The role of social preferences in the organization of a gregarious mammal colony

by

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Examining Committee Membership

The following served on the examining committee for this thesis. The decision of the Examining Committee is by majority vote.

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Author's Declaration

This thesis consists of material all of which I authored or co-authored: see Statement of Contributions included in the 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.

Statement of Contributions

Julia Sunga was the sole author for Chapters 1 and 8, which were written under the supervision of Hugh Broders and not intended for publication.

This thesis consists of six (6) manuscripts that have been published or are prepared for publication. For published manuscripts, permission from the journals has been obtained via email confirmation of journal policies. As lead author of these chapters, I contributed to conceiving study designs, carrying out data analysis, and drafting and submitting manuscripts. My coauthors provided guidance during each step of the process and provided feedback on analytical methods and manuscript drafts.

Exceptions to sole authorship of material are as follows:

Chapter 2 of this thesis was published in 2021 in PLOS ONE (citation below). This study was conceptualized in cooperation with Hugh Broders and received significant input on manuscript drafts from Hugh Broders and Quinn Webber.

> Sunga, J., Webber, Q.M.R., and Broders, H.G. (2021). Influence of number of individuals and observations per individual on an estimate of subgroup structure. PLOS ONE. 16(6):e0252471. doi:10.1371/journal.pone.0252471.

Chapter 3 of this thesis was published in the journal Animal Behaviour (citation below). This study was conceptualized in cooperation with Hugh Broders and received significant input on method refinement from Quinn Webber. Edits and ideas were also contributed by Jessica Humber and Bruce Rodrigues.

> Sunga, J., Webber, Q.M.R., Humber, J., Rodrigues, B., and Broders, H.G. (*2022*). Roost fidelity partially explains maternity roosting association patterns in *Myotis lucifugus*. Animal Behaviour. **194**: 67-78. doi:10.1016/j.anbehav.2022.09.008.

Chapter 4 of this thesis is in preparation for submission. I am responsible for all aspects of the manuscript and have received input and editorial feedback from Hugh Broders, Jessica Humber, and Evan Woelk Balzer, with data collection contributions from Ipshita Tomar.

Chapter 5 of this thesis is in preparation for submission. I am responsible for all aspects of the manuscript and have received input and editorial feedback from Hugh Broders and Quinn Webber.

Chapter 6 of this thesis is being prepared for submission. I am responsible for all aspects of this manuscript and have received input and editorial feedback from Hugh Broders and Caleb Ryan.

Throughout the manuscripts, I use the pronoun “we” in place of “I” to reflect the collaborative nature of this work, with special reference to my co-authors and collaborators in each independent manuscript chapter.

Abstract

Social preferences are often demonstrated to exist in “intelligent”, long-lived species, such as cetaceans and primates, where individuals have the opportunity to form relationships with conspecifics through repeated interactions. The long lifespan of bats combined with the regular roost switching behaviour of females in some temperate species, presents opportunity for females to build and act on social relationships. However, regular roost switching also poses a challenge for teasing apart the individual influences of social and habitat preferences. To gather evidence for the influence of social preference, I tested predictions of a hypothesis that bats select daily roosts based on social preferences. Using a system of little brown myotis (*Myotis lucifugus*) individually marked with passive integrated transponder tags and passively monitored roost boxes in Newfoundland, Canada, I quantified the number of days bats spent in each roost, and the number of days spent sharing a roost with other marked bats to characterize patterns in co-roosting association. I found that patterns of roost use do not entirely explain the frequency of roosting association between pairs of female bats. Further, association patterns showed predictable changes following estimated parturition dates, estimated based on nighttime roost revisit behaviour, as adult females are expected to experience changes in selective pressures and mobility with the onset of the lactation period. I also found that patterns of roosting association between individual bats often persisted for more than 5 years and could even persist for up to 10 years following the first observed interaction. Using this same dataset, I also address the effect of missing information on estimates of social network structure, providing a deeper understanding of the ability of these results to inform on the structure of the underlying population. Overall, my findings add to evidence that supports that bats act on social preferences, and thus make a case for social complexity in bat groups. These findings further suggest that, perhaps due to their similarly long life spans, bats may be more similar to their large-bodied, “intelligent”, mammal counterparts than previously expected.

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I am grateful to my supervisory committee, Dr. Heidi Swanson and Dr. Brad Fedy, for providing guidance and constantly challenging me to think deeper about my work and its impacts on the wider field of wildlife conservation.

None of the chapters in my project would have been possible without the contributions of many previous researchers who put countless hours into data collection efforts in Newfoundland, including Karissa Appleby, Nicole Besler, Michael Blackwood, Lynne Burns, Mackenzie Donahue, Cody Fouts, Amanda Gallant, Alicia Irwin, Laura Johnson, Shelley Moores, Jordi Segers, and Kayley Smith. We would also like to acknowledge the important contributions of Jessica Humber, Bruce Rodrigues, and the entire Salmonier Nature Park Staff over the last 10 years, and many other Department of Environment and Conservation Staff who have participated.

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You do this with a special flare that simultaneously helps me maintain my sanity while holding on to that little bit of zany.

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Thank you all.

Land Acknowledgements

As a settler in this nation we call Canada, I have a responsibility to understand and acknowledge the history of the peoples that lived and continue to live on these lands where I conduct my work and where my research data was collected. I respectfully acknowledge that:

Waterloo, where I worked and lived for a large portion of my PhD, is situated on the Haldimand Tract, land that was granted to the Haudenosaunee of the Six Nations of the Grand River, and within the territory of the Neutral, Anishinaabe, and Haudensaunee peoples.

Guelph, where I currently reside, is part of the treaty lands and territory of the Mississaugas of the Credit First Nation of the Anishinaabeg Peoples and is home to many First Nations, Inuit, and Métis people today.

Pinery Provincial Park and the surrounding Lambton County, where I spent my summers conducting field work, was inhabited by the Chippewa, Odawa, and Potawatomi peoples, collectively the Anishinaabeg, at the time of transfer to the Crown by treaty as part of the Huron Tract Purchase under Treat #29, the Sombra Township Purchase under Treaty #7 and the Long Woods Purchase under Treat #21.

The island of Newfoundland (Ktaqmkuk), where much of the data I present in this thesis was collected, are the ancestral homelands of the Mi’kmaq and Beothuk Peoples.

As a settler, I strive to be a responsible steward of these lands and to respect the cultures, ceremonies, and traditions of all who call it home.

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List of Abbreviations

1. PIT – passive integrated transponder
2. e.g. – for example
3. HWI – half weight index
4. SRI – simple ratio index
5. SE – standard error
6. i.e. – that is
7. *sp* – pertaining to multiple species
8. g – grams
9. VC – visitor's centre
10. HQ – headquarters
11. HB – private farmhouse property
12. cm – centimeters
13. CV SRI – coefficient of variation of the simple ratio index
14. *M* – *Myotis*
15. RFID – radio-frequency identification
16. AMOC – at most one changepoint
17. AIC_c – Conditional Akaike's Information Criterion
18. km – kilometers
19. SD – standard deviation
20. CV HWI – coefficient of variation of the half weight index
21. LAR – lagged association rate
22. MRQAP – multiple regression quadratic assignment procedure
23. df - degrees of freedom
24. WNS – white-nose syndrome
25. h – hours
26. min – minutes

List of Symbols

1. R_{com} – community assortativity coefficient
2. ≈ – approximately
3. % – percent
4. ≥ – greater than or equal to
5. Q – modularity
6. < – less than
7. > – greater than
8. p – p value (probability of obtaining test result given a specific hypothesis, usually the null)
9. β – parameter estimate in regression model
10. R^2 – coefficient of determination (R squared)
11. ≤ – less than or equal to
12. º – degrees
13. km^2 – kilometers squared
14. ± – plus or minus
15. * – significant
16. n – number of individuals
17. ºC – degrees Celsius
18. km/h – kilometers per hour
19. K – number of parameters
20. ΔAIC – difference in Conditional Akaike’s Information Criterion Value
21. w_i – Akaike model weight
22. Σw_i – sum of model weights
23. ΔCº – change in temperature
24. ΔAH – change in absolute humidity
25. t – test statistic
26. m/s – meters per second

Chapter 1

General Introduction

The tendency for animals to live in groups, hereafter group behaviour, has arisen multiple times in the animal kingdom (Wilson 2000; Goodenough et al. 2010). Thus, one can observe a wide variety of interaction types between individual animals and organizational patterns of animal groups. Observing and quantifying the patterns of group behaviour, in the structure of animal groups or the nature of interactions between individuals, can inform the proximate benefits that may have been most influential in the evolution of group behaviour for a species (Hinde 1976). The mechanisms that result in the formation and maintenance of animal groups can be broadly classified into two categories: active and passive. Active mechanisms refer to those where animals seek conspecifics for benefits directly associated with these interactions (Krause and Ruxton 2002; Frère et al. 2010) while passive mechanisms refer to instances where animals associate by aggregating around a common resource such as food or shelter. Active mechanisms can then be further broken down into animals seeking any conspecific, or showing social preferences where individuals seek certain conspecifics with which to interact. Passive and both levels of active mechanisms are not mutually exclusive, and may function at different levels of organization simultaneously, resulting in a hierarchical structuring of animal groups (Lusseau et al. 2006; Frère et al. 2010; Burns et al. 2015). By understanding the fitness benefits to individuals that drive a group's behaviour and organization, we can not only understand why animal groups are organized in any given way, but also better identify the resources and connectivity needed to maintain stable animal groups and thus persistent populations.

One way to examine group structure is to determine the strength, nature, and distribution of connections among individuals. When quantifying connections among individuals in a group, connections can be distributed randomly, where association strengths or frequency are relatively evenly distributed among all individuals, as seen in some small colonies or communities of Bechstein's bats (*Myotis bechsteinii*; Kerth et al. 2011) Alternatively, connections can be distributed nonrandomly, in which certain individuals interact more frequently or more intensely with certain conspecifics over others. In landscapes where resources are homogeneously distributed, social preferences and active mechanisms are more easily distinguished from passive mechanisms, but teasing apart these types of factors can be more difficult in the far more common heterogeneous landscapes (Aureli et al. 2008). In a landscape with homogeneously distributed resources, nonrandom patterns of association strongly suggest a role of social attraction or social preferences. However, in heterogeneous environments, the roles of passive and active mechanisms must be specifically targeted by controlling for passive factors such as the distribution of a resource.

Social network analysis is being increasingly applied to understand the behaviour of animals in groups. Specifically, associations between individuals are investigated to characterize relationships, and the relationships across the entire group or population are quantified to describe overall social structure, also known as network topology (Hinde 1976; Whitehead 2008; Hoppitt and Farine 2018). Network topology can be characterized by a variety of measures, including network density; the number of connections compared to the number of possible connections in a network (Wey et al. 2008), or modularity; a measure of the number of connections within subunits versus among subunits of the network (Newman 2006), which facilitates comparisons with other networks in different environments, or simulated models that account for different null hypotheses.

