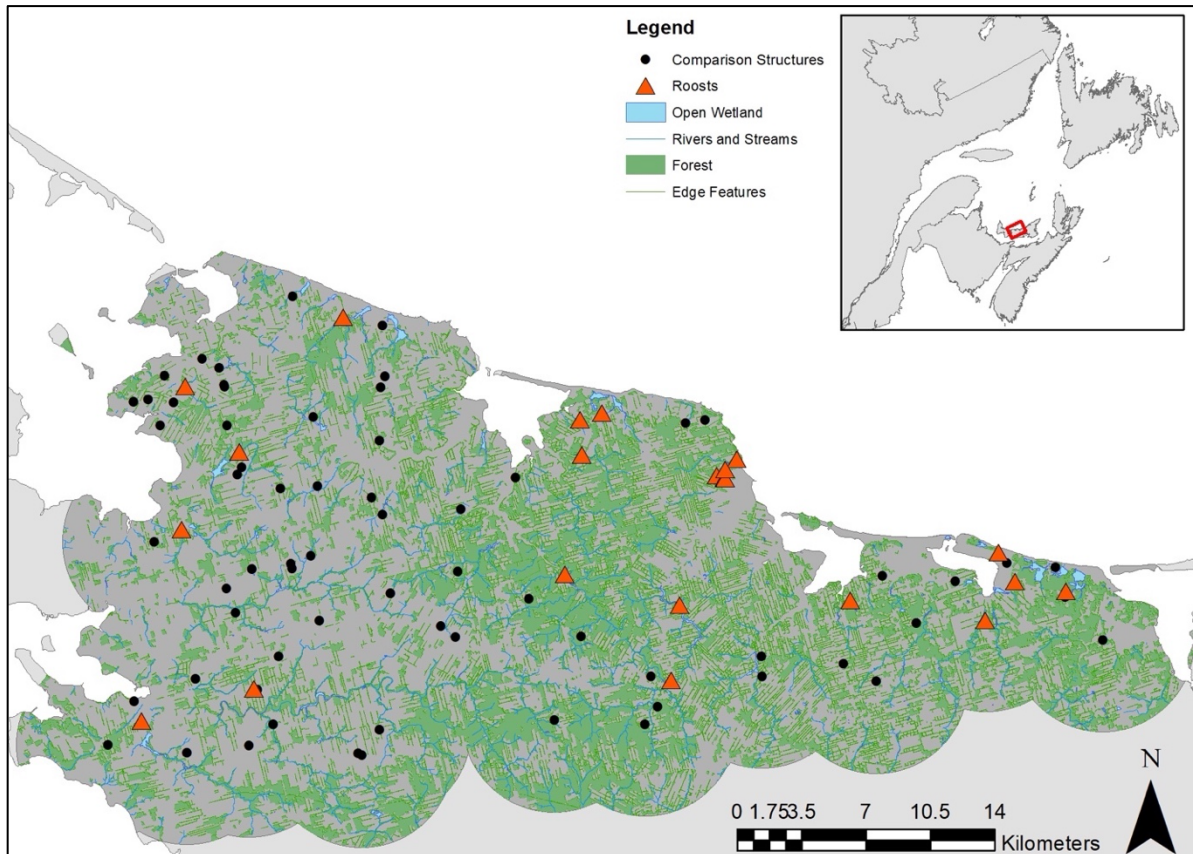
Figure 2.1 Houses used as roosts by little brown myotis (*Myotis lucifugus*) on Prince Edward Island in the summer of 2019 and comparison houses randomly selected for statistical comparison from within a pooled 5 km buffer set from each known roost.

Little brown myotis selected roosts that were generally closer to forests and bodies of water than comparison structures (Table 1). The best-supported model had considerably higher weight than any other model ($\omega_i = 0.73$; all other models $\omega_i \leq 0.10$)(Table 2). There was little, if any, support for the null model ($\omega_i < 0.001$). The 95% confidence model set contained three models, which were composed exclusively of

the distance to forest ($\hat{\beta}$ = -6.36, SE = 2.96) and distance to open wetland parameters ($\hat{\beta}$ = -1.18, SE = 0.51)(Table 3). The odds of a structure being selected for roosting changed by 0.31 times for each 1 km increase in distance to open wetland, and by 1.7×10^{-3} times for each 1 km increase in distance to forest. The direction of parameter estimates for were consistent across all models for both distance to forest and distance to open wetland. All models demonstrated reasonable

Table 2.1 Summary of geographic characteristics of houses used as roosts by little brown myotis (*Myotis lucifugus*) and randomly selected comparison houses on Prince Edward Island. Units are km^2 for area measurements, km for distance, and km/km^2 for density. The parameters Forest Area, Length of Rivers and Streams, and Open Wetland Area were calculated as the sum of the feature measure within a 5 km buffer drawn around each roost and comparison structure location. Edge Density was calculated as the sum of the length of forest edge and treed linear features within a 5 km buffer divided by its area (78.54 km^2).

	Comparison		Roost	
	Mean	SD	Mean	SD
Distance to Forest	0.19	0.19	0.07	0.09
Distance to Open Wetland	1.07	0.70	0.56	0.58
Distance to Rivers and Streams	0.52	0.27	0.37	0.29
Forest Area	13.35	6.76	13.29	6.88
Open Wetland Area	0.41	0.33	0.55	0.48
Edge Density	5.86	1.95	5.81	1.98
River and Stream Length	50.63	25.78	36.01	24.96

Table 2.2 Models and associated parameters predicting roost structure selection of little brown myotis (*Myotis lucifugus*) on Prince Edward Island. The parameters Forest Area and Length of Rivers and Streams were calculated as the sum of the feature measure within a 5 km buffer drawn around each roost and comparison structure location. Models are organized according to their quasi Akaike's Information Criterion adjusted for small sample sizes (AIC$_c$) and corresponding weights (ω_i). R^2 is the Nagelkerke's pseudo-R^2.

Model	Parameter(s)	K	ΔAIC$_c$	ω_i	R^2
Foraging Accessibility*	Distance to Open Wetland + Distance to Forest	3	0	0.73	0.254
Distance to Open Wetland*	Distance to Open Wetland	2	3.98	0.10	0.165
Distance to Forest*	Distance to Forest	2	4.55	0.08	0.157
Wetlands	Distance to Open Wetland + Open Wetland Area	3	5.03	0.06	0.182
Commuting	Distance to Forest + Edge Density	3	6.29	0.03	0.163
Wetland Area	Open Wetland Area	2	12.08	<0.001	0.038
Null	Intercept	1	12.30	<0.001	0.000
Foraging Quantity	Forest Area + Open Wetland Area	3	14.22	<0.001	0.039
Edge Density	Edge Density	2	14.39	<0.001	0.000
Forest Area	Forest Area	2	14.39	<0.001	0.000
Tree Features	Edge Density + Forest Area	3	16.53	<0.001	0.000

Models in the 95% confidence set are denoted with *

Table 2.3 Model averaged weighted parameter estimates, estimated unconditional standard error (SE), and relative importance of all parameters in the 95% confidence set of models predicting roost structure selection of little brown myotis (*Myotis lucifugus*) on Prince Edward Island. Odds ratio represents the change in odds of roost structure selection with a 1 km increase of the parameter. Relative importance is the sum of AIC$_c$ weights of all models including the parameter of interest.

Parameter	Estimate	SE	Odds ratio (CI)	Relative Importance
Distance to Open Wetland	-1.18	0.51	0.31 (0.11 - 0.83)	0.89
Distance to Forest	-6.36	2.96	1.7×10^{-3} (5.2×10^{-6} - 0.57)	0.84

2.4 Discussion

As predicted, roosts were nearer to forests and open wetlands than comparison structures, and the most supported model reflected the combined importance of proximity to these features for roost selection. Similar distance measures are informative for roost selection in a variety of other species, including *Miniopterus schreibersii* and *Rhinolophus mehelyi* (Rainho and Palmeirim 2011), *M. yumanensis* (Evelyn et al. 2004), *Nyctalus noctula* and *M. daubentonii* (Boonman 2000). Generally speaking, these positive relationships between roost selection and proximity to forest and aquatic features are considered to be made according to the energetic benefits of reduced commuting distances (but see Brigham 1991). Relative to the known range of foraging distances in little brown myotis (<1 km: Broders et al. 2006 to >5 km: Randall et al. 2014), the low observed distance between roosts and open wetlands (0.56 ± 0.58 km) indicates strong selection for proximity to open wetland. Notably however, the estimated odds ratio associated for distance to open wetland was greater and its estimated parameter estimate less variable than those for distance to forest. Given the relatively high degree of support for the top-ranked model in light of the low support for its constituent univariate models, roost selection appears to reflect a shared importance of forest and wetland features. If the study area contains a sufficient quantity of roosts such that bats can make selections according to not just one, but both of these variables, it follows that they would.

My results also demonstrate a distinct difference between the influences of proximity and quantity of landscape features on bat roost selection. Contrary to my prediction, there was no support for the influence of either forest area or open wetland area on roost selection. Previous work has demonstrated that wetlands and forest edges are generally favoured by foraging little brown myotis (Nelson and Gillam 2017, Thomas and Jung 2019), but it is unclear whether a critical degree of feature availability is necessary to support a population of this species. If the primary benefit of forests is to provide near edges for safe commuting at dusk, it follows that the total area would not be influential.

Regardless, in a system like Prince Edward Island where the landscape is generally homogeneous, it is possible that if little brown myotis select roosts according to feature availability, there is too little landscape variation to detect it. The pseudo-R^2 value for the top model further indicates that there are other factors that explain important roost selection variation within this system.