Despite the flexibility of these techniques, there are multiple challenges associated with the application of social network analysis to natural systems. Most notably, in natural systems it is rarely feasible to observe all interactions between all individuals within a population. In these cases, researchers must make careful decisions about how to prioritize sampling effort, while tempering conclusions with what is possible given their available data. Previous studies have emphasized the importance of ensuring sufficient observations of individuals or pairs of individuals (dyads) before they are included in analyses, with some suggesting a blanket, minimum 20-observation threshold for dyad inclusion (Frantz et al. 2009; Franks et al. 2010). These studies primarily focus on estimates of individual network position or relationships between dyads, and further work is needed to understand how missing individuals or observations influence estimates of wider network topology. Another common challenge is selecting time periods that are biologically relevant to the process of interest as networks must be calculated through aggregations of interactions across a given time period (Araujo et al. 2017; Bonnell and Vilette 2020).

Across years, social networks may undergo the addition of new individuals through birth or immigration and the loss of individuals through mortality or emigration. Further, cyclical periods of absence such as migration patterns may result in year-to-year changes in structure. These changes can be assessed through interannual comparisons of network topology (Shizuka et al. 2014), and measures such as the lagged association rate can be used to characterize the stability of relationships over time (Whitehead 2008). Within years, seasonal changes in reproductive status and climatic conditions change individual needs, leading to shifts in relationships among individuals and therefore the structure of the overall network (Hamede et al. 2009; Brent et al. 2013; Olson and Barclay 2013; Kusch and Lane 2021). Despite potential ease of observation of these seasonal changes, it is not always simple to tease apart the roles of factors like reproduction and seasonal variation, as in many cases, these events are heavily correlated in time.

On an even smaller scale, daily, or even hourly, changes in individual needs can manifest as changes in daily network structure. An example of this are societies that display fission-fusion dynamics, in which groups frequently split apart and rejoin in changing conformations and locations (Aureli et al. 2008; Ramos-Fernández and Morales 2014). These sorts of societies are often described in groups such as dolphins (*Tursiops sp.*; Connor et al. 2000, Lusseau 2003) and elephants (Elephantidae; de Silva and Wittemyer 2012), species classically thought of as highly intelligent. In some cases, these societies are considered “multi-level societies” whereby fission events are always divided along the same spatial or social boundaries resulting in consistent subgroup composition (Grueter et al. 2020). Although not all animal societies may meet this strict definition of multi-level society, it’s possible that some individuals interact more frequently with certain subsets of individuals, constituting social “communities” (Newman 2006). Societies displaying fission-fusion dynamics provide the opportunity to investigate underlying mechanisms of group behaviour, through the quantification of subgroup structure and comparison to extrinsic factors.

Bats are an interesting model taxon for assessing the role of social preference and environmental conditions on group behaviour. This is because many species of bats experience multiple selective pressures that specifically necessitate interaction with conspecifics, including a need for social thermoregulation (Willis and Brigham 2007; Czenze et al. 2017; Webber and Willis 2018), and the potential for information transfer regarding the locations of roosts and foraging sites (Wilkinson 1992; Hernández et al. 2020). Some temperate bat species form summer maternity colonies that display fission-fusion dynamics in their day-roosting patterns across multiple roosting locations (Fenton and Barclay 1980; Kunz and Racey 1998; Willis and Brigham 2004; Chaverri et al. 2007b; Garroway and Broders 2007; Kerth 2008; Johnson et al. 2013). Thus an individual's decision of where to roost on any given day is likely driven by a need for social thermoregulation, and the various characteristics of a given roost (Rhodes et al. 2006; Olson and Barclay 2013; Patriquin et al. 2013). These decisions are important to bats because environmental conditions and the use of torpor not only effect immediate adult survival, but also influence the timing of parturition and the probability of offspring survival (Racey and Swift 1981; Frick et al. 2010).

Although bats benefit from interaction with conspecifics, the question remains of whether their daily roosting decisions are influenced by preferences for specific associates; the bat sociality hypothesis (Kerth 2008). As bats return to maternity areas over multiple years (Willis and Brigham 2004; Kerth and Petit 2005; Arnold 2007; Metheny et al. 2008), and roost with the same individuals multiple times throughout and among summers, there is opportunity for both passive (roost choice) and active (associate choice) mechanisms of decision making to act simultaneously. Due to their frequent roost switching behaviour, it has previously been assumed that nonrandom patterns of association in bat colonies are due to active, social preferences (Wilkinson et al. 2019), but it is also possible that variation in roost preferences may explain these patterns. The separate roles of active and passive mechanisms have been formally tested in *Desmodus rotundus*, where nonrandom patterns of association appeared to persist even when roost preferences were controlled for in null models (Wilkinson 1985), but whether this is the case for many other species of bats remains to be determined.

Little brown myotis (*Myotis lucifugus*) are a gregarious, temperate bat species found throughout North America, in which females form maternity colonies that can exceed hundreds or even thousands of individuals (Davis and Hitchcock 1965). Meanwhile other temperate hibernating species, including Bechstein's bats (*Myotis bechsteinii*), tend to form smaller colonies of 5-20 individuals (Kerth and König 1999; Kerth et al. 2011). These little brown myotis maternity colonies break into daily roosting subgroups of females, which may consist of hundreds of individuals within a single roost (Olson and Barclay 2013) . Adult males roost separately from these maternity colonies. During the maternity period, females give birth to single up in the late spring or early summer, though on rare occasions may give birth to two. These pups weigh ≈30% of their mother's body weight at birth and are dependent on nursing from their mother for at least 21 days until volancy (Krochmal and Sparks 2007). Adult female and male and female juveniles then leave maternity colonies in the late summer for swarming and hibernation sites before the annual cycle repeats again (Fenton 1997).

Given the importance of social thermoregulation for female bats in maternity colonies, it was expected that these groups not only interact actively, seeking conspecifics, but, given their long life history and repeated interactions, have sufficient opportunity to form and act on social preferences for certain conspecifics. Using a population of adult, female, little brown myotis implanted with passive integrated transponder (PIT) tags, and a system of 11 monitored roost boxes in Salmonier Nature Park, Newfoundland, Canada (Figure 1.1A) my project characterized the general structure of bat maternity colonies by quantifying roosting associations among individuals and investigated to what extent social preferences may influence the observed structure. First, I examined our inferential capabilities by testing the effects of missing data on estimations of community structure (Chapter 2). I then approached 4 objectives to better understand the roost-use decisions of individual bats and the social organization of bat maternity colonies:

1. Assessed the presence of nonrandom association patterns and determining to what degree these patterns could be attributed to roost fidelity (Chapter 3),
2. Used changes in roosting behaviour to assess parturition timing among individuals, across years (Chapter 4) and among locations with the addition of four monitored roost boxes ≈400 km NW at Pynn’s Brook, Newfoundland, Canada (Figure 1.1B),

3. Determined how social structure varies with reproductive period and environmental conditions within years (Chapter 5) to assess consistency in roost and associate preference within a single season,
4. Quantified changes in network structure across years to assess consistency in roost and associate preferences across multiple years and long periods of absence (Chapter 6).

Together, my findings provide a more detailed description of a bat maternity colony, both in the patterns of interaction among individuals, and the factors that influence colony structure. Through a clearer understanding of social dynamics of bat maternity colonies, we may better understand how habitat and connectivity needs of temperate bat groups relate to the important functions of sociality in bat populations.

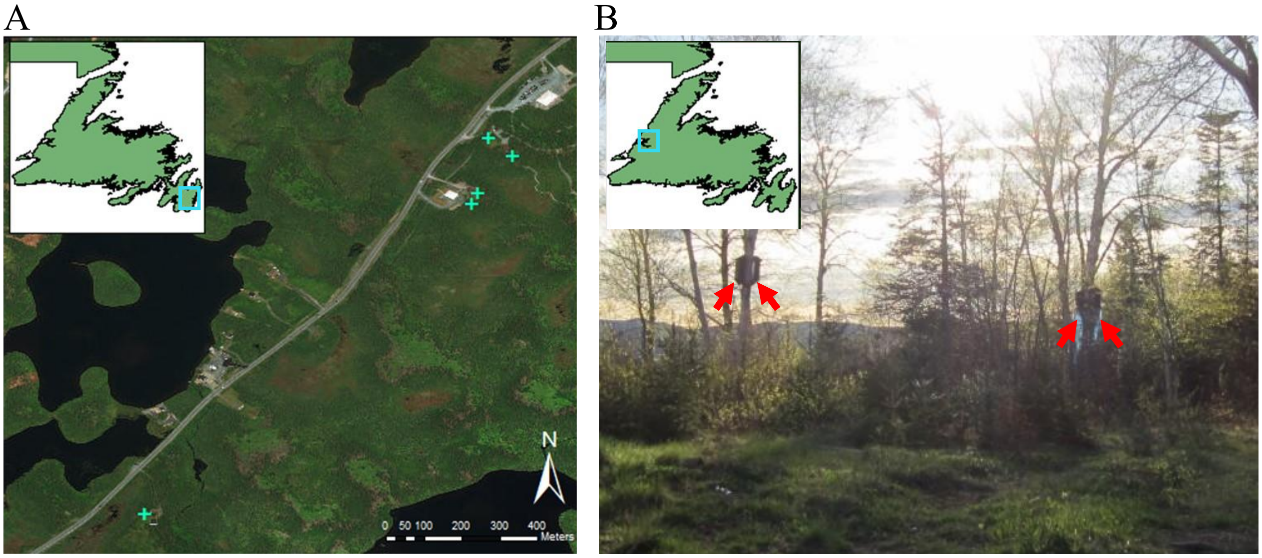


Figure 1.1. A) Location of monitored, 4-chambered artificial roost boxes in Salmonier Nature Park (Lat: 47.3º, Long: -53.3º) where each blue cross represents two monitored boxes mounted on one pole with inset map showing approximate location on the island of Newfoundland and B)

photograph depicting four, monitored 4-chambered artificial roost boxes mounted on two trees in Pynn’s Brook (Lat: 49.1º, Long: -57.5º) where each box is indicated with a red arrow and with inset showing approximate location on the island of Newfoundland.

Chapter 2

Influence of number of individuals and observations per individual on a model of community structure

2.1 Overview

Social network analysis is increasingly applied to understand animal groups. However, it is rarely feasible to observe every interaction among all individuals in natural populations. Studies have assessed how missing information affects estimates of individual network positions, but less attention has been paid to metrics that characterize overall network structure such as modularity, clustering coefficient, and density. In cases such as groups displaying fission-fusion dynamics, where subgroups break apart and rejoin in changing conformations, missing information may affect estimates of global network structure differently than in groups with distinctly separated communities due to the influence single individuals can have on the connectivity of the network. Using a bat maternity group showing fission-fusion dynamics, we quantify the effect of missing data on global network measures including community detection. In our system, estimating the number of communities was less reliable than detecting community structure. Further, reliably assorting individual bats into communities required fewer individuals and fewer observations per individual than to estimate the number of communities. Specifically, our metrics of global network structure (i.e., graph density, clustering coefficient, R_{com}) approached the ‘real’ values with increasing numbers of observations per individual and, as the number of individuals included increased, the variance in these estimates decreased. Similar to previous studies, we recommend that more observations per individual should be prioritized over including more individuals when resources are limited. We recommend caution when making

conclusions about animal social networks when a substantial number of individuals or observations are missing, and when possible, suggest subsampling large datasets to observe how estimates are influenced by sampling intensity. Our study serves as an example of the reliability, or lack thereof, of global network measures with missing information, but further work is needed to determine how estimates will vary with different data collection methods, network structures, and sampling periods.

2.2 Introduction

Social network analysis permits an in-depth understanding of population-level social structure and has been widely applied to study the organization of animal groups (Bejder et al. 1998; Whitehead 1999; Webber and Vander Wal 2019). Social groups may vary in size, composition, and structure, and large groups may show hierarchical organization, with higher order groups comprised of subgroups (Newman 2006; Aureli et al. 2012). These subgroups are not always static in structure, demonstrating fission-fusion dynamics, as they merge and split through space and time, and consistencies in subgroup composition may result in the delineation of social communities (Aureli et al. 2008; Whitehead 2008; Sueur and Maire 2014). Social communities, hereafter ‘communities’, are defined by the appearance of social preference among discrete clusters of individuals that associate more strongly with members of the same community than with members of other communities (Mourier et al. 2012). For fission-fusion societies, individuals can interact to varying extents with conspecifics from multiple social communities making the identification of community boundaries difficult. Community structure can still be delineated, when sufficient data exists, based on repeated or consistent subgroup composition and associations among individuals. An understanding of the degree to which associations between individuals persist, and the locations where associations occur, can provide insight into whether community formation is the result of passive processes such as use of a common resource, or active processes such as social preference among conspecifics, among other factors (Bejder et al. 1998; Whitehead 1999; Croft et al. 2011; Papageorgiou et al. 2019; Grueter et al. 2020). Testing hypotheses about social structure in groups with fission-fusion dynamics requires sufficient data on interactions among individuals to reliably assign community membership (Webber and Vander Wal 2019).

A common challenge for studies using social network analysis in natural systems is collecting enough data to reliably estimate elements of the group's social structure, particularly as they relate to social communities. Specifically, the proportion of a group, or total number of individuals sampled, and the number of observations per individual must be sufficient to reflect the dynamics of the true network. In a recent review of social network literature, Webber & Vander Wal (2019) identified the median number of individuals included per network was 15 (range 4–1406), but many studies did not indicate what proportion of the overall population this may represent. Further, the minimum number of observations included per individual varies widely among studies and can have important effects on network estimates. For example, based on assessment of individual network metric performance, Farine and Strandburg-Peshkin (2015) recommended that there should be at least 20 observational periods where a pair of individuals is observed either together or apart (see also Lusseau et al. 2008; Whitehead 2008; Franks et al.

2010; Silk et al. 2015; Hoppitt and Farine 2018). Other studies select a median number of observations per individual as a decision rule (i.e. Mourier et al. 2012), which, in well sampled populations, may unnecessarily omit individuals or pairs of individuals that have fewer observations than the designated threshold. In contrast, in poorly sampled populations, the median number of observations per individual may retain individuals that do not have sufficient information with which to estimate their network position. Generally, increasing the minimum number of observations required per individual reduces the number of individuals that can be included in an analysis, effectively decreasing the estimated network size and increasing the proportion of the population that is analytically considered as ‘missing’ (Silk 2018). Multiple studies have assessed the effect of missing data on the estimation of animal social networks, largely focusing on impacts on estimates of an individual’s position in the network (e.g., degree, centrality) (Frantz et al. 2009; Franks et al. 2010; Silk et al. 2015; Hoppitt and Farine 2018). Specific thresholds can vary based on the network metrics of interest and the type of network, but important broad patterns relating to the effect of missing data are consistent across most studies. Across all network sizes, studies have suggested minimums of 10-50% of the population sampled and unsurprisingly, the more observations that can be obtained of these individuals, the better (Franks et al. 2010; Silk et al. 2015). However, Davis et al. (2018) also note that in some systems, increased sampling may not be a priority because at some point networks become ‘saturated’ such that further sampling does not markedly increase estimate accuracy unless all individuals or interactions can be observed, a nearly impossible feat in many animal groups. Importantly, requirements of a minimum number of observations per dyad or median threshold should vary with the type and timing of the social system being studied (Frantz et al. 2009), the behaviour or interaction of interest and the method of sampling that is applied (Davis et al. 2018). Thus, recommendations may vary among different social systems (e.g., those displaying fission-fusion or multilevel dynamics). It has also been recommended to more intensely sample a smaller proportion of the population when resources are limited (Franks et al. 2010; Silk et al. 2015). However, for fission-fusion societies, the potential for ephemeral social connections, which can impact the functions and consequences of animal societies (e.g., information transfer and disease transmission; Granovetter 1973), differs from societies with more stable community composition. Meanwhile, too few observations per individual may lead to spurious estimates of the strength of connections between individuals and approximations of network structure. Further work is needed to determine the suitability of these recommendations across different types of animal groups. We therefore expect a need to balance minimum requirements for observations to accurately assess individual connections, while also including as many individuals as possible to model a larger proportion of the overall population.

When investigating a new system, various strategies can be applied to assess the robustness of estimates to missing data, and to determine what amount of data is needed for a desired level of confidence. Bootstrapping is the simplest method to apply, where aspects of the network are repeatedly assessed to derive multiple estimates of a statistic to characterize its distribution (Franks et al. 2010; Shizuka and Farine 2016). This technique, particularly that of resampling with varying numbers of samples included, is integral to the community assortativity estimate process described by Shizuka and Farine (2016) and has also been applied to assess the robustness of network measures (Franks et al. 2010; Silk et al. 2015). Further, a variation of bootstrapping, jackknifing, in which data is systematically removed, is commonly used to assess the error associated with estimates of lagged associate rates (Whitehead 2008). Bayesian methods can be applied to assess the uncertainty around edge weight estimates (Farine and Strandburg-Peshkin 2015).

Here, we use bootstrapping to examine the impact of varying number of observations per individual and number of individuals included in social network analysis on estimates of global network structure, particularly as they relate to the presence of communities, in a group displaying fission-fusion dynamics. Generally, it is expected that sample size is inversely correlated with the discrepancy between the true network structure and estimates of it, but that reasonable estimates can be obtained with missing data. Using an empirical dataset of a large group of little brown myotis (*Myotis lucifugus*) displaying fission-fusion dynamics, we quantified the impacts of two distinct sampling considerations on estimates of global network metrics and community structure. Specifically, we assessed how variation in each of the number of individuals and number of observations per individual affected the discrepancy of the sub-sampled network in estimates of graph density, clustering coefficient, the number of communities, and the assortment of individuals into communities.

2.3 Methods

2.3.1 Sample Population

We used data from a long-term study of wild little brown myotis roosting in artificial structures at Salmonier Nature Park, Newfoundland, Canada in 2016. Individuals were implanted with passive integrated transponder (PIT) tags and readers (Trovan, Ltd. United Kingdom) were deployed at 11 roost boxes within a ≈1 km^2 area of the park, each of which were regularly used throughout the study period. Other natural and anthropogenic roosts existed in the area that were not monitored. Readers recorded observations of when individuals entered and exited roost boxes and the last observation before sunrise constituted the assigned daytime roost locations of individual bats. Dyadic associations were based on the gambit-of-the-group assumption (Whitehead 2008), such that individuals were assumed to associate if they roosted in the same box on the same day. This assumption in commonly used in studies of bat roosting behaviours (examples include Kerth and König 1999; Garroway and Broders 2007; Mavrodiev et al. 2021). It is known that there were missing observations and that at least 50% of individuals in the population were not tagged nor included in this study. Although it may, this dataset is not intended to represent the true population as characterization of the actual true population is not the purpose of this study. Rather, our aim is to quantify differences in estimates between samples where all available information is included, to those with only partial data.

All animal handling protocol was approved by the animal care committee of Saint Mary's University, Halifax, Nova Scotia (AUP #16-12). Wildlife scientific research permits were also obtained from the Government of Newfoundland and Labrador, Department of Fisheries and Land Resources, Forestry and Wildlife Branch (# WLR2016-12).

2.3.2 Generating the 'observed' network

All detections were filtered for adult female bats that were each observed on ≥ 40 days, which resulted in 99 individuals. For each individual, 40 of their observations (day records of an individual bat in a particular roost) were randomly selected to generate a balanced dataset (all individuals observed an equal number of times, albeit not on the same days) from which we calculated an ‘observed’ social network that spanned 131 observation days. These numbers were selected to provide more observations per individual than has been assessed in other studies, e.g., Franks et al. (2010) which assessed reliability up to a maximum of 20 censuses, while still allowing multiple levels of sub-setting of the number of individuals included. Although a network with a maximum of 40 observations removes additional information on individuals in an already incomplete dataset, we used this threshold to remove any impact of individuals with uneven numbers of available observations. Further, the ‘observed’ network was not assumed to be a reliable estimate of the true underlying population, and as such, all findings and implications focus on discrepancies between metrics of the observed network with estimates based on sub-sampled networks.

From our data, we calculated an observed network based on the instances of co-roosting, which represent individuals observed in the same roost on the same day. We first calculated the Half Weight Index (HWI) (Whitehead 2008) between all dyads based on the proportion of days spent roosting together or apart using package “asnipe” (Farine 2013). The HWI represented edges in the network. We selected HWI, as opposed to the simple ratio index (SRI), as our association index of choice based on the sampling regime of our study. Although SRI is being increasingly recommended as an association index, the HWI accounts for missing individuals within a given sampling period (Whitehead 2008). In this system, it is likely there are a number of unmonitored roosts within the study area and given we allowed for a maximum of 40 observations out of a possible 131 nights on which observations were possible, it is reasonable to expect there are many days when only one bat in a given dyad is detected. Based on our observed network, we calculated three global social network metrics. First, we calculated modularity (Q), which is a measure of the number of edges within communities compared to the expected number if all edges were placed randomly (Newman 2006). Based on network modularity, we estimated the number of communities using the "igraph" package *cluster_fast_greedy* community detection algorithm (Csárdi and Nepusz 2006), a process which iteratively divides the network until the ratio of within to among community connections peaks. Second we calculated the clustering coefficient (function: *transitivity*), defined as the proportion of triads that have three edges compared to the number of triads with two edges (Farine and Whitehead 2015). Third, we calculated graph density (function: *edge_density*), defined as the number of observed edges across the whole network divided by the number of possible edges (Farine and Whitehead 2015). Both graph density and clustering coefficient were calculated using the R package "igraph" (Csárdi and Nepusz 2006).