Another explanation for the observed pattern may be the prevalence of maternity roosts within the roost structure sample. At least three roosts identified with radio telemetry are maternity roosts, and their conspicuous nature likely biased the community-reported roosts toward them. During the active season, energetic investments associated with reproduction are disparate among males and females (Gustafson 1979, Kurta et al. 1989, Reynolds and Kunz 2000). Females adjust commuting distances in response to their relatively high reproductive energy demands, by reducing home range size (Henry et al. 2002) and making frequent return trips during the night (Anthony et al. 1981). Therefore, females in particular should select roosts near foraging areas. Indeed, Segers and Broders (2014) noted a similar pattern in their work in Nova Scotia. The only tree roost identified in my trapping was occupied by a male, which reflects sex-based roost preferences identified in other work (Broders et al. 2006, Johnson et al. 2019). My results therefore likely present evidence of how differential constraints and selective pressures among sexes manifest themselves in roost selection.

One major consideration for these results is that I was unable to examine the physical characteristics of the sampled roost and comparison structures. The microclimate characteristics of bat boxes (Wilcox and Willis 2016), tree roosts (Willis and Brigham 2007), and anthropogenic structures (Johnson et al. 2019) are associated with preferential use, and may represent important but unmeasured variation in my data. At least seven of the roosts in this study are thought to be > 100 years old. Old structures are commonly used by little brown myotis, and especially reproductive females (Anthony et al. 1981, Henry et al. 2002, Broders and Forbes 2004, Randall et al. 2014). Such roosting structures may not represent a limited resource in the study area (Miller et al. 2003), given the agricultural history of the

region and recent bat population declines due to white-nose-syndrome (Blehert et al. 2009, Frick et al. 2010*a*, Cheng et al. 2021). Anecdotally, homeowners at numerous roosts also shared stories of bats inhabiting their homes for decades, which also suggests that roost selection decisions made in an outdated landscape composition context may persist through site fidelity (Norquay et al. 2013). Collectively, it is important to note that the influence of nearby foraging resources may be tempered by yet-unmeasured characteristics of the suite of available nearby structures.

There remain several caveats to note. First, the selected buffer range was chosen as a conservatively large estimate of the features available to foraging bats, and further radio-telemetry data may reveal landscape effects at much smaller scales (e.g., Coleman et al. 2014). For example, if reproductive females require foraging resources at smaller spatial scales during lactation, measures of feature quantity within a 5 km buffer may not identify important variation at the local scale. Further, features like waterbodies or forest patches may vary according to qualities not captured by my geospatial data. For example, light and chemical pollution may affect site use (Stone et al. 2009, 2015, Threlfall et al. 2013, Secord et al. 2015, Straka et al. 2016). These outstanding questions represent important further areas of study, especially given the need to identify and maintain the critical habitat of species affected by white-nose syndrome (Environment and Climate Change Canada 2018).

This study demonstrates a preference for proximity to open wetlands and forested areas in the roost selection of little brown bats. Because flight is an energetically expensive (Winter and Von Helversen 1998) but unavoidable component of bat foraging, it follows that reducing commuting distances may be an important way bats improve the net energetic benefit of each foraging flight. The lack of support for area measures suggests that such energy budget constraints are an important factor in determining central place quality in little brown myotis. However, inter-annual site fidelity (Norquay et al. 2013), sociality (Kazial et al. 2008) and even personality (Webber and Willis 2020) indicate suggest that resource selection in little brown myotis is a complex process that cannot be explained with presence-

availability analyses alone. I therefore recommend the integration of roost structure analysis with assessments of seasonal and inter-annual roost-switching to contextualize roost selection patterns within the life history characteristics of this species. Such research will clarify how sociality in long-lived animals influences habitat selection in changing environments, and provide management with a better understanding of critical habitat for the endangered little brown myotis.

Chapter 3

Active Season Body Mass Patterns of Little Brown Myotis and Northern Myotis

3.1 Introduction

Though selective pressure, populations evolve behavioural strategies to maximize fitness (Stearns 1976). Because behaviour happens in the context of environmental conditions, these strategies must be considered in light of abiotic and biotic influences (e.g., Burles et al. 2009) and the behavioural or phenotypic flexibility they elicit in animals (Pigliucci 2001, Snell-Rood 2013). These nuances may be especially evident in seasonal environments whose annual weather patterns are characterized by distinct periods of temperature and precipitation intensity (Bonan 2002, Sunday et al. 2011). For example, many bird species spend the summer at breeding grounds in the northern part of their range and migrate towards the tropics during the winter (Newton and Dale 1996). Conversely, some mammals remain near their summer territories and occupy hibernacula during the winter (e.g., Grizzly Bears; Nelson et al. 1983).

Patterns of behaviour in temperate hibernating bats, such as little brown myotis (*Myotis lucifugus*) and northern myotis (*M. septentrionalis*) are notably influenced by seasonality. These long-lived insectivorous mammals use prolonged torpor to hibernate through the cold winter when food is not available (Fenton and Barclay 1980, Whitaker and Gummer 1992, Caceres and Barclay 2000, Czenze and Willis 2015). During hibernation, individuals suppress their metabolic rate and subsist on fat reserves acquired in the preceding active season (Thomas et al. 1990, Carey et al. 2003, Geiser 2004). The demands of hibernation illustrate the necessity of not only physiological adaptations associated with long-term torpor, but behavioural ones as well. Indeed, these adaptations have important implications for inter-annual survival (Frick et al. 2010*b*, Norquay and Willis 2014), and places special emphasis within these species on the ability to access and capitalize on food resources.

One important manifestation of resource use is mass gain, which is facilitated by a net positive energy budget. For volant insectivorous species like little brown myotis and northern myotis, energy intake varies with insect availability, ambient temperature, wind speed, and precipitation, such that foraging efficiency is diminished on nights with lower temperatures and high winds and/or precipitation (Fenton 1969, Anthony et al. 1981, Ciechanowski et al. 2007). High precipitation in temperate areas is furthermore associated with delayed parturition (Grindal et al. 1992, Linton and Macdonald 2018, 2020) and reduced swarming site activity in fall (Parsons et al. 2003). Just as these factors affect energy intake in bats, they may also affect energy expenditures. In particular, low ambient temperatures increase the costs of euthermia and explain, at least in part, torpor use throughout the year (Speakman and Rowland 1999, Willis et al. 2006, Dzal and Brigham 2013, Besler and Broders 2019).

In addition to features like thermoregulatory activity, foraging, and hibernation, adult bats' annual energy budgets must also support reproduction, whose characteristics differ markedly between females and males (Fenton 1969; Schowalter 1980; Kunz et al. 1998). Adult males undergo relatively inexpensive spermatogenesis throughout the summer and subsequently copulate promiscuously at swarming sites in the fall (Thomas et al. 1979, Schowalter 1980, Norquay and Willis 2014). This late annual investment may explain, at least in part, why males emerge from hibernation later than females (Czenze and Willis 2015) and persist in areas with relatively lower prey abundances during the summer (Barclay 1991).

The comparatively larger female investment takes place in spring and early summer (Wimsatt 1960), and the Thrifty Female Hypothesis suggests females should give birth as soon as possible each year to maximize overwinter survival of offspring (Frick et al. 2010*b*, Jonasson and Willis 2011, Norquay and Willis 2014, Czenze et al. 2017). However, the optimal time of parturition will vary with past and present environmental conditions (Linton and Macdonald 2020), geographic region (Rodrigues, Zahn, Rainho, and Palmeirim 2003), and individual characteristics such as body condition or age (Linton and Macdonald 2019). Indeed, the relatively early female spring emergence (Davis and Hitchcock 1965,

Norquay and Willis 2014, Czenze and Willis 2015) often coincides with limited insect abundance and unfavourable environmental conditions (e.g., low temperature, precipitation, wind) which necessitate torpor use to conserve energy and recover from hibernation (Humphries et al. 2003, Czenze and Willis 2015, Besler and Broders 2019). However, because torpor use delays parturition and weaning (Racey and Swift 1981), poor spring foraging conditions may in turn delay parturition such that reproductive females and their offspring struggle to gain sufficient pre-hibernation energy stores.

In fall, bats of all age classes and sexes maximize their net energy budgets to gain fat and thus survive hibernation. There are two proposed mechanisms by which they may do so; increase energy intake through hyperphagia or decrease energetic costs though torpor use. Hyperphagia is a dramatic increase in foraging intensity, and has been documented in little brown myotis at swarming sites in Vermont (Kronfeld-Schor et al. 2000) and Ontario (Mcguire et al. 2009) but see (Mcguire et al. 2016). Additionally, bats may drastically decrease their thermoregulatory costs through a transition from daily euthermia to daily torpor (Stawski et al. 2014), as noted by (Speakman and Rowland 1999) and suggested by Mcguire et al. (2016). Because these strategies must account for deteriorating foraging conditions, mating, and differences in age-dependent foraging efficiency (Mcguire et al. 2009), it is challenging to identify when and how prehibernation mass gain takes place. Further, disparate patterns of mass change prior to hibernation (Kunz et al. 1998) indicate that reproductive pressures may necessitate a temporally disparate implementation of these strategies, regardless of what they may be.

Given the magnitude of reproductive and prehibernation investments in temperate bats, disparate behavioural strategies among sexes, age classes, and species should confer distinct annual patterns of body mass change. Unfortunately, contemporary body mass comparisons are often limited to paired mean comparisons at points throughout a year (e.g., Kunz et al. 1998, Rughetti and Toffoli 2014) which may fail to capture meaningful variation across seasons. Available records of mass variation patterns of little brown myotis and northern myotis (Fenton 1970, Schowalter 1980, Kunz et al. 1998, Speakman and

Rowland 1999, Kronfeld-Schor et al. 2000, Townsend et al. 2008, Mcguire et al. 2009, 2016, Lacki et al. 2015) have identified some regional characteristics of body mass variation in these species, but I seek to expand on this work through more comprehensive inter-year comparisons. As climate change alters the phenology of hibernating species (e.g., ground squirrels; Lane et al. 2012) and prey such as insects (Forrest 2016), it is increasingly important to develop quantitative ways to assess patterns of annual phenology within and among species, and especially those whose phenology is closely linked with environmental conditions.