We then assessed evidence for the division of the network into communities. We generated 1000 random networks using "spatsoc" (Robitaille et al. 2019) to randomly swap individuals among roosting subgroups on a given day, while maintaining the number of available roosting boxes and individuals constant within days, generating distributions of Q, clustering coefficient, and graph density values. These parameters were held constant to create null model networks that reasonably approximated possible network structure if all roosting decisions were random. A p-value was calculated, via Monte Carlo methods, based on the percent of random network Q values that fell above that of the original ‘observed’ network, where a p-value of < 0.05 indicated significant evidence for community structure. This measure may only support an inference that there is evidence for community structure and does not provide confidence in the estimated number of communities or the assignment of individuals to these communities. Next, using a metric proposed by Shizuka and Farine (2016), we examined the confidence in the assignment of individuals to communities by calculating a community assortativity coefficient (R_{com}). The R_{com} method uses bootstrapping of the ‘observed’ network to calculate consistency in individual community assignment, resulting in a network-level value between -1 and 1. Values closer to 1 indicate high confidence in community assortment while values closer to 0 indicate little confidence in community assortment. Shizuka and Farine (2016) recommend a threshold of 0.5 for reasonable confidence in community assortment. We used 1000 bootstraps to calculate R_{com} and this process was repeated 10 times to obtain an average value for the ‘observed’ network.

2.3.3 Sampled Networks

In this study, we assessed the influence of two distinct sampling considerations, the number of individuals included, and the number of observations included per individual. All sample networks were based on randomly selecting a subset of individuals and observations from the above generated ‘observed’ network. Individuals were randomly sampled to generate subsets of 5, 10, 15, 20, 25, 35, 50, 75, and 99 (all) individuals. Within each of these network sizes, we randomly selected 1, 5, 15, 10, 20, 30, or 40 (all available from ‘observed’ network) observations for each individual to generate balanced sample networks. This sampling process was repeated

100 times for each combination of number of individuals and number of observations per individual. A sample network of 99 individuals with 40 observations per individual was not created as this would represent the complete ‘observed’ network.

For all sample networks, the number of subgroups and Q were estimated as above for the ‘observed’ network. P-values of Q were calculated by generating 1000 random networks for each sample network and comparing the distribution of Q values via Monte Carlo methods as above. These random networks shuffled the roost in which an individual bat roosted on a particular day, and were generated with “spatsoc” as above (Robitaille et al. 2019). Those with a p-value < 0.05, indicating significant evidence for subgroups structure were assigned a YES (1), while those with a p-value > 0.05 were assigned a NO (0). In all sample networks, we also estimated network graph density and clustering coefficient as for the ‘observed’ network.

For each of the 100 sample networks related to each sampling regime, we assessed the accuracy in assignment of dyads to communities compared to the observed. Specifically, we generated individual-by-individual matrices, each of which indicated whether a dyad was estimated to occupy the same or different communities and whether this assignment was consistent with the observed network. We then generated a proportional measure of similarity. The similarity measure was a proportion that ranged from 0 to 1, where 0 indicated that no dyads were assigned to communities correctly based on the ‘observed’ network, and 1 indicated that all dyads were correctly assigned to communities compared to the ‘observed’ network.

Finally, R_{com} values were also calculated as outlined by Shizuka and Farine (2016). The number of bootstraps was set to 1000, regardless of the network size. Although this may be redundant in smaller networks, this ensured sufficient subsampling for all sample networks. On occasion, particularly in networks with only 1 observation per individual, no connections between individuals were present in the sample network, resulting in a Q value of zero and returning a network where the number of detected communities was equal to the number of individuals present. This scenario does not constitute community structure and because there was no ability to assign individuals to communities the community logistic value was coded as a NO (0) while R_{com} values were set to 0.

2.3.4 Statistical Analyses

To assess how sampling regime affected estimates of community structure, the absolute value of the difference in estimated number of communities between the ‘observed’ network and the sample networks was calculated. Multiple linear regression was used to assess whether the independent variables of the number of observations, the number of individuals, and the interaction between these factors influenced the difference between the sample and ‘observed’ network in estimated number of communities. Both response and independent variables were log-transformed to meet model assumptions of heteroscedasticity of residuals. We also applied a multiple linear regression to assess the influence of these factors on the proportion of similarity of dyadic community assignment between sample networks and the ‘observed’ network.

For all sample networks, we calculated the absolute difference from the ‘observed’ network for measures of graph density and clustering coefficient. Here, we also applied multiple linear regressions of the number of individuals, the number of observations per individual, and the interaction of these terms to assess their impact on these metric estimates. For our assessment of graph density, both independent and response variables were log transformed to meet assumptions of homoscedasticity of residuals. The transformation was not required for the analysis of clustering coefficient.

Often, network analysis simply aims to determine whether there is sufficient evidence of community structure in a study population (e.g., Garroway and Broders 2007). A logistic regression was performed on whether there was evidence for community structure ($p < 0.05$) in the sample networks as there was in the ‘observed’ network. Number of individuals, number of observations per individual, and their interaction were used as the independent variables and the response variable was whether there was significant evidence for community structure (1), or insufficient evidence (0; $p > 0.05$).

We also tested how different sampling regimes affected the ability to confidently assort individuals based on community assortativity ($R_{com} > 0.5$; Shizuka & Farine, 2016). Other assortativity measures, measures of how strongly nodes associate with those most like themselves, have been reported to be artificially high in poorly sampled systems (Franks et al. 2010). Thus, a linearly increasing R_{com} value was not expected with the addition of more information. We therefore tested the probability of obtaining a R_{com} estimate that indicated confidence in individual assortment ($R_{com} \geq 0.5$), without overestimating this confidence by exceeding the value of the ‘observed’ network. Values within this range were coded as acceptable (1) while those above or below this range as unacceptable (0). A logistic regression was then performed with this binary response variable and the number of observations, number of individuals, and the interaction between these factors as independent variables. All sampling, randomizations, network metric calculation, and statistical analysis were performed in R version 4.0.0 (R Core Team 2020)

2.4 Results

2.4.1 Relationship between sampling regime and global network measures

The ‘observed’ network of 99 individuals with 40 observations per individual was estimated, with significant support to have community structure ($Q = 0.285$, $p < 0.0001$) with 3 communities estimated. The ‘observed’ network also had a graph density of 0.675, a clustering coefficient of 0.828 and a R_{com} of 0.858, indicating a high-level of confidence in the assortment of individuals into communities. Across all sample networks, the estimated number of communities ranged from 2 to 95 (median = 4, SE ± 0.177). Multiple linear regressions revealed that each of the number of individuals ($\beta = 1.069$, SE = 0.012, $p < 0.001$), number of observations per individual ($\beta = 0.297$, SE= 0.0166, $p < 0.001$), and the interaction between these terms ($\beta = -0.368$, SE= 0.005, $p < 0.001$) explained discrepancy between the estimated number of communities in the ‘observed’ network and the number estimated by sample networks ($p < 0.001$, $R^2 = 0.871$). Generally, error associated with our estimates was large (range 0-92, SE = 0.376) when the number of observations was low (< 10) and increased when more individuals were included with few (< 10) observations (Figure 2.1). Regardless of the number of individuals included the number of communities was consistently estimated to be between 2 to 4 (within one of the ‘observed’ network) when at least 15 observations per individual (96.4%) were included compared to when 10 or fewer observations were included (14.6%) in the analysis. Across all numbers of individuals, the confidence in estimates of the number of communities exceeded 50%

only when 20 or more observations per individual (of the 40 possible) were available and was at or near 0 with less than 10 observations for all numbers of individuals (Table 2.1).

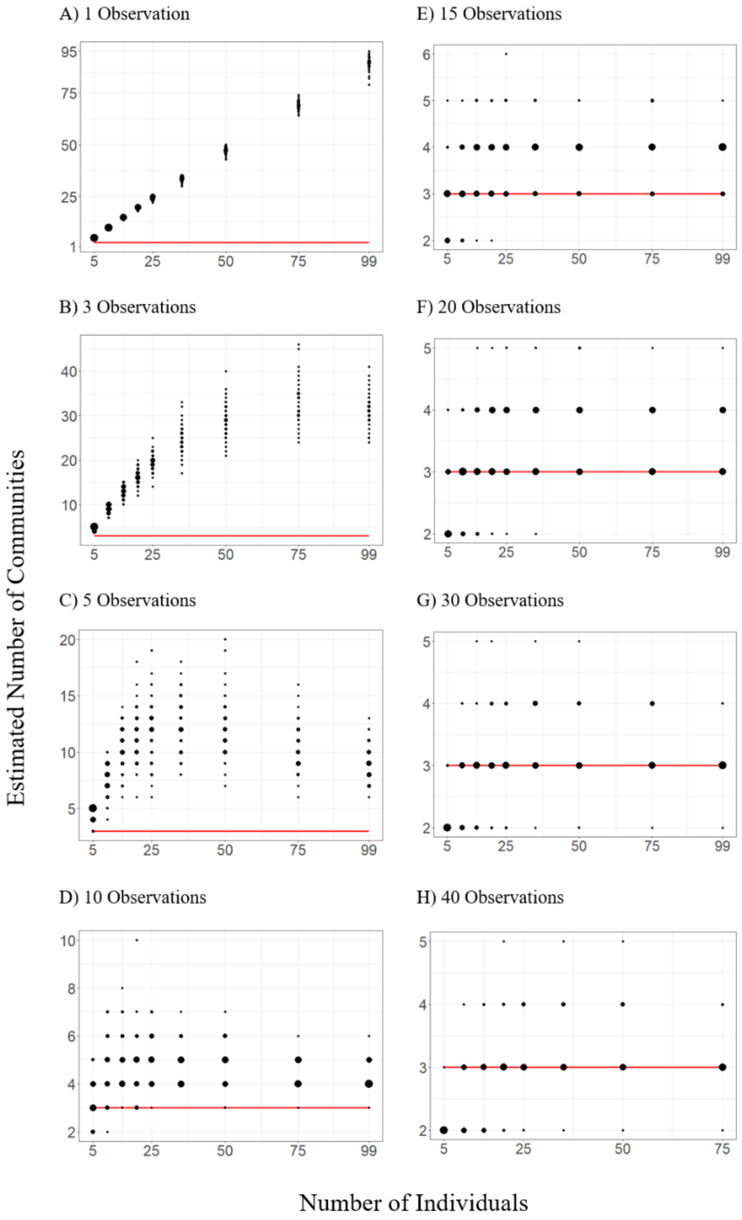


Figure 2.1 Variation in the estimated number of communities under various scenarios of number of individuals sampled and the number of observations per individual (panels A-H). Point sizes are scaled based on the number of times a value occurred. The red horizontal line represents the actual number of communities in the 'observed' population from which all other scenarios were sampled (subgroups = 3). Note, the changing y-axis scale among panels.

Table 2.1 All sampling regimes (number of individuals and number of observations per individual) where there was sufficient evidence to detect community structure in at least half of all 100 replicates. Sufficient evidence for community structure was based on a $p < 0.05$ when comparing values of Q in sample networks to that of randomized networks. The number of replicates (0-100) with a community assortativity (R_{com}) value considered acceptable at greater than the minimum threshold of 0.5 but less than the 'observed' network (0.858) are reported and the number of replicates (0-100) that correctly estimated the presence of 3 communities.

Number of Individuals	Number of Observations	Evidence for Community Structure ($p<0.05$)	Acceptable R_{com}	Correct # of Communities
5	40	50	25	6
10	20	60	56	67
10	30	81	59	55
10	40	95	55	44
15	15	62	77	39
15	20	80	68	53
15	30	96	74	67
15	40	100	63	58
20	15	76	72	44
20	20	94	72	49
20	30	99	78	65
20	40	100	59	71
25	10	54	72	2
25	15	88	66	35
25	20	99	78	44
25	30	100	74	68
25	40	100	58	70
35	10	77	58	0
35	15	98	62	29
35	20	100	79	50
35	30	100	84	61
35	40	100	61	68
50	10	95	33	6
50	15	100	79	31
50	20	100	91	43
50	30	100	75	62
50	40	100	52	68
75	10	100	40	3

75	15	100	91	25
75	20	100	93	52
75	30	100	83	66
75	40	100	57	85
99	10	100	46	3
99	15	100	98	24
99	20	100	97	54
99	30	100	96	89

The absolute difference in graph density estimates between the ‘observed’ and sample networks was significantly correlated ($R^2 = 0.797$, $p < 0.001$) with the number of observations per individual ($\beta = -0.108$, SE= 0.003, $p < 0.001$), the number of individuals ($\beta = 0.009$, SE = 0.002, $p < 0.001$), and the interaction between these terms ($\beta = -0.008$, SE = 8.987×10^{-4}, $p < 0.001$) in the log transformed model. Graph density estimates increased towards the true value of 0.675 with increasing numbers of observations per individual while variance in estimates decreased with more individuals included (Fig 2.2B, D, F, H). Clustering coefficient changed similarly, with the absolute difference between ‘observed’ and sample estimates related to the number of observations per individual ($\beta = -0.021$, SE= 2.467×10^{-4}, $p < 0.001$), the number of individuals ($\beta = -0.003$, SE= 1.037×10^{-4}, $p < 0.001$), and the interaction between these terms ($\beta = 5.604 \times 10^{-5}$, SE= 5.730×10^{-6}, $p < 0.001$) in a linear model ($R^2 = 0.690$, $p < 0.001$). Mean estimates of clustering coefficient generally increased similarly with more observations per individual, regardless of the number of individuals, while increasing the number of individuals reduced the variance in clustering coefficient estimates (Figure 2.2A, C, E, G).

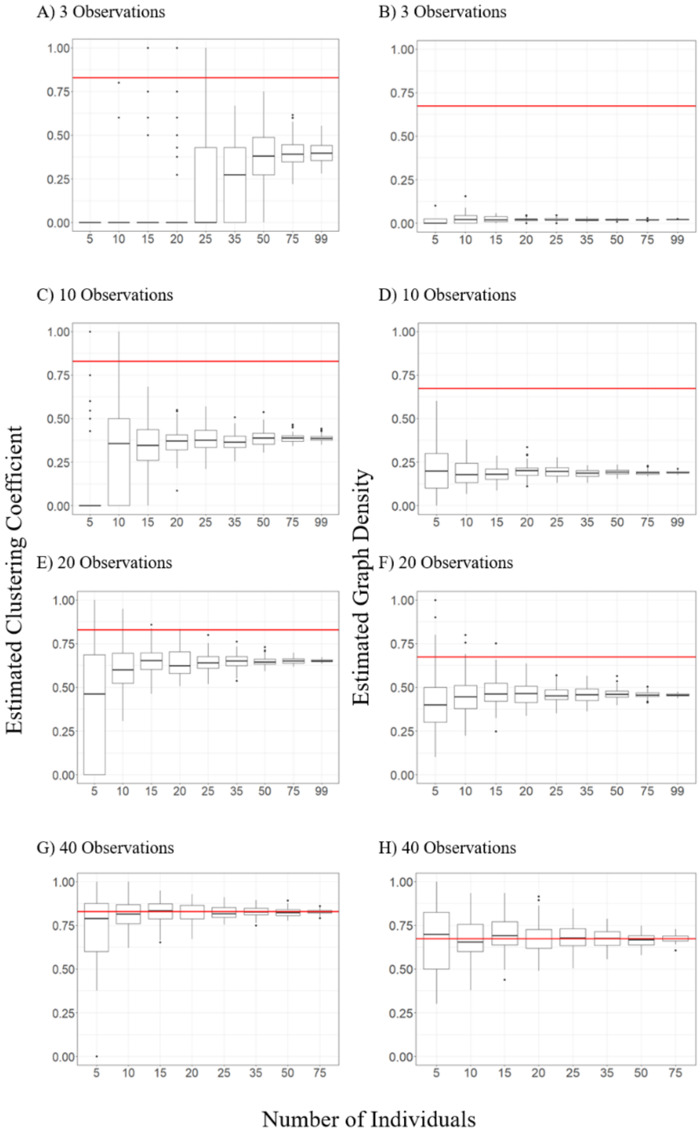


Figure 2.2 Influence of number of individuals and number of observations per individual on estimates of network clustering coefficient (panels A, C, E, and G) and graph density (panels B, D, F, and H). Boxes represent the 25th to 75th percentile of values with the centre line representing the median value. The horizontal red line indicates observed values of graph density (0.675) and clustering coefficient (0.828) based from the 'observed' network. Full figures for

each measure with all tested numbers of observations per individual can be found in A2.1 and A2.2.

2.4.2 Relationship between sampling regime and evidence for community structure

Analysis of the p-values of Q indicated a significant increase in the probability of correctly concluding the presence of community structure with additional individuals ($\beta = 0.004$, SE = 0.002 $p = 0.010$) and observations ($\beta = 0.050$, SE = 0.005, $p < 0.001$), and an interactive effect between these variables (β 0.005, SE = 2.709×10^{-4}, $p < 0.001$). With < 10 observations per individual, the probability of correctly concluding the presence of community structure did not exceed 75% even with all individuals included. With ≥ 10 observations per individual, the probability of detecting community structure exceeded 50% with < 30 individuals sampled (Figure 2.3A). At least 10 observations per individual were required to detect the presence of community structure in at least 50% of replicates using the p value of Q (Table 2.1).

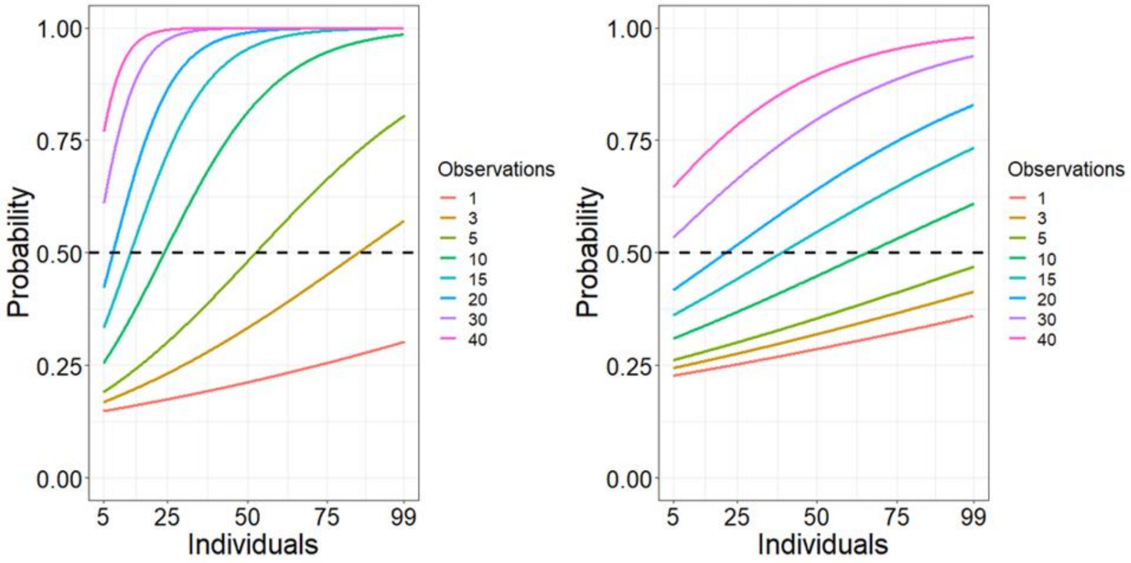


Figure 2.3 Probability of detecting community structure (A) and confident assortment of individuals (B). Detection of communities (A) is based on the p-value of modularity (Q; $p < 0.05$) and confident assortment of individuals (B) is based on obtaining a community assortativity coefficient (R_{com}) value that indicates a reasonable ability to assort individuals into communities (≥ 0.5) without overestimating this ability based on the 'observed' network (≤ 0.858).

2.4.3 Relationship between sampling regime and community assignment

R_{com} values ranged from 0 to 1 (median = 0.669, SE ± 3.810×10^{-3}) across all sampling regimes. We observed a significant relationship between the probability of obtaining a R_{com} value indicating reasonable ability to assort individuals into communities ($0.5 < R_{com} < 0.858$) and the independent variables of number of individuals ($\beta = 0.006$, SE = 0.001, $p = 0.01$) and number of observations per individual ($\beta = 0.043$, SE = 0.003, $p < 0.001$; Figure 2.3B). The interaction term between the two independent variables was also significant ($\beta = 7.066 \times 10^{-4}$, SE = 9.248×10^{-5}, $p < 0.001$). At least 15 observations per individual were needed to obtain a R_{com} value above 0.5 but less than the 'observed' network value of 0.858 in at least 50% of replicates (Table 2.1). The proportion of R_{com} estimates that fell within this range occasionally decreased with more observations per individual due overestimates (Figure 2.4D). With 10 observations or fewer, R_{com} was overestimated relative to the observed network in 33.0% of replicates. With 15 or more observations per individual, estimates of R_{com} fell within the acceptable range in 68.7% of replicates and overestimated in 16.9% regardless of the number of individuals included (Figure 2.4A, C, E, G).

The proportion of dyads correctly assigned to communities based on the 'observed' network significantly increased with increasing numbers of observations per individual ($\beta = 0.005 \times 10^{-3}$, SE = 1.637×10^{-4}, $p < 0.0001$) and was also significantly affected by the interaction between the number of observations per individual and the number of individuals included in the model ($\beta = 7.061 \times 10^{-5}$, SE = 3.803×10^{-6}, $p < 0.0001$). The number of individuals was not a significant predictor of the correct assortment of dyads ($p = 0.887$). As with graph density and clustering coefficient, increases in similarity were seen with more observations per individual, while the inclusion of more individuals reduced the variance in similarity results (Figure 2.4B, D, F, and H).