The goal of this project was to characterize the active season mass variation patterns of little brown myotis and northern myotis. To achieve this goal, I set three objectives. First, I evaluated summer mass variation patterns in adults to identify how their form, magnitude, and variation differed according to sex and species. Second, I similarly examined patterns of mass variation in fall, but included juveniles to determine whether they displayed a similar capacity to gain mass as adults, and whether such gain took place at a similar time. My last objective was to identify whether the temporal distribution of summer mass variation in females could be explained by weather conditions in either spring or summer.

3.2 Methods

To achieve these objectives, I selected data from projects conducted in the Canadian provinces of New Brunswick, Nova Scotia, Prince Edward Island, Ontario, and the island of Newfoundland between 1999 and 2019. In these projects, bats were captured with mist nets (Avinet, Dryden, New York, USA) and harp traps (Austbat Research Equipment, Lower Plenty, Victoria, Australia) by different research groups and assessed for standard morphometric and diagnostic criteria, including sex, age class (adult or juvenile; Kunz and Anthony 1982), and mass to two decimal places. The capture dates were recorded as Julian Date (1-365), and individual observations were grouped according to year, province, age-class (adult/juvenile), sex, and species (e.g., adult male *M. lucifugus* captured in Nova Scotia in 2013; hereafter

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'group'). To exclude swarming behaviour in summer analyses, I classified summer captures as those that occurred before August 11 (approximately Julian Day 222)(Burns and Broders 2015) at locations other than known or suspected hibernacula. I made no temporal constraint for juvenile records in fall, because it was assumed that the importance of surviving their first winter should orient all their fall behaviour in that first year around doing so. Adult records were only included for fall analysis if they occurred at known or suspected hibernacula and swarming sites. I chose a location criterion for adults because the migration to such sites represents a choice to engage in a new suite of behaviours. Furthermore, monitoring at such sites in Nova Scotia suggest very low summer occupancy until the swarming period in fall (Burns and Broders, unpublished data).

For summer, I selected groups representing each of the possible adult sex/species combinations (e.g., adult male *M. lucifugus*; hereafter 'collection') that had the best sampling regime (i.e., based on the temporal distribution and quantity of sampling). Each chosen group included at least nine unique nights of sampling with no sampling gaps longer than 20 days so that biologically relevant phenomena (e.g., pregnancy) would be detectable even when sampling regimes were irregular (Chen et al. 2002, Lepot et al. 2017). Similarly, I selected fall data from capture efforts according to the same criteria, for 15 groups, including adults and juveniles of both sexes in three consecutive years (2009-2011).

Given these groups, I fitted LOESS (Cleveland 1979, Cleveland and Devlin 1988) nonparametric fits (span = 0.75) through the full sample of body mass values of each group and trimmed each fit to the widest possible range for which captures were available in all groups; Julian Dates 158-207 (approximately June 7 - July 26) for summer and 227-262 (approximately August 15 - September 19) for fall. I chose not to fit exclusively between these dates because doing so would lose accuracy provided by captures outside that range in years with more sampling. I chose a quadratic fit instead of a linear fit because quadratic smoothing is preferable when the data includes informative curvature (Cleveland and Devlin 1988). Similarly, I selected a span value of 0.75 because my interest was primarily in identifying

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large-scale trends rather than daily fluctuations, thus necessitating a wider evaluation window (Cleveland and Devlin 1988).

To test whether differences among group mass variation patterns could be explained on the basis of sex or species, I first constructed a Dynamic Time Warp (DTW; Sakoe and Chiba 1971, Berndt and Clifford 1994) dissimilarity matrix among the time series of each group with the R package *dtwclust* (Sardá-Espinosa 2019). Dynamic Time Warping is a time series comparison technique that determines the optimal nonlinear alignment between pairs of time series that minimizes the sum of absolute differences between the two series (Rabiner et al. 1978). In DTW analysis, the order of points in time series is retained, but their distribution through time is nonlinearly 'warped' such that each point is paired with one or more points in a comparison sequence (Berndt and Clifford 1994). Dissimilarity between two or more series is therefore evaluated according to their features, regardless of whether they have the same onset, duration, or amplitude (Sakoe and Chiba 1971, Aghabozorgi et al. 2015). One common application is in speech analysis, in which shared phrases can be identified among speakers, despite differences in volume or pace of speech (Amin and Mahmood 2008). In ecology, this technique may also be used to generate a dissimilarity matrix among annual time series to determine whether sampled populations share biologically significant features, regardless of when those features appear in the sampling period. Given a DTW dissimilarity matrix, I then performed a Ward's Distance unsupervised hierarchical clustering exercise (Ward 1963) and organized the outcome as a dendrogram.

To facilitate comparison among groups, I made inferences based on the characteristics of each fitted line. In both summer and fall, I calculated the first derivatives of each fitted line as an estimate of the intensity, direction, and variability of mass change in each group. In summer, I also identified the earliest and latest fitted value as a metric of early and late season variation among groups. Because the fitted period of fall sampling was comparatively short and I was primarily interested in how bats prepare for hibernation, I instead estimated the greatest magnitude in mass change within each group's fitted

window. I also examined fall fitted lines for evidence of a sudden onset in rapid mass gain. In cases where a clear onset was not evident, I estimated the second derivate of mass change in fall, whose greatest values indicated when the rate of mass gain changed the most, and thus estimated when the onset of rapid mass gain occurred.

To test for the influence of foraging conditions on the timing of parturition, I selected all summer female groups from the historical dataset with available local environmental data (n = 9) according to the same eligibility criteria as previous and fitted them in the same way. Given the resulting fitted lines, I selected the highest fitted mass value as an estimate of the group mean parturition date. I collated environmental data for each of these groups, which consisted of the hourly temperature, hourly wind speed (m/s) and hourly precipitation (mm) for each sampling location and were taken from the nearest Environment and Climate Change Canada weather station that logs hourly data (Appendix B). Using these variables, a foraging index, created by Linton and Macdonald (2018), was used to assess the hourly foraging conditions in April - July. A score of 0 (temp. < 7 º C; wind > 5 m/s; rain > 0.75mm), 0.5 (7 º C ≤ temp. ≤ 10 º C ; 4 m/s ≤ wind ≤ 5 m/s; 0.25 mm ≤ rain ≤ 0.75mm), or 1 (temp. > 10 º C; wind < 4 m/s; rain < 0.25mm) was assigned to each hour between sunset and sunrise (determined using *SunCalc*; Thieurmel and Elmarhraoui 2019) to represent poor, moderate, and good foraging conditions, respectively. A spring suitable foraging condition (SSFC; April and May) and summer suitable foraging condition (JSFC; June and July) was then calculated for each cohort using the arithmetic average of the hourly foraging condition (Linton and Macdonald 2018). In groups whose parturition inflection dates were estimated from bats captured at multiple locations, I used a weighted average in which the respective weight of a station was equal to the proportion of bats caught at that location relative to the rest of the cohort. After testing for normality, I tested for a correlation between the estimated parturition date and SSFC and JFSC each with linear regression.