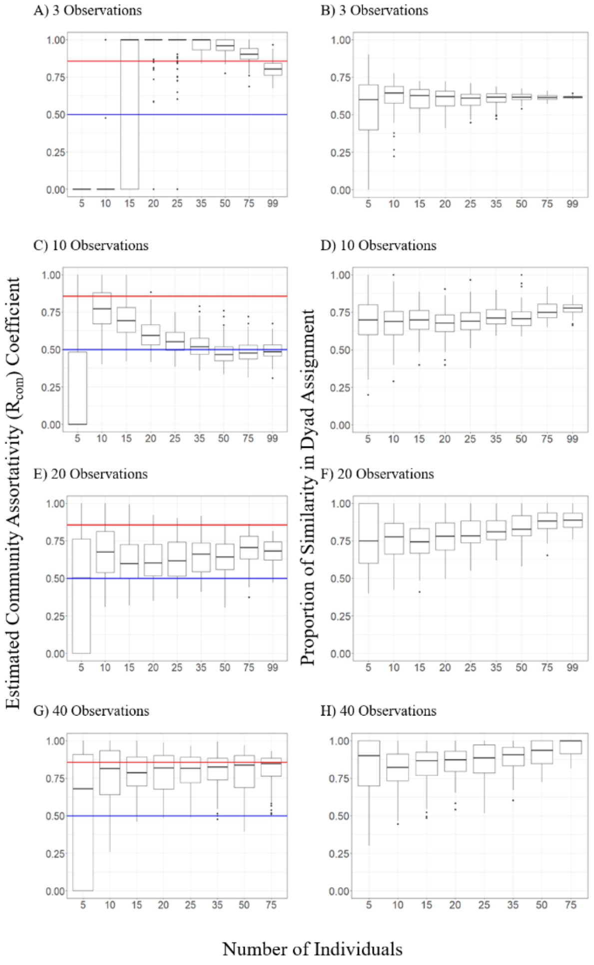


Figure 2.4 Distribution of community assortativity coefficients (Rcom; panels A, C, E, and G) and proportion of correctly assigned dyads (panels B, D, F, and H) as a factor of the number of individuals and the number of observations per individual included in the network. Boxes represent the 25th to 75th percentile of values with the centre line representing the median value. In panels A, C, E, and G, the blue line indicates the suggested minimum threshold of R_{com} (0.5) and the red line indicates the R_{com} value of the 'observed' network (0.858). Values that fell within this range were deemed acceptable and therefore represent sample networks with reasonable confidence in the assortment of individuals into subgroups. Full figures for each measure with all tested numbers of observations per individual can be found in A2.3 and A2.4.

2.5 Discussion

In most studies of animal behaviour, it is recommended to include as much information as possible to estimate characteristics with the greatest probability of accuracy and to ensure reliable inference. Social network analysis is no exception, particularly when the gambit-of-the-group method is applied to deducing social connections (Franks et al. 2010). However, in ecological studies, sampling is often limited by factors such as logistical challenge and cost. We quantified the effects of both the number of individuals and the number of observations per individual on the reliability of metrics that characterize a fission-fusion social network created using the gambit-of-the-group assumption. When looking at other global network metrics including graph density, the number of connections compared to the number of possible connections, and clustering coefficient, a metric based on the connections among triads, discrepancies from the observed network decreased most notably when including more observations per individual, while including more individuals reduced the variance in estimates. Further, the ability to detect community structure, assort individuals into communities, and estimate the number of communities in the network improved with the inclusion of more data but the addition of more individuals and more observations did not have equal impacts on these different estimates. Thus, when designing studies of animal behaviour, there can be considerable trade-offs between these two sampling considerations and the metrics of interest.

Our results are consistent with prior studies based on estimates of individual network position (Silk et al. 2015; Hoppitt and Farine 2018) that recommended only including individuals for which a minimum number of observations have been recorded, and that adding more individuals cannot make up for a lack of repeated observations of individuals or interactions

(Carter et al. 2019). We found that the presence of communities and confidence in individual assortment into communities could often be estimated with missing data but, in our dataset, 15 or more observations per individual were needed to consistently achieve an estimate within 2 of the 'observed' number of communities present, regardless of the number of individuals present. Additionally, including a larger number of individuals with fewer than 10 observations per individual greatly increased the average discrepancy between sample estimates and the 'observed' network. As these results demonstrate, including many individuals with insufficient information per individual has the potential to result in increased error when estimating group-level metrics. Yet, the use of overly conservative minimum observation thresholds when estimating network properties may reduce our ability to detect weak connections, which can be essential for understanding other aspects of the overall network structure (Granovetter 1973). It is therefore important to balance including as many individuals as possible with ensuring that all included individuals have been sampled sufficiently.

To select a sampling regime with sufficient potential to estimate animal social networks, our results demonstrate the potential error that can occur. We suggest that other studies with sufficiently large data sets perform similar subsampling tests to assess how their estimates respond to missing data and provide some suggestion of how requirements may change based on study objectives. For most studies interested in aspects of global network structure, the priority is to determine whether the network shows evidence of any community structure. In our 'sample' populations, conclusions consistent with the 'observed' population regarding the presence of community structure could be made with as few as 10 observations and less than 50% of the population sampled, when using Monte Carlo methods to obtain a p-value for Q. The number of observations per individual had a strong impact on the ability to detect community structure, as networks with < 10 observations with any number of individuals were not reliable and could not detect the presence of communities without nearly all individuals being sampled and even then, still demonstrated some uncertainty. These findings support the recommendations of Franks et al. (2010), who suggested that when resources are limited, researchers should prioritize sampling fewer individuals more intensely rather than sampling more individuals less intensely and support that network metrics can be robust to missing individuals when enough observations are provided (Frantz et al. 2009). However, these results do not provide information on whether the estimated number of communities is accurate, or how well the estimated communities assort individuals.

To accurately estimate the number of communities present in this social network, far more information, and therefore a more intense sampling regime, was required than was needed to simply detect that communities were present. Overall, our ability to accurately estimate the number of communities was limited. Success for any particular sampling regime did not exceed 80% with the exception of having 30 observations per individual and 100% of individuals included or 40 observations per individual and 75 of 99 individuals included. A feat that may be unreasonable for many ecological studies. Estimates of the number of communities did generally improve with the inclusion of more individuals or more observations per individual but it was again important that at least 10 observations per individual were included. With 20-30 observations, the correct number of communities was estimated over 50% of the time, even with only 15 individuals included. These findings are again in agreement with the recommendation of Franks et al. (2010) to ensure a sufficient number of observations per individual. Further, it has been previously demonstrated that the ability to estimate attributes of animal networks, and therefore the amount of information needed to detect a biological effect, is dependent on the relative effect size of the attribute under study (Carter et al. 2019). Given the densely overlapping nature of communities in fission-fusion societies, it is possible that estimates of communities numbers would perform better in less highly connected networks with the same sampling regime (Frantz et al. 2009; Ding et al. 2016), as community delineation would be more pronounced in these instances.

Silk et al. (2015) suggested that global measures of social networks would perform poorly when individuals are missing from a network. With both global estimates of network graph density and clustering coefficient, our results suggest that missing observations had more impact on estimated values than missing individuals. Further, the ability to provide significant evidence for the presence of community structure based on p-values of Q and the modest ability to estimate the number of communities present despite missing individuals, provided sufficient numbers of observations shown here contradicts Silk et al. (2015)'s proposition. This may be due to the fact that some global metrics can be greatly influenced by the omission of single individuals that bridge two subgroups or communities (Lee et al. 2006; Silk et al. 2015) however those connections are more likely to be missed if only a small number observations of individuals are recorded. Our results suggest that when selecting a social network metric to determine the presence of communities for populations that are under-sampled, Q may be a robust choice in the face of missing information, while measures such as clustering coefficient showed little accuracy with limited numbers of observations, and great uncertainty with limited numbers of individuals. However, further work is needed to ensure that the performance of these metrics is not unique to our specific network structure. Additionally, the performance of global metrics may vary based on the type of sampling method used in a given study, and the definition of edges in a network (Davis et al. 2018).

Regardless of the number of communities, the ability to consistently assort individuals to communities is useful for understanding network structure and asking questions about mechanisms of group and community formation. Although assignment of individuals to communities can be uncertain, even with only 3 observations per individual and 5 individuals, dyads were generally assigned correctly over 50% of the time. The proportion of similarly assigned dyads increased most obviously with the addition of more observations per individual and was less variable with more individuals included thus showing a relationship similar to that of network graph density and clustering coefficient. R_{com} suitably increased with greater similarity in dyad assignment to communities based on the 'observed' network. R_{com} provides an opportunity to estimate the confidence in the assortment of individuals to specific communities (Shizuka and Farine 2016) when the underlying network is not available for comparison as we have here. Generally, our analysis of R_{com} demonstrated the performance of assigning individuals to communities was more variable than detecting communities via p-values of Q, but more consistent than estimating the exact number of communities within any given sampling regime. There was a tendency to overestimate the R_{com}, a similar result to other assortativity measures, such as assortment into groups by sex or other traits of the individuals (Franks et al. 2010). It is unsurprising that the R_{com} may be vulnerable to the same issues. Specifically, we found that R_{com} was often overestimated when individuals were observed < 10 times. This may be due to less variation between bootstrap removals of individuals when networks contained fewer observations. As the number of observations increased beyond 20 per individual, we found that R_{com} stabilized, a result which is corroborated by Franks et al. (2010) and emphasizes the benefit of increasing the sampling intensity for each individual.

Unlike other studies on the effects of missing information on network estimates, we do not suggest any specific thresholds for estimation of global network metrics as our results may not be reflective of the exact error trends in other study systems. Specifically, our ‘observed’ network has only a small number of communities, and it is expected that with more communities, estimates from subsamples would be more variable, and the ability to assort individuals in these communities would decline. Thus, more subdivided networks may require a larger proportion of the population to be sampled, and/or more observations per individual to appropriately characterize the network community structure. In addition, the difference in average strength of connections within and among communities may be more variable in other networks. In networks where communities are less connected, such as those of other bat species, *Thyroptera tricolor* (Vonhof et al. 2004), fewer observations per individual may be appropriate to delineate communities. Important considerations for differences in the rate of interactions and variability in network structure will also impact sampling protocols (Davis et al. 2018). Finally, our ‘observed’ network does not contain all individuals and interactions that occur in the population, and thus it is unknown how well our ‘observed’ network represents the true, underlying population of bats in our study area. This topic would benefit from further study on how global network estimates preform when the underlying population is known with more certainty, for example, using captive populations that are continuously monitored. As our network serves as only an example of how estimates of global network metrics may vary in a specific type of fission-fusion system, we recommend that, as these types of larger datasets become more readily available, researchers continue to assess how subsampling and therefore missing data influences network estimates. There may be additional benefits to testing how community detection, R_{com}, the estimated number of communities, and accuracy of assignment to communities vary with network size, as the effect of sampling effort on the accuracy of other network measures has been found previously to vary with overall network size (Silk et al. 2015). Given that our ‘observed’ network of 99 tagged individuals was much smaller than what is expected in the true population, and in some other social networks assessed to date (exceeding 1000 individuals, Webber and Vander Wal 2019), predictive ability may be higher in actual bat social networks when the same proportions of the population are observed. Another potential avenue of future research is to assess how R_{com} can be adapted for less stable animal social societies, including those of bats. It is likely that increasing connectivity among communities despite high densities of connections within subgroups, as is typical in fission-fusion societies, negatively influences our ability to correctly assort individuals to a subgroup. A modification of R_{com} has been suggested for instances where an individual is a part of multiple communities simultaneously (Montilla et al. 2019), and perhaps a similar modification is needed for societies displaying fission-fusion dynamics. Further study is necessary to determine how both network size and structure can influence the consequences of sampling and data filtering prior to generating network models based on a portion of the overall population (Frantz et al. 2009; Silk et al. 2015).