3.3 Results

The 12 summer groups (Fig. 3.1) assorted into four DTW clusters, which were statistically distinguishable by species and sex (Fig. 3.2). The only exception to this assortment was the group of female northern myotis captured in 2009 in Newfoundland, which was most similar to the male little brown myotis cluster. Of all the clusters, female little brown myotis were the most differentiated from the others (cophenetic distance = 313.57), including the female northern myotis (cophenetic distance = 429.11). Male groups of both species demonstrated steady rates of mass increase throughout the summer, but the rate of change in female groups was much more variable (Levene's Test: $p < 0.001$ for both sexes)(Fig 3.3).
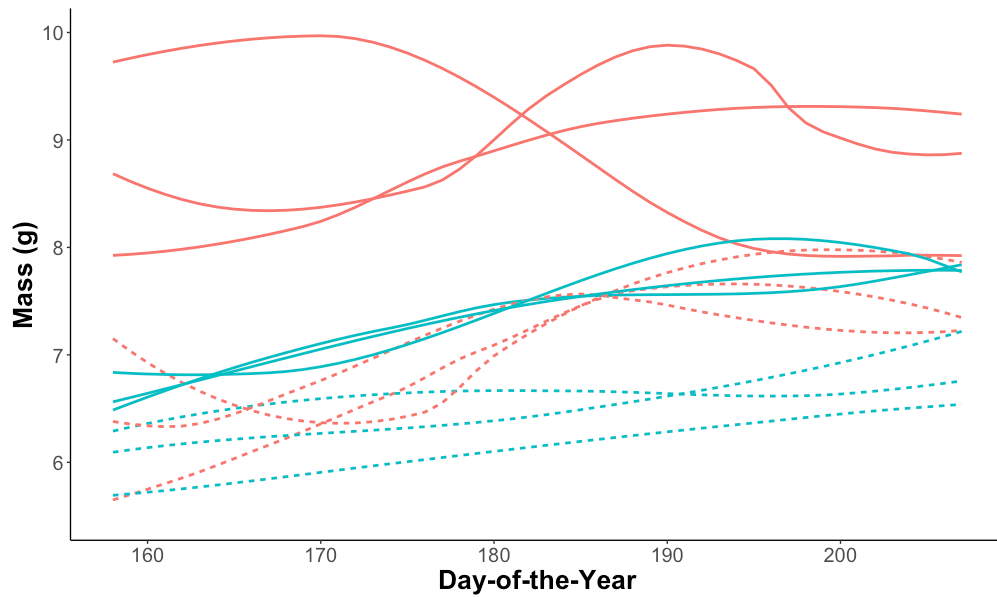
Figure 3.1 Fitted summer mass variation patterns of adult little brown myotis (*Myotis lucifugus*; solid lines) and northern myotis (*M. septentrionalis*; dashed lines) captured between Julian Day 158-207. Female groups are denoted in orange and male groups are denoted in blue.
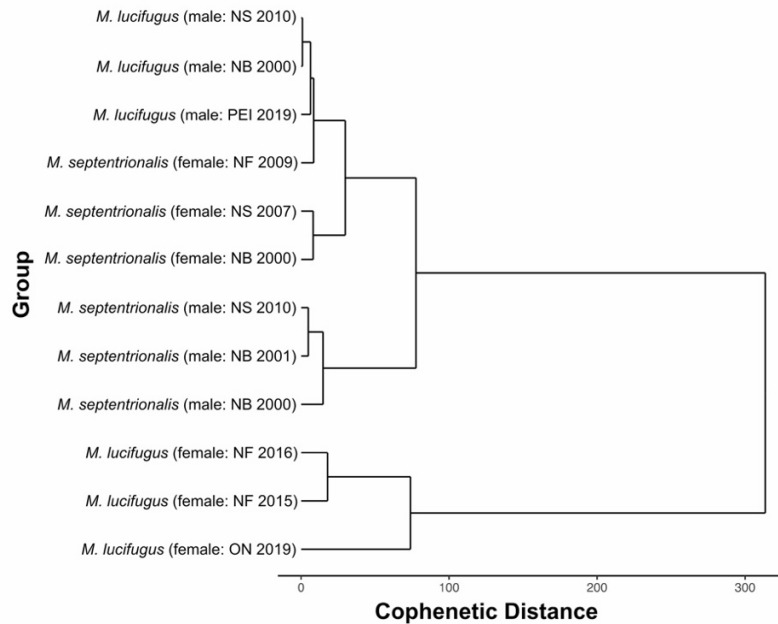
Figure 3.2 Hierarchical Dynamic Time Warp distance clustering dendrogram of time series constructed from summer mass variation patterns of adult little brown myotis (*Myotis lucifugus*) and northern myotis (*M. septentrionalis*) captured in in New Brunswick (NB), Nova Scotia (NS), Prince Edward Island (PEI), Newfoundland (NF) and Ontario (ON) between 2000 and 2019. The distance among clusters is cophenetic, which indicates the point at which a pair of adjoined clusters may be combined.
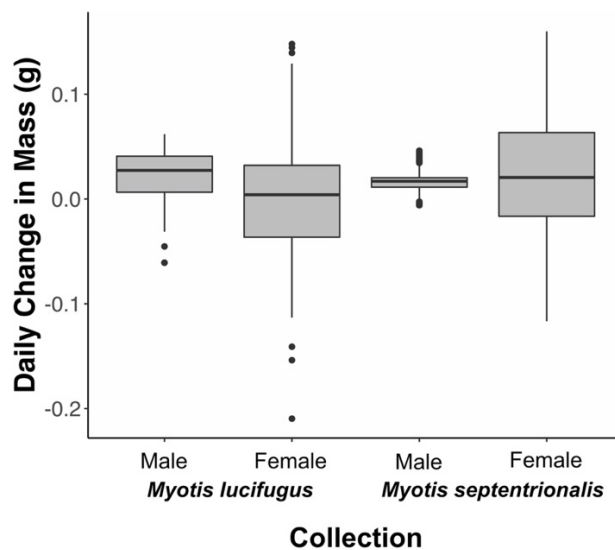
Figure 3.3 Distribution of the summer daily body mass change in collections of adult male and female little brown myotis (*Myotis lucifugus*) and northern myotis (*M. septentrionalis*) captured in Eastern Canada between 2000 and 2019. Each boxplot is comprised of 49 points, each representing the estimated daily change in body mass for the group. Error bars represent standard error of the estimated mean daily change in body mass.

The 15 fall groups (Fig. 3.4) assorted into three DTW clusters, which were largely distinguishable according to species (Fig. 3.5). Differences by age class were less evident in northern myotis than little brown myotis, and juvenile little brown myotis were more closely associated with adult northern myotis than conspecific adults or juvenile northern myotis. The greatest differentiation was found among the two species-associated clusters (cophenetic distance = 208.50). With the exception of juvenile northern myotis (t-test, p = 0.01), the fall estimated rates of mass gain were generally similar among sexes in both species, and were less variable in juveniles than adults (Levene's Test, p < 0.001 for both species)(Fig. 3.6). The estimated onsets of mass gain took place between Julian Day 227 and 255 (Table 3.4). Between the two species, rapid mass gain generally began earlier in little brown myotis and in adults of both species, but the age-associated pattern was less distinct.
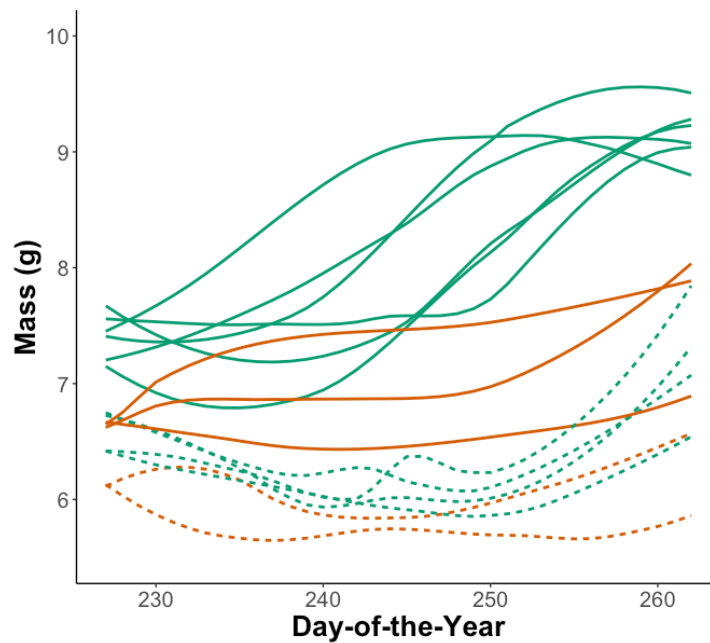
Figure 3.4 Fitted fall mass variation patterns of little brown myotis (*Myotis lucifugus*; solid lines) and northern myotis (*M. septentrionalis*; dashed lines) captured in Nova Scotia between Julian Date 227-262. Adult groups are denoted in green and juvenile groups are denoted in orange.
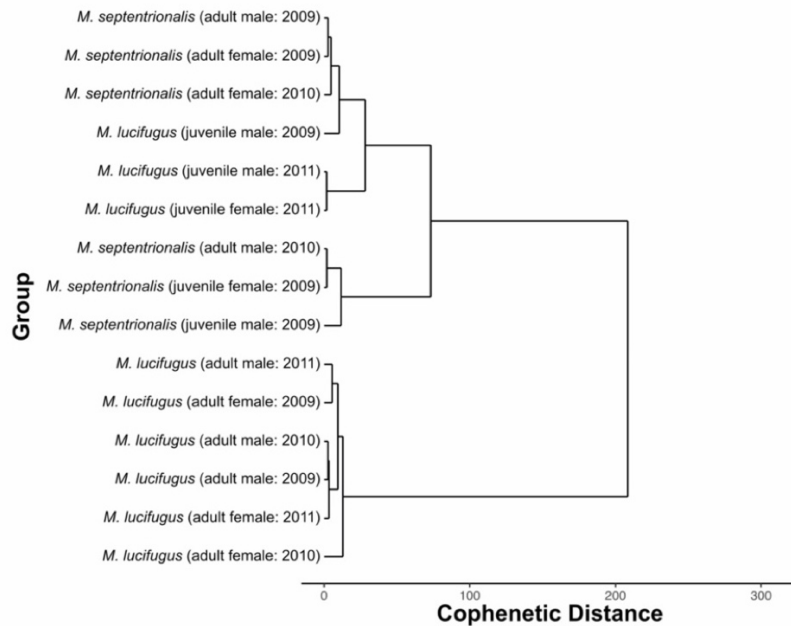
Figure 3.5 Hierarchical Dynamic Time Warp distance clustering dendrogram of time series constructed from fall mass variation patterns little brown myotis (*Myotis lucifugus*) and northern myotis (*M. septentrionalis*) captured in Nova Scotia between 2009 and 2011. The distance among clusters is cophenetic, which indicates the point at which a pair of adjoined clusters may be combined.
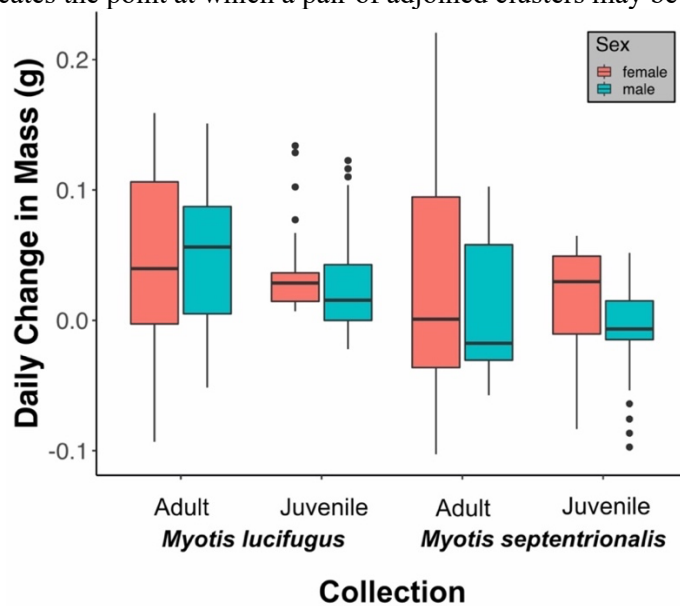
Figure 3.6 Distribution of the fall daily body mass change in collections of little brown myotis (*Myotis lucifugus*) and northern myotis (*M. septentrionalis*) captured in Nova Scotia between 2000 and 2019. Each boxplot is comprised of 35 points, each representing the estimated daily change in body mass for the group during the sampling period. Error bars represent standard error of the estimated mean daily change in body mass.