The temporal extent of data collection also has the potential to influence social network structure and assignment of individuals to communities. Specifically, our data were collected over a relatively long period of time (131 days) representing the full range of dates when at least one animal was observed in the study area. This results in the multiple observations of an individual not necessarily occurring on the same days as observations for other individuals. Although it is likely that days where individuals were not observed occurred when individuals were not present in the system and therefore not associating with the observed animals. Always observing individuals synchronously, as is the case in many animal network study systems, is expected to improve network estimates and possibly result in fewer observations per individual being required to achieve comparable levels of reliability (Davis et al. 2018). A shorter, more heavily sampled time period should provide increased confidence in R_{com} and estimates of the number of communities but, shorter time-periods represent only a snapshot of the social environment. Networks are inherently dynamic systems and inferences across too narrow a temporal window may overestimate the strength of relationships between individuals and communities or miss important transient connections (Blonder et al. 2012; Pinter-Wollman et al. 2014; Zhao et al. 2018; Bonnell and Vilette 2020). Further, obtaining 20 observations but over a very long time-period would likely be insufficient as more samples would be needed to appropriately reflect such a dynamic system throughout the entire study period. Thus, when designing studies, researchers must carefully consider the temporal period of network formation that is biologically relevant for their study species (e.g. reproductive period or breeding season), and the expected rate of interactions or behaviour of interest, and select an appropriate sampling method and frequency for the designated period (Davis et al. 2018).

2.5.1 Conclusions

Overall, our study suggests that global metrics, including the detection of community structure and appropriate assortment of individuals into communities, can be robust to missing information while estimating the exact number of communities is less reliable. When designing a study, results in our system support the suggestion of Franks et al. (2010) to prioritize sampling a smaller part of the population with greater intensity when resources are limited, rather than more of the population at lower intensity. For some measures, accuracy to the true value improves with more observations per individual, while variation in estimates decreases with more individuals included. Generally, we recommend that researchers include as many individuals and observations as is feasible, but we urge caution when including individuals with limited numbers of observations. To best design sampling protocol, researchers must consider their study system, sampling logistics, decide which measures are most important, and determine what level of reliability is desired. The levels of reliability that we present here reflect that of a highly connected, fission-fusion group and results may differ for different network sizes and characteristics (Frantz et al. 2009). Our results represent a clear example of the uncertainty in global metric estimates that may exist in samples of animal social networks and continued work is needed to determine how the effects of missing information vary with different types of animal societies. As large datasets becoming increasingly available, and when it is uncertain whether enough individuals or observations have been collected, we demonstrate a benefit to subsampling and repeatedly calculating network metrics, as we have here, to determine if estimates stabilize as the full available sample size is approached.

Chapter 3

Roost fidelity partially explains maternity roosting association patterns in *Myotis lucifugus*

3.1 Overview

Resources that draw individuals to a specific location may result in the formation of groups and development of individual social preferences. Simultaneously considering both ecological and social factors can therefore reveal underlying mechanisms of group formation and organization. Females of some temperate bat species roost in groups during the spring and summer months within which they give birth to and nurse their pups. Females switch roosts frequently but the factors that influence roost switching remain poorly understood. To characterize the structure of a bat maternity group and gather evidence for the role of social preference in shaping this structure, we used roost co-occurrence data from little brown myotis (*Myotis lucifugus*) implanted with passive integrated transponder tags and roost boxes monitored with passive readers in Salmonier Nature Park, Newfoundland, Canada. By developing informed null models, we more directly investigate hypotheses that may explain why bats roost together. Although our results suggest that association patterns of maternity groups can largely be explained by similar interindividual patterns in bats' roosting frequencies within a given roost box (roost fidelity), other factors are likely to contribute to the observed structure. We thus provide support for the potential influence of roost and social preferences in shaping maternity group structure.

3.2 Introduction

Sociality and group-living behaviour have evolved repeatedly among animals (Wilson 2000). Fitness benefits of sociality may include improved foraging success, energy conservation, and reduced predation risk (Goodenough et al., 2010; Wilson, 2000). In many animal societies, including primates and cetaceans, groups of varying sizes and composition split and merge over time, a phenomenon described as fission-fusion dynamics (Aureli et al. 2008; Sueur and Maire 2014; Farine and Whitehead 2015). When a group undergoes a fission event into smaller components, these components are referred to as subgroups, which are often composed of individuals that interact or associate at a specific instance in time. Individuals that are regularly found in the same subgroup, both in the frequency and duration of these interactions, can be considered part of the same social community (Krause and Ruxton 2002), which can be composed of overlapping subgroups through space and time (Newman 2006). It has been hypothesized that social community structuring is more common in large groups where individuals are unlikely to actively maintain associations evenly with all individuals due to the lack of opportunity, the lack of cognitive ability, or selective pressures (Aureli et al. 2012; Ramos-Fernández and Morales 2014) and thus, develop preferences for certain conspecifics.

One of several nonmutually exclusive hypotheses proposed to explain community structuring and association patterns among individuals is that individuals associate passively due to aggregation around dynamic resources such as food, or static resources such as nesting or denning sites (Krause and Ruxton 2002; Frère et al. 2010). Another, nonmutually exclusive hypothesis is that conspecifics associate actively, seeking specific individuals to interact with (Burns et al., 2015; Frère et al., 2010; Lusseau et al., 2006). Thus, there may be multiple factors simultaneously structuring animal groups. For example, active associations driven by social preferences, i.e. the active choice of an individual to interact with a certain conspecific, can occur within passive aggregations around a common resource. Active associations within passive aggregations of animals have been demonstrated in a range of taxa, including pods of dolphins (*Tursiops sp*; Lusseau et al., 2006), and foraging groups of baboons (*Papio ursinus*) within a troop (Bonnell et al. 2017). In this scenario, animals may regularly associate with certain individuals despite only small areas of home range overlap or, conversely, avoid individuals despite extensive home range overlap (Frère et al. 2010) due to social preferences. In landscapes where resources are distributed uniformly, a group of animals driven exclusively by passive mechanisms will appear as random and uniform patterns of associations across the population, while an actively driven network will have nonrandom patterns in associations. However, when resources are clustered across a landscape, nonrandom patterns may indicate passive aggregation around a resource, and not necessarily an active effort for individuals to associate with certain conspecifics. Passive aggregation around clustered resources may appear as apparent social structure even if individuals do not preferentially associate with one another (Spiegel et al. 2016). For example, in a nonsocial species of crab (*Carcinus maenas*), apparent social structure was induced through certain patterns of food distribution (Tanner & Jackson, 2012). Linking the distribution of resources with patterns of association may help explain the causes and consequences of emergent structure of animal groups.

Multiple species of temperate bats exhibit complex fission-fusion dynamics (Kunz and Racey 1998), where the drivers of fission and fusion events remain poorly understood. In spring and early summer, females form maternity groups where they give birth to and raise young. Temperate bats tend to have relatively high roosting area fidelity and return to the same maternity areas over multiple years (Davis & Hitchcock, 1965; Fenton, 1969). Each day, the maternity group is separated into subgroups, each roosting in a different location such that the composition and location of these subgroups changes from day-to-day (Kerth and König 1999; Willis and Brigham 2004; Wilkinson et al. 2019). Among the primary benefits of group living in temperate bats is social thermoregulation, where energy expenditure for pregnant and lactating females is inversely related to subgroup size (Willis and Brigham 2007). Daily roost preferences and therefore fission and fusion events may be influenced by stable (i.e. tree species or size) and dynamic (i.e., temperature) roost characteristics that facilitate the physiological requirements of an individual (Rhodes and Wardell-Johnson 2006; Olson and Barclay 2013; Patriquin et al. 2013; Waag et al. 2021). If roost-related factors were the only drivers of group formation and fission-fusion events, roosting subgroups should be formed passively, based on individual selection for these roosts.

An additional hypothesis for explaining group structure in bats is that maternity groups are organized based on active mechanisms, namely social preferences for roosting with certain conspecifics (Kerth and König 1999; Willis and Brigham 2004; Patriquin et al. 2010; Kerth et al. 2011). The benefits of social thermoregulation, and other possible benefits of co-roosting, provide the opportunity for individuals to familiarize themselves with roost-mates and form social preferences for roosting with certain individuals (Willis and Brigham 2007; Webber and Willis 2018). Nonrandom roosting association patterns have been observed in big brown bats

(*Eptesicus fuscus*) and northern long-eared bats (*Myotis septentrionalis*), where individuals roost more frequently than expected by chance with certain individuals even when regularly switching between roosts (Willis and Brigham 2004; Garroway and Broders 2007). These nonrandom roosting association patterns may point towards the presence of social preferences in female temperate bats, however individuals or groups of individuals may also have different preferences for specific roost characteristics when switching. As such, it remains unclear whether these nonrandom association patterns are only due to social preferences, only differences in roost preferences, or some combination of these and other factors as these mechanisms may act simultaneously (Wilkinson 1985).

Little brown myotis (*Myotis lucifugus*) are among the most widespread species of hibernating bats in North America. Many females return to the same maternity roosting areas year-after-year and are known to roost in maternity groups that display fission-fusion dynamics (Olson and Barclay 2013). Within a maternity group, different subgroups of bats will use different roosts on any given day, and the composition of these subgroups may indicate the presence of communities as in other species. Given their gregarious nature and maternity site fidelity, and the fission-fusion dynamics in areas of heterogenous roosting resources (Waag et al. 2021), little brown myotis present a compelling model system to tease apart the contributions of roost preferences and social preferences to maternity group organization. Here, we aimed to characterize the roosting organization of a maternity group of little brown myotis in Newfoundland, Canada and investigate whether there is evidence that social preference explains at least some of the emergent organization of this maternity group structure. Given the hypothesis that bats make decisions based on social preference for certain individuals, we predicted that 1) within maternity groups, there are nonrandom patterns of roosting association among individuals that cannot be entirely accounted for by roost fidelity. At a smaller spatial scale, we also predicted that 2) among bats frequently using roosts within a geographical subset of the study location (herein: local groups), roost fidelity would not entirely account for observed roosting association patterns.