There was a significant relationship between the estimated date of parturition and spring foraging condition (SSFC: $R^2 = 0.792$, Pearson: $p = 0.001$, df = 7)(Fig. 3.7), but not with summer foraging condition (JSFC: $R^2 = 0.643$, Pearson: $p = 0.017$, df = 7)(Fig. 3.8). The summer foraging condition estimate from Nova Scotia in 2012 was an outlier (Cook's Distance = 0.465), and was thus excluded from summer analysis.
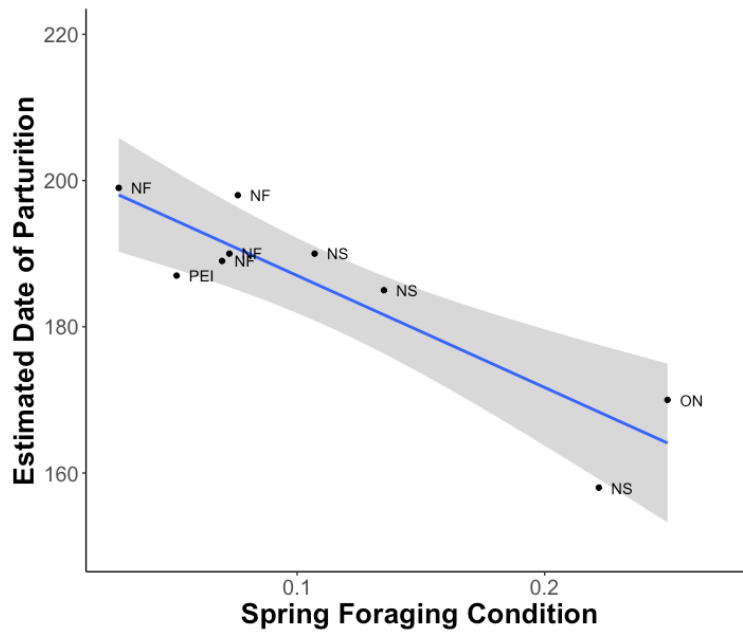
Figure 3.7 Linear relationship between spring foraging condition and the estimated date of parturition in little brown myotis (*Myotis lucifugus*) and northern myotis (*M. septentrionalis*) captured in New Brunswick (NB), Nova Scotia (NS), Prince Edward Island (PEI), Newfoundland (NF) and Ontario (ON) between 2005 and 2019. Each point represents the estimated date of parturition for one group.
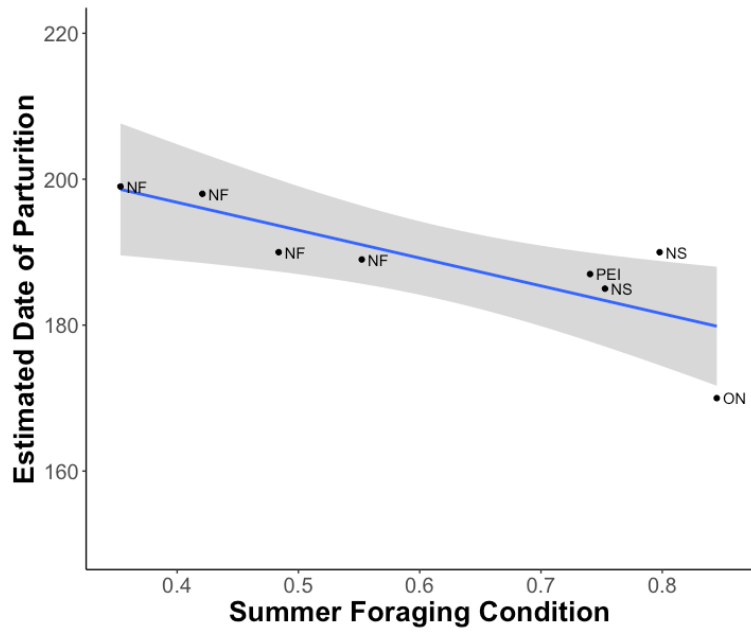
Figure 3.8 Linear relationship between summer foraging condition and the estimated date of parturition in little brown myotis (*Myotis lucifugus*) and northern myotis (*M. septentrionalis*) captured in New Brunswick (NB), Nova Scotia (NS), Prince Edward Island (PEI), Newfoundland (NF) and Ontario (ON) between 2005 and 2019. Each point represents the estimated date of parturition for one group.

Table 3.1 Sampling characteristics of groups of adult little brown myotis (*Myotis lucifugus*) and northern myotis (*M. septentrionalis*) captured in New Brunswick (NB), Nova Scotia (NS), Prince Edward Island (PEI), Newfoundland (NF) and Ontario (ON) during the summer between 2000 and 2019. Earliest Capture and Latest Capture denote the date (Julian Date) of the first and last capture in each group, and the largest gap in sampling within those dates is Largest Gap. The sample size, number of unique capture nights, and total number of capture sites are given as n, Nights, and Sites respectively. Groups added for parturition analysis are indicated with *.

Species	Sex	Year	Province	Earliest Capture	Latest Capture	Largest Gap	n	Nights	Sites
M. lucifugus	male	2000	NB	151	222	15	27	14	1
M. lucifugus	male	2010	NS	122	209	16	124	21	7
M. lucifugus	male	2019	PEI	158	221	15	22	12	5
M. lucifugus	female	2015	NF	139	220	9	294	31	2
M. lucifugus	female	2016	NF	154	216	9	153	19	2
M. lucifugus	female	2019	ON	134	219	11	298	21	6
M. lucifugus *	female	2012	NS	147	214	17	142	12	9
M. lucifugus *	female	2013	NF	158	214	18	616	26	2
M. septentrionalis	male	2000	NB	142	222	13	37	18	1
M. septentrionalis	male	2001	NB	156	207	17	20	9	1
M. septentrionalis	male	2010	NS	120	209	17	31	15	4
M. septentrionalis	female	2000	NB	142	222	9	30	17	1
M. septentrionalis	female	2007	NS	149	209	9	29	14	2
M. septentrionalis	female	2009	NF	156	217	12	28	14	2
M. septentrionalis *	female	2005	NS	154	216	7	62	20	2
M. septentrionalis *	female	2009	NF	156	217	18	28	14	2

Table 3.2 Summary of the LOESS-fitted interpolations of mass values of groups of adult little brown myotis (*Myotis lucifugus*) and northern myotis (*M. septentrionalis*) captured during the summer in New Brunswick (NB), Nova Scotia (NS), Prince Edward Island (PEI), Newfoundland (NF) and Ontario (ON) between 2000 and 2019. Earliest Mass and Latest Mass describe the fitted mass value on Days-of-Year 158 and 207 respectively, and Change denotes the net difference in mass between those values. Standard Error (SE) describes the error of each full LOESS fit (span = 0.75), including all values between the earliest available capture until at the latest available capture, up to Day-of-Year 222. Groups added for parturition analysis are indicated with *.

Species	Sex	Year	Province	SE	Earliest Mass (g)	Latest Mass (g)	Change (g)
M. lucifugus	male	2000	NB	0.59	6.49	7.84	1.35
M. lucifugus	male	2010	NS	0.50	6.56	7.79	1.22
M. lucifugus	male	2019	PEI	0.60	6.84	7.77	0.94
M. lucifugus	female	2015	NF	1.10	7.93	9.24	1.31
M. lucifugus	female	2016	NF	1.27	8.69	8.88	0.19
M. lucifugus	female	2019	ON	1.03	9.72	7.92	-1.80
M. lucifugus *	female	2012	NS	0.77	8.16	8.43	-0.97
M. lucifugus *	female	2013	NF	0.84	7.39	7.19	1.03
M. septentrionalis	male	2000	NB	0.52	5.69	6.54	0.85
M. septentrionalis	male	2001	NB	0.82	6.29	6.76	0.47
M. septentrionalis	male	2010	NS	0.68	6.09	7.22	1.12
M. septentrionalis	female	2000	NB	0.65	5.65	7.35	1.70
M. septentrionalis	female	2007	NS	0.67	6.38	7.23	0.85
M. septentrionalis	female	2009	NF	1.46	7.15	7.86	0.71
M. septentrionalis *	female	2005	NS	0.91	6.61	7.02	0.39
M. septentrionalis *	female	2009	NF	1.46	7.15	7.86	0.71

Table 3.3 Sampling characteristics of groups of little brown myotis (*Myotis lucifugus*) and northern myotis (*M. septentrionalis*) captured in Nova Scotia during the fall between 2009 and 2011. Earliest Capture and Latest Capture denote the date (Julian Date) of the first and last capture in each group, and the largest gap in sampling within those dates is Largest Gap. The sample size, number of unique capture nights, and total number of capture sites are given as n, Nights, and Sites respectively.

Species	Sex	Year	Age	Earliest Capture	Latest Capture	Largest Gap	n	Nights	Sites
M. lucifugus	female	2009	adult	227	274	4	162	25	6
M. lucifugus	male	2009	adult	227	279	5	242	27	6
M. lucifugus	male	2009	juvenile	227	279	12	49	17	6
M. lucifugus	female	2010	adult	226	273	10	97	22	9
M. lucifugus	male	2010	adult	209	276	17	189	29	12
M. lucifugus	female	2011	adult	223	269	8	65	12	6
M. lucifugus	male	2011	adult	223	269	8	167	16	6
M. lucifugus	female	2011	juvenile	198	269	15	48	14	11
M. lucifugus	male	2011	juvenile	198	269	12	71	15	10
M. septentrionalis	female	2009	adult	227	267	12	87	19	6
M. septentrionalis	male	2009	adult	227	274	7	129	21	6
M. septentrionalis	female	2009	juvenile	227	265	7	41	16	6
M. septentrionalis	male	2009	juvenile	227	274	9	67	17	6
M. septentrionalis	female	2010	adult	226	262	10	70	21	11
M. septentrionalis	male	2010	adult	209	276	17	130	26	13

Table 3.4 Summary of the LOESS-fitted interpolations of mass values of groups of little brown myotis (*Myotis lucifugus*) and northern myotis (*M. septentrionalis*) captured during the fall in Nova Scotia between 2009 and 2011. Earliest Mass and Latest Mass describe the fitted mass value on Days-of-Year 227 and 262 respectively, and Max Change denotes largest net difference present between any two fitted values in the sampling period. Standard Error (SE) describes the error of each full LOESS fit (span = 0.75), including all values between the earliest available capture until at the latest available capture.

Species	Sex	Year	Age	SE	Earliest Mass (g)	Latest Mass (g)	Max Change (g)	Onset
M. lucifugus	female	2009	adult	1.00	7.67	9.28	2.10	244
M. lucifugus	male	2009	adult	1.21	7.20	9.07	1.92	229
M. lucifugus	male	2009	juvenile	0.77	6.67	6.89	0.46	241
M. lucifugus	female	2010	adult	1.02	7.15	9.23	2.44	239
M. lucifugus	male	2010	adult	1.03	7.45	8.80	1.69	227
M. lucifugus	female	2011	adult	0.94	7.56	9.04	1.53	249
M. lucifugus	male	2011	adult	1.10	7.41	9.51	2.20	238
M. lucifugus	female	2011	juvenile	0.64	6.65	7.89	1.24	227
M. lucifugus	male	2011	juvenile	0.77	6.62	8.04	1.41	249
M. septentrionalis	female	2009	adult	0.52	6.73	7.32	1.38	248
M. septentrionalis	male	2009	adult	0.71	6.75	7.07	1.00	248
M. septentrionalis	female	2009	juvenile	0.89	6.11	6.57	0.73	245
M. septentrionalis	male	2009	juvenile	0.61	6.13	5.86	0.48	255
M. septentrionalis	female	2010	adult	0.91	6.42	7.84	1.84	249
M. septentrionalis	male	2010	adult	0.63	6.42	6.54	0.69	251

3.4 Discussion

The summer body mass variation patterns of adult male and female little brown myotis and northern myotis were both visually and statistically distinguishable. Indeed, female patterns contained mid-season parturition peaks and were more variable than those of males. It is unsurprising that female little brown myotis were the most differentiated from the other groups, given both their peaks and their relatively greater mass than northern myotis (Van Zyll de Jong 1985, Kurta et al. 1989, Kunz et al. 1998, Reynolds and Kunz 2000, Jung et al. 2006). Furthermore, the low and consistent early-summer mass values for male groups suggests that early summer period is characterized by some combination of late emergence (Czenze and Willis 2015) and small net positive energy budget balances. Similarly, the variance in early summer female mass supports the contention that female emergence times may vary according to factors like body condition, reproductive status, or weather which may differ among groups (Frick et al. 2010*b*, Jonasson and Willis 2011).

The fall clustering outcomes indicate lower behavioural differentiation relative to summer and did not provide evidence for differentiation according to sex. There was weak visual evidence for delayed rapid mass gain in juveniles, whose onset estimates were generally similar to adults in the same year. Temporal asynchrony in rapid mass gain was evident in Kunz et al. (1998), but Mcguire et al. (2009) observed no clear period of juvenile rapid mass gain during their study. In light of these studies, my clustering and onset estimates suggest that that if juveniles achieve and sustain high rates of mass gain like adults, it occurs later Nova Scotia than could be observed within the sampling period. Despite an upward bend in many of the fitted juvenile lines, the relatively low variation and mean in mass gain rates in juveniles suggests that their prehibernation strategy may be better characterized as a single long effort following parturition. Conversely, I found clear evidence that adults undergo a transition from summer behaviour to a period of rapid mass gain characterized by rates as high as 0.1g/day (Fig. 3.6), like those

observed in Kunz et al. (1998). Regardless of which factors drive this difference, my work provides further support for the existence of age-dependent prehibernation strategies in both little brown myotis and northern myotis.

One contributing factor to the timing of age- or sex-specific strategies by individuals is weather. In adult female bats, I found that the association of weather with the estimated date of parturition in was especially strong in spring. The relatively greater importance of spring weather over summer is intuitive, considering that gestation begins very shortly after emergence (Wimsatt 1945, O'Farrell and Studier 1973), and that favourable springs should facilitate earlier parturition, regardless of the quality of the subsequent summer. One proposed mechanism for this relationship is non-random pre-emergence arousal patterns in little brown myotis, which suggest that females in good body condition capitalize on rare warm early-spring nights (Czenze and Willis 2015, Czenze et al. 2017). Years with more favourable nights early in the spring may provide benefits to emergent females in a wider range of body conditions, and therefore move the mean parturition date up. Alternatively, spring conditions may simply dictate the timing of emergence and thus the onset of gestation and associated rapid mass gain. Although Czenze and Willis (2015) demonstrated that emergence timing at a hibernaculum in Manitoba was associated with barometric pressure changes, Meyer et al. (2016) found no such relationship at a hibernaculum further South in Wisconsin. In context with the known influence of body mass on emergence timing (Frick et al. 2010*b*, Norquay and Willis 2014, Czenze and Willis 2015), it is therefore less likely that foraging conditions drove early emergence, but instead facilitated gestation for those females that had already emerged.

In summer sampling, all male groups demonstrated consistently positive and less variable rates of daily mass change than female groups, but it should be noted that the mid-summer negative slopes associated with female groups can generally be attributed to the effect of parturition on a group's mean mass. Regardless, female groups demonstrated higher rates of mass gain than concurrent male groups,

especially during early summer. This disparity indicates that if pregnancy is facilitated by favourable

foraging conditions (Anthony and Kunz 1977, Arlettaz et al. 2001) male body mass is not affected to the

same degree, likely due to the lack of pressure to develop significant sperm stores so early in the season.

The presence of this pattern in male little brown myotis and northern myotis groups across years supports

the contention that male temperate bats minimize their net energy budget throughout the summer (Barclay

1991, Wilkinson and Barclay 1997), due to the higher costs of flight at greater body masses (Winter and

Von Helversen 1998). Complementing further mass variation analysis with temperature-sensitive radio

telemetry data (e.g., Barclay et al. 1996) may clarify whether these patterns are driven by lower rates of

foraging (Barclay 1991), increased use of torpor (Kurta and Kunz 1988), or less efficient foraging

(Wilkinson and Barclay 1997). In particular, such analysis would identify the relationships between

nightly foraging frequency or duration and daily patterns of thermoregulation.

There are some important considerations to these results. First, the variation in a LOESS-fitted

line is a function of the chosen span parameter (Cleveland and Devlin 1988). Because I selected a

conservative span parameter (0.75), I conceded that the fitted lines would not capture short term changes

in average mass. Similarly, derivatives calculated for each group also reflect the variability introduced by

the span parameter, and thus do not reliably capture short-term variation. For this reason, I do not

consider the short-term fluctuations in fall fits to be informative, but instead used the distribution of

derivatives to contextualize my conclusions. Additionally, group composition accounted for sex, year, and

province, but included captures pooled from sites across each province, which may have masked intra-site

variation. I recognize both sampling frequency and site distribution as major limitations in analyses of

historical datasets like this one, and emphasize the value of ongoing long-term monitoring.

Collectively, each objective of this project supports the hypothesis that sex- and age-specific

energy allocation regimes of little brown myotis and northern myotis confer similarly disparate patterns of

body mass variation. In particular, my results illustrate the drastic body mass changes of females in early

summer, and the concurrent low rates of body mass change in males. Further, I demonstrate that weather conditions are important for the reproductive success of female temperate hibernating bats. Fall analysis identified the presence of disparate prehibernation strategies among adults and juveniles. Both the summer and fall patterns were identifiable through time series clustering, and demonstrate its use as a viable technique for characterizing body mass patterns among populations. In tandem with time series modelling, it should be considered as a viable tool to identify phenological patterns in populations with important annual behaviours (e.g., moulting birds: Sjöberg 1988)

Chapter 4
Discussion

In this thesis, I examined two important aspects of active season (summer and fall) temperate bat behaviour. First, I tested the hypothesis that little brown myotis on Prince Edward Island select roosts according to a preferences for certain landscape features or composition. In particular, I examined the relationship between roost location and the accessibility or availability of forest, linear, and freshwater landscape features. Second, I sought to characterize active season mass variation patterns of little brown myotis (*Myotis lucifugus*) and northern myotis (*M. septentrionalis*). I compared these patterns among bats according to age, species, and sex, and subsequently related summer mass variation to foraging conditions. To meet these outcomes, I used a combination of radio telemetry, community science, and historical capture records.

In Chapter 2, I identified a strong positive relationship between roost location and the distance to both open wetlands and forest stands. This outcome likely reflects energetic cost savings associated with a reduced commute distance between a central place (i.e. the roost) and foraging resources, a prediction of the marginal value theorem (Charnov 1976). Close physical associations between maternity roosts and water bodies have been identified in several other systems (Evelyn et al. 2004, Rainho and Palmeirim 2011, Segers and Broders 2014), but the structure of such geographic relationships may vary according to the foraging strategy of central place foragers. For example, the bald eagle (*Haliaeetus leucocephalus*) nest site selection response to anthropogenic disturbance is variable (Andrew and Mosher 1982, Thompson and McGarigal 2002, Guinn 2004), which may be attributed to how individuals tolerate perceived danger relative to foraging benefits.

Despite evidence for the importance of proximity to certain landscape features, there was no support for a relationship with nearby (within 5 km) forest area, open wetland area, or edge density.

Although each of these features may have important biological implications for commuting and foraging little brown myotis, it appears as they are not informative at the measured spatial scale in this system. The scale-dependent influence of forest cover on roosting northern myotis (Kaminski et al. 2020) indicates that further study is necessary to determine whether similar patterns exist in little brown myotis. Previous work has identified forest cover (Bergeson et al. 2015), road density (Fagan et al. 2018), snag availability (Broders and Forbes 2004), and proximity to water (Kalcounis-Rüppell et al. 2005) as potentially important characteristics. In context with sexual disparities in anthropogenic roost selection (Randall et al. 2014, Johnson et al. 2019), these results suggest that roost selection is a complicated process that reflects reproductive, foraging, and thermoregulatory aspects of active season behaviour.

In Chapter 3, I examined sex-, species-, and age-specific differences in active season body mass variation patterns in little brown myotis and northern myotis. In spring and summer, these differences were most pronounced among conspecific males and females, likely due to temporally disparate reproductive investments. The estimated timing of parturition derived from these patterns was strongly associated with spring and summer foraging conditions. Of these, spring foraging conditions had a stronger influence on the estimated date of parturition. Collectively, this pattern indicates not only an energetically significant disparity among adult males and females, but an important reproductive link between female behaviour and weather. The influence of weather on parturition timing was noted in Linton and Macdonald (2018), and aligns with the Thrifty Female Hypothesis (Jonasson and Willis 2011, Czenze et al. 2017), which predicts a strong association between female reproductive behaviour and net energetic expenditures.

I also illustrated patterns of prehibernation mass gain, which were generally similar among sexes within species. Adults demonstrated slightly greater variation in the rate of mass gain than juveniles, but the greatest distinction existed among the two species, with little brown myotis demonstrating earlier onsets of mass gain than northern myotis. These results indicate that, like other hibernating mammalian

taxa, reproductive and age-related constraints influence annually predictable cycles of energy expenditure (Michener and Locklear 1990, Buck and Barnes 1999, López-Alfaro et al. 2013). In bats, juvenile overwinter mortality is estimated to be far higher than that of adults (Sendor and Simon 2003, Ellison et al. 2007, Frick et al. 2010*b*), which is likely the result of lower fat reserves entering hibernation. Similarly, fall and spring body condition predicts emergence timing of females (Norquay and Willis 2014, Czenze and Willis 2015), whose early emergence offers the best opportunity for early (and therefore successful) reproduction. These relationships suggest that how an individual prepares for hibernation affects not only overwinter survival, but reproductive success as well.

This work demonstrates how two key aspects of temperate bat biology; roosting and foraging, are affected by environmental conditions. As synanthropic roosters, little brown myotis appear to take into consideration not only the relative quality of buildings relative to trees or crevices (Henry et al. 2002, Broders et al. 2006, Olson and Barclay 2013, Randall et al. 2014, Johnson et al. 2019), but also how these structures relate to the landscape around them. Similarly, it appears as though reproductive females of both species capitalize on favourable weather conditions to undergo parturition sooner in the year, unlike males, whose biggest reproductive investment comes in fall (Thomas et al. 1979) alongside prehibernation mass gain. These strategies demonstrate how individuals address their energy budgets with respect to life history characteristics. As a long-lived mammal, such flexibility complements interannual site fidelity (Norquay et al. 2013), gregariousness (Olson and Barclay 2013), and dynamic torpor use (Dzal and Brigham 2013, Besler and Broders 2019) to improve year-to-year fitness in changing environments.

Whereas this study provides two important assessments of how temperate bats meet reproductive and hibernation demands, further work is needed to quantify the fitness effect of these behaviours and how they vary among individuals and populations. Notably, I pooled mass data across individuals and capture sites, and could thus only make general inferences about populations. In systems where passive

integrated transponder (PIT) tags are being used, PIT readers and automated scales at roost entrances could bring much finer resolution to mass variation analyses. Such work could more precisely estimate the timing of parturition, or examine how foraging bout timing (Henry et al. 2002) changes throughout the reproductive period. Paired with mass measurements, phenological assessments would support work like Frick et al. (2010) or Czenze and Willis (2015), which examined survival and emergence timing in little brown bats. Further, PIT data could provide greater definition to roost selection analyses, and delineate individual preferences in relation to aspects like known age or reproductive condition.

Another important next step will be to address structural characteristics of roosts used by little brown myotis. Roost selection is a complex decision-making process, and landscape-level analyses alone cannot adequately explain its variation. Recent work supports the contention that microclimate is an important indicator of roost use in little brown myotis (Wilcox and Willis 2016, Hoeh et al. 2018) and that sociality likely plays a role as well (Waag et al. 2021). Supplementing our understanding of tree roosting behaviour (Kalcounis-Rüppell et al. 2005, Broders et al. 2006, Olson and Barclay 2013, Bergeson et al. 2015) with structural analyses like those done in other bat species (Neubaum et al. 2007, Fagan et al. 2018) will provide key details for critical habitat identification and artificial roost construction.

In response to the classification of little brown myotis and northern myotis as endangered (Environment and Climate Change Canada 2018), management entities are tasked with identifying and maintaining critical habitat for these species. In Chapter 2, I determined that on Prince Edward Island, roosts are likely to be situated in places that minimize their distance to both forests and open wetlands. Although my models presented no support for the influence of landscape feature quantity on roost selection, proximity measures emphasize the importance of retaining these features for foraging and commuting bats.

The relationship between foraging conditions and mass variation identified in Chapter 3 also has important conservation implications. This study, like others, provides strong evidence that favourable weather conditions facilitate reproductive behaviour in bats (Burles et al. 2009, Frick et al. 2010*b*, Linton and Macdonald 2018, 2020). Although climate change is expected to have a more drastic effect on temperature regimes at northern latitudes (Holland and Bitz 2003, Cohen et al. 2014), the long-term effect of warmer or more extreme annual weather patterns on bats is yet unknown. Further, these species may experience phenological decoupling of prey availability, as has been observed in other aerial insectivores (Visser and Both 2005). Viewed with the same energy budget lens, conservation should seek to promote energetically favourable roosts to alleviate stress enacted through adverse weather conditions and decreased foraging efficiency. For this reason, identifying and protecting valuable roosts may be a practical way to support recovering bat populations. Supplementing such habitat conservation measures with ongoing behavioural research like the projects in this study will offer increasingly targeted support and further our understanding of their biology.

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Appendix

Appendix A
Raw Roost Selection Structure Data

		Distance to Feature (km)				Feature Area (km^2)		Feature Length (km)		
Type	Source	Rivers and Streams	Open Wetland	Forest	Edge	Forest	Open Wetland	Rivers and Streams	Edge	Edge Density (km / km^2)
Comparison	Random	0.11	0.06	0.13	0.13	8.76	0.24	64.19	344.75	4.39
Comparison	Random	0.37	0.72	0.23	0.23	10.95	0.58	48.34	458.90	5.84
Comparison	Random	0.07	2.80	0.20	0.13	10.05	0.38	16.94	381.95	4.86
Comparison	Random	0.19	1.64	0.15	0.15	9.13	0.33	57.33	434.26	5.53
Comparison	Random	1.02	1.69	0.06	0.06	21.27	0.99	29.28	507.12	6.46
Comparison	Random	0.78	2.50	0.01	0.01	7.99	0.20	12.87	308.83	3.93
Comparison	Random	0.65	1.63	0.14	0.14	6.22	0.40	15.30	272.69	3.47
Comparison	Random	0.14	0.39	0.11	0.05	12.05	0.12	63.10	506.34	6.45
Comparison	Random	1.00	1.81	0.94	0.29	20.70	0.45	77.88	528.19	6.73
Comparison	Random	0.24	1.60	0.27	0.27	18.16	0.06	85.83	508.33	6.47
Comparison	Random	0.41	0.43	0.08	0.08	31.12	0.15	117.97	645.46	8.22
Comparison	Random	0.38	0.96	0.17	0.02	26.27	0.11	93.14	663.78	8.45
Comparison	Random	0.51	1.35	0.01	0.01	9.11	0.39	35.01	267.81	3.41
Comparison	Random	0.91	0.92	0.33	0.33	12.03	1.55	15.11	311.60	3.97

Comparison	Random	0.45	1.26	0.71	0.29	10.31	0.40	41.84	323.77	4.12
Comparison	Random	1.05	1.71	0.02	0.02	9.37	0.52	39.35	472.51	6.02
Comparison	Random	0.37	0.64	0.26	0.03	26.66	0.45	102.78	707.64	9.01
Comparison	Random	0.46	0.46	0.07	0.07	18.40	1.40	19.59	432.18	5.50
Comparison	Random	0.69	0.35	0.30	0.05	9.23	0.95	26.40	291.14	3.71
Comparison	Random	0.80	1.52	0.07	0.04	11.32	0.22	49.90	522.82	6.66
Comparison	Random	0.06	0.18	0.08	0.08	12.74	0.33	57.06	848.93	10.81
Comparison	Random	0.90	0.96	0.31	0.31	8.90	0.44	34.47	452.52	5.76
Comparison	Random	0.41	1.02	0.21	0.12	4.46	0.06	10.53	229.30	2.92
Comparison	Random	1.06	2.43	0.18	0.18	8.05	0.45	58.75	368.96	4.70
Comparison	Random	0.68	1.37	0.22	0.13	6.70	0.15	20.68	349.33	4.45
Comparison	Random	0.58	0.68	0.24	0.10	15.45	0.25	53.79	787.21	10.02
Comparison	Random	0.45	0.22	0.14	0.14	9.42	0.23	62.59	339.48	4.32
Comparison	Random	0.62	0.45	0.00	0.01	10.97	0.66	56.02	432.83	5.51
Comparison	Random	0.15	0.67	0.05	0.04	34.90	0.06	110.28	553.97	7.05
Comparison	Random	0.45	0.27	0.20	0.20	9.84	0.33	61.55	341.61	4.35
Comparison	Random	0.76	2.21	0.31	0.22	6.99	0.43	18.07	314.90	4.01
Comparison	Random	0.53	0.39	0.16	0.16	6.55	0.21	38.26	240.96	3.07
Comparison	Random	0.66	0.76	0.02	0.02	10.47	0.23	52.26	490.18	6.24
Comparison	Random	0.75	1.65	0.02	0.02	13.53	0.26	48.08	828.96	10.55
Comparison	Random	0.72	0.75	0.26	0.04	10.74	0.19	20.25	444.10	5.65
Comparison	Random	0.97	1.06	0.25	0.25	8.86	0.45	34.64	454.86	5.79

Comparison	Random	0.21	0.80	0.00	0.15	25.11	0.26	88.92	668.97	8.52
Comparison	Random	0.49	0.55	0.30	0.30	10.89	0.45	55.14	406.31	5.17
Comparison	Random	0.38	1.03	0.35	0.22	9.34	0.47	51.11	379.22	4.83
Comparison	Random	0.35	2.24	0.02	0.02	32.82	0.15	103.12	627.45	7.99
Comparison	Random	0.51	0.25	0.01	0.01	9.39	0.23	60.83	331.94	4.23
Comparison	Random	0.40	0.48	0.01	0.01	15.98	0.44	43.15	654.11	8.33
Comparison	Random	0.35	0.70	0.04	0.04	22.95	0.11	73.32	580.42	7.39
Comparison	Random	0.38	2.28	0.35	0.05	12.54	0.10	68.74	402.06	5.12
Comparison	Random	0.30	1.95	0.60	0.47	22.04	0.05	92.26	524.17	6.67
Comparison	Random	0.77	1.64	0.48	0.40	10.04	0.30	53.43	340.27	4.33
Comparison	Random	0.40	0.06	0.07	0.07	13.99	1.51	11.56	303.13	3.86
Comparison	Random	0.29	0.23	0.10	0.06	11.52	0.44	56.01	888.36	11.31
Comparison	Random	0.15	0.84	0.13	0.13	11.97	0.39	59.81	468.48	5.96
Comparison	Random	0.66	2.56	0.03	0.03	5.12	0.05	15.38	273.10	3.48
Comparison	Random	0.60	1.76	0.15	0.15	12.39	0.94	35.43	451.21	5.74
Comparison	Random	0.26	1.09	0.08	0.08	19.81	0.27	60.96	633.93	8.07
Comparison	Random	0.51	0.61	0.02	0.02	14.81	0.91	26.95	448.40	5.71
Comparison	Random	0.75	1.30	0.01	0.01	13.07	0.93	39.04	484.52	6.17
Comparison	Random	0.31	0.38	0.01	0.01	8.30	0.10	28.02	415.75	5.29
Comparison	Random	0.50	1.62	0.24	0.04	16.91	0.44	74.42	517.29	6.59
Comparison	Random	0.76	0.19	0.03	0.03	9.94	0.42	50.62	439.71	5.60
Comparison	Random	0.47	0.51	0.22	0.08	3.56	0.00	9.61	173.98	2.22

Comparison	Random	0.66	1.46	0.59	0.59	12.49	0.43	60.56	460.95	5.87
Comparison	Random	0.05	0.06	0.25	0.16	13.36	0.23	56.17	479.90	6.11
Comparison	Random	0.98	1.29	0.15	0.15	9.46	0.46	53.73	426.04	5.42
Comparison	Random	0.80	1.59	0.83	0.14	20.35	0.45	76.43	520.38	6.63
Comparison	Random	0.34	0.69	0.03	0.03	10.84	0.69	51.32	470.42	5.99
Comparison	Random	0.58	1.50	0.02	0.02	17.68	0.22	47.55	612.30	7.80
Comparison	Random	0.28	1.19	0.07	0.07	9.80	0.21	61.26	360.19	4.59
Comparison	Random	0.17	0.49	0.41	0.15	7.14	0.58	27.59	246.05	3.13
Roost	Balzer	0.79	0.85	0.16	0.16	10.03	0.10	18.59	441.67	5.62
Roost	Balzer	0.45	0.29	0.01	0.01	7.00	0.07	11.62	312.64	3.98
Roost	Balzer	0.87	0.77	0.04	0.04	9.88	1.55	10.68	260.30	3.31
Roost	Balzer	0.76	0.75	0.30	0.30	8.90	0.10	16.84	413.80	5.27
Roost	Balzer	0.10	1.72	0.08	0.08	16.97	0.48	39.35	579.28	7.38
Roost	Balzer	0.79	0.78	0.33	0.33	8.93	0.10	16.96	415.10	5.29
Roost	Balzer	0.18	0.83	0.08	0.06	11.04	0.47	24.92	394.53	5.02
Roost	Balzer	0.30	0.28	0.02	0.02	17.44	1.40	17.09	388.88	4.95
Roost	Balzer	0.66	0.72	0.01	0.01	16.14	1.55	21.47	404.62	5.15
Roost	Balzer	0.39	0.34	0.01	0.01	8.12	0.10	15.76	387.19	4.93
Roost	Balzer	0.18	0.14	0.04	0.04	11.37	0.47	21.79	396.65	5.05
Roost	CWHC	0.08	0.14	0.09	0.09	7.81	0.54	44.06	277.91	3.54
Roost	CWHC	0.36	0.67	0.10	0.10	11.19	0.41	46.79	345.65	4.40
Roost	CWHC	0.59	0.12	0.01	0.01	9.89	0.42	50.40	434.78	5.54

Roost	CWHC	0.08	2.43	0.05	0.05	6.90	0.31	18.86	335.64	4.27
Roost	CWHC	0.02	0.08	0.01	0.01	36.37	0.14	101.21	716.31	9.12
Roost	CWHC	0.13	0.16	0.11	0.11	17.99	0.48	73.32	811.88	10.34
Roost	CWHC	0.82	0.55	0.01	0.01	12.23	0.13	31.12	637.86	8.12
Roost	CWHC	0.32	0.22	0.02	0.02	20.90	1.14	37.96	588.59	7.49
Roost	CWHC	0.05	0.05	0.07	0.07	23.22	0.57	90.50	736.86	9.38
Roost	CWHC	0.08	0.38	0.03	0.03	9.96	0.71	48.99	465.94	5.93
Roost	CWHC	0.22	0.08	0.07	0.07	10.13	0.93	33.95	294.90	3.75

Appendix B

Weather Station Information

Latitude	Longitude	Name	Station ID	Year	Province	Count	Distance (km)
44.930205	-63.322052	DEBERT	42243	2005	NS	62	54.6
44.930205	-63.322052	DEBERT	42243	2006	NS	78	54.6
44.438182	-65.216519	KEJIMKUJIK 1	6923	2007	NS	1	4.04
44.930205	-63.322052	DEBERT	42243	2007	NS	28	54.6
48.78493	-54.213417	TERRA NOVA NAT PARK CS	27142	2009	NF	8	30.83
50.529393	-57.38976	FEROLLE POINT (AUT)	9034	2009	NF	20	57.9
43.556236	-65.453543	BACCARO PT	46007	2012	NS	3	11.81
44.37418	-65.030255	KEJIMKUJIK 1	6923	2012	NS	21	14.14
44.616123	-63.434336	SHEARWATER RCS	47187	2012	NS	16	6.44
44.769795	-64.423364	KENTVILLE CDA CS	27141	2012	NS	14	33.36
45.512278	-62.071631	TRACADIE	41575	2012	NS	29	32.33
45.596577	-63.122363	DEBERT	42243	2012	NS	9	30.43
45.902232	-61.096977	PORT HAWKESBURY ESKASONI FIRST NATION	48668	2012	NS	4	34.46
45.95602	-60.786756	AUTOMATIC WEATHER STATION	49748	2012	NS	25	11.51

		ESKASONI FIRST NATION					
46.110449	-60.862553	AUTOMATIC WEATHER STATION	49748	2012	NS	21	26.89
47.260322	-53.284788	ST JOHNS WEST CLIMATE	48871	2013	NF	417	47.08
49.093622	-57.535893	CORMACK RCS	50677	2013	NF	199	26.7
47.260322	-53.284788	ST JOHNS WEST CLIMATE	48871	2015	NF	278	47.08
49.093622	-57.535893	CORMACK RCS	50677	2015	NF	19	26.7
47.260322	-53.284788	ST JOHNS WEST CLIMATE	48871	2016	NF	131	47.08
49.093622	-57.535893	CORMACK RCS	50677	2016	NF	26	26.7
43.21164	-81.81554	SARNIA CLIMATE	44323	2019	ON	50	45.83
43.22567	-81.8639	SARNIA CLIMATE	44323	2019	ON	1	43.39
43.25023	-81.81393	SARNIA CLIMATE	44323	2019	ON	48	48.27
43.25093	-81.84967	SARNIA CLIMATE	44323	2019	ON	41	45.98
43.25137	-81.8254	SARNIA CLIMATE	44323	2019	ON	1	47.59
43.25176	-81.84901	SARNIA CLIMATE	44323	2019	ON	75	46.08
43.25268	-81.85139	SARNIA CLIMATE	44323	2019	ON	2	45.98
43.266368	-81.811244	SARNIA CLIMATE	44323	2019	ON	1	49.5
43.26956	-81.83027	SARNIA CLIMATE	44323	2019	ON	1	48.48
46.403678	-63.064619	HARRINGTON CDA CS	30308	2019	PEI	5	10.47
46.415825	-63.09451	HARRINGTON CDA CS	30308	2019	PEI	5	9.89
46.46477	-63.30543	HARRINGTON CDA CS	30308	2019	PEI	2	17.01
46.490563	-63.39518	HARRINGTON CDA CS	30308	2019	PEI	27	23.78

| 46.492309 | -63.398438 | HARRINGTON CDA CS | 30308 | 2019 | PEI | 2 | 24.1 |
| 46.49725 | -63.39805 | HARRINGTON CDA CS | 30308 | 2019 | PEI | 25 | 24.46 |