3.3 Methods

3.3.1 Data Collection

We captured 1604 little brown myotis in and around Salmonier Nature Park (47.3ºN, 53.3ºW) during 2012–2019. Bats were captured between 15 May and 19 August of each year using mist nets (Avinet, Dryden, NY. U.S.A.) and harp traps (Austbat Research Equipment, Lower Plenty, Victoria, Australia) and implanted with passive integrated transponder (PIT) tags. Based on emergence count data, this PIT-tagged sample is expected to have comprised <50% of the bats present in the area. At the time of data collection, the study site was negative for *Pseudogymnoascus destructans*, the fungal pathogen that causes white-nose syndrome however, as a precaution, we designated all equipment to one location to reduce the risk of spreading *P. destructans*. Following capture, we recorded age, sex, and reproductive status for each individual. Bats were identified as young- of- the- year or as adults based on calcification of the fourth metacarpal (Anthony 1988), with only adult female bats included in this study.

Bats were marked with PIT tags (0.09 g; EID-ID100 implantable transponders; EIDAP Inc., Brampton, Ontario, Canada; Trovan Electronic Identification Systems, North Ferriby, U.K.), implanted subcutaneously between the scapulae. In Salmonier Nature Park, transponder antennae (LID650, Dorset Identification, Aalten, The Netherlands) were placed at 11 artificial, four-chamber roost boxes within a 1.1 km^2 area of the park and collected data on roost entry and exit between April and September each year. Ten of the 11 roost boxes were paired on five poles and one box was on the side of a barn. The roosts were broadly centred around three smaller localities, the visitor's centre (VC; 4 boxes), the headquarters (HQ; 4 boxes) and a private property in the southwest end of the study area (HB; 3 boxes). All boxes were present in the park at these locations since 2008, 4 years prior to beginning of monitoring efforts in 2012. The boxes were roughly 63 × 61 × 15 cm with a single opening, and each box can hold over 200 bats, based on emergence counts. All roost boxes were 3 - 5 m above ground level.

In 2012, capture effort was limited to one small locality of the study area and many captures occurred late in the season. Thus, we began our social network analysis the following year, in 2013, the first year in which we observed bats throughout the maternity period. Only detections recorded between 28 April and 30 September of each year were included to better focus analysis on the spring and summer maternity seasons. Based on emergence counts and visual assessments at roost boxes, roost groups of > 100 bats were common. As bats may visit multiple roosts in a night, we assigned day roosts based on the last detection before sunset. In 96.9% of all assigned day roost records, the last observation before sunset was in agreement with the last observation prior to sunrise earlier that day, and so we expect our assignments are reliable. We restricted the data set to include only individuals for which there were ≥20 day roost records within a year to reduce spurious conclusions about individuals and their associations with other bats, based on a formal assessment of reliability of network metrics with missing data using a subset of the data presented here (Sunga et al. 2021a [Chapter 2]). We used a conservative threshold to censor individuals, specific to our data set, because previous work has emphasized the importance of including sufficient information on each individual to ensure reliable conclusions regarding social relationships (Franks et al. 2009; Sunga et al. 2021a [Chapter 2]), while others emphasize the importance of calibration data when conducting social network analysis (Hoppitt and Farine 2018).

There were known PIT-tag reader malfunctions at two boxes in the HQ area of the study from 8 July to 30 July in 2018 where no data were collected. One box in the HQ area also missed some detections between 29 May and 21 June 2013. At the three boxes at HB in 2016, no PIT-tag reader data were collected from 18 July until the end of that season. One roost box at the HB location degraded in 2018 and was not monitored in 2019, while this same box was not monitored in 2014. Given that reader malfunctions occurred only for relatively short periods, at three or fewer roost boxes in any given year, and that only bats with sufficient numbers of observations were included in each year, resulting data are assumed to be suitable for assessing roost use patterns and association patterns among bats that frequently used the monitored boxes. Despite only having a single entrance on each box, we expect that a small proportion of the roost entries and exits were unrecorded; however, given the large sample of recorded entries and exits (total 1, 089, 663 records during 2012 - 2019) and the assumption that missed recordings were random, we had the power to adequately characterize the structure of this system of tagged bats.

Finally, approximately 80% of adult females tagged in any given year returned the subsequent year while 60% of tagged juvenile females returned (*unpublished data*).

3.3.2 Ethical Note

All animal handling protocol was approved by the animal care committee of Saint Mary's University, Halifax, Nova Scotia (AUP #number 16-12) and the University of Waterloo, Waterloo, Ontario (AUP #number 30066). Wildlife scientific research permits were also obtained from the Government of Newfoundland and Labrador, Department of Fisheries and Land Resources, Forestry and Wildlife Branch for each year of the study.

All handling and PIT tagging was performed by trained project members. Animals were held individually after capture and prior to processing. During PIT tagging, a cloth was placed over the individuals eyes/head to reduce stress during the procedure, and following the tagging, bats were held for 5 minutes to allow surgical adhesive to dry and to ensure animals were in good health prior to release. Holding and handling times were kept to a minimum and all were released at the point of capture.

3.3.3 Network Construction

All network analyses were conducted in R version 3.4.4 (R Foundation for Statistical Computing, Vienna, Austria, http://www.r-project.org). Associations between bats were assessed based on the gambit-of-the-group assumption, where two individuals were assumed to be associated if they were in the same roost on the same day (Whitehead 2008; Franks et al. 2010). We therefore quantified the ratio of times two individuals (dyad) roosted in the same roost box on the same day compared to the number of times those individuals roosted separately, or only one bat was detected in the system, and considered this as a proxy for the strength of connections between dyads also known as the simple ratio index (SRI; Cairns & Schwager, 1987). Given that bats leave the study site each year to hibernate, and not all individuals return, we generated and analyzed networks separately for each year.

3.3.4 Social network randomization procedures

By altering the construction of null model networks, hypotheses that explain community organization can be more directly tested (Farine 2017). Two types of null models were tested, a “naïve” null model that did not account for roost fidelity, and a roost fidelity-corrected null model. The naïve null models were created using “spatsoc” (version 0.1.9; Robitaille et al. 2019), such that the number of roosts used and the number of tagged individuals within a roost on a given day were held constant with what was observed on that day, while the roost an individual was found in was randomized. To construct null models that accounted for roost fidelity, roost occurrences were randomized among days, such that the number of days a bat spent in any particular roost throughout the maternity season remained constant, but the given day that it spent at that roost was changed. This procedure maintained the proportion of days an individual spent in each roost but randomized which bats may have shared a given roost on a given day, thus generating a random network of associations among individuals roughly based on overlap in roost fidelity (Farine 2017). The date an individual used a roost was randomized only among those in which the individual was observed in the system so that our models were not influenced by factors that may have caused bats to leave the system entirely. Each of these processes were repeated to generate 1000 null models of each type, for each year of the study, across the whole study area and thus the whole monitored maternity group.

We also investigated the potential of hierarchical organization within this study system, particularly the presence of detectable communities among bats that frequently used roosts within the same smaller locality of the study area. Similar to previous studies investigating the presence of subcommunities (Mourier et al. 2012), and due to the appearance of a correlation between community structure and roosting areas, individuals were grouped into local groups based on the roosting area they had the highest recorded fidelity to in each year: Visitor's Centre (VC; four boxes on two poles), Headquarters (HQ; four boxes on two poles), or a private residence (HB; three boxes, two on one pole and one on an adjacent building within 5 m of the pole). If an individual had an equal number of detections between multiple roosting areas in one year, then it was included in each local group. In 2015, only two individuals were assigned to the HB roosting area, so we did not conduct analysis for this local group network. Among all years, the VC local group was consistently the largest, an outcome which may be due to uneven capture effort among roosting areas (Table 3.1). In 2013, 2015, and 2016, one individual was found to use two roosting areas equally and so was included in both local groups, and in 2014, two individuals were included in multiple local groups. Analysis was then conducted for each local group in each year. The same randomization procedures as above were then applied to each local group network to generate 1000 nonroost fidelity-corrected null models and 1000 roost fidelity-corrected null models for comparison against the observed model.

Table 3.1 Number of bats in each year of analysis that were first captured near each roosting area within the study system. Values are based on the bats that were included in each year of analysis and do not indicate the year in which all included individuals were first captured.

Year	HB Captures	HQ Captures	VC Captures
2013	9	44	117
2014	28	88	183
2015	4	39	106
2016	33	63	181
2017	41	59	164
2018	38	36	117
2019	37	40	126

3.3.5 Assessment of network structure

For the actual and null model networks in each year for both whole maternity groups and local groups, we calculated the coefficient of variation of the simple ratio index (CV SRI). We then compared the actual value to the distribution of values from the null model networks and calculated the proportion of null model CV SRI values that were greater than or equal to the corresponding actual CV SRI value (97.5 percentile) which would support the presence of nonrandom patterns of association among individuals. We also calculated modularity (Q), a measure of the density of connections within and among estimated communities using the *cluster_fast_greedy* algorithm in “igraph” (Csárdi and Nepusz 2006) and compared the actual network value to the distribution of null network values to calculate the proportion of null model Q greater than or equal to the corresponding actual Q. This measure, when compared between the actual and null model networks, allows an assessment of whether significant evidence exists for the presence of social communities. For both CV SRI and Q, the p value represents the proportion null model networks with higher values than that of the actual network. For each whole maternity group and local group network, we also calculated the community assortativity coefficient (R_{com}) by bootstrapping which individuals were included 500 times (Shizuka and Farine 2016) and re-estimating community membership to determine whether individuals could be reliably assorted into communities. Values > 0.5 indicate reasonable strength in the assortment of individuals into communities (Shizuka and Farine 2016).

Networks were visualized using Gephi 0.9.2 (Bastian et al. 2009). Nodes were positioned using the Force Atlas layout algorithm with default parameters of 200 repulsion strength, 10 attraction strength and a maximum displacement of 10. Edges were scaled by weight such that edges with a higher SRI appear thicker.

3.3.6 Correlation between roost fidelity similarity and association strength

As a further test of the relationship between roost fidelity and network structure, we calculated the correlation between roost fidelity and association strength between individuals. We first calculated an individual × roost box matrix where the values corresponded to the proportion of observed days an individual spent in each roost box. We then applied the function *simil* from the package “ecodist” (Goslee and Urban 2007) to compare the individual × roost box matrices for all combinations of individuals and calculate a similarity score for their roost fidelity. This resulted in an individual × individual matrix where the values were a measure of the similarity in proportion of days spent in each roost box (roost fidelity).

We then conducted a Mantel test to correlate similarity in roost fidelity with the individual × individual matrix of association strength (SRI) with the expectation that greater similarity in roost fidelity would be positively correlated with SRI values. Mantel tests were conducted using the *mantel* function in “ecodist” (Goslee and Urban 2007) set to 10, 000 permutations. We used the Spearman-ranked Mantel test to account for skew in the similarity of roost use values.

3.4 Results

During 2013-2019, there were 76,097 day roost records recorded in Salmonier Nature Park, Newfoundland. Of the 155 possible days of detection from 28 April until 30 September, no year had fewer than 100 days with at least 1 day roost record in any roost box, with most days with no recordings occurring in May and September. Monitored roosts varied in their use by tagged bats, with box 111 in HB used the least, with an average of 62 day roost records per year, while box 108 in VC was used the most with an average of 2940 day roost records per year. The number of recorded PIT-tagged bats sharing a roost (subgroup size) also varied considerably ranging from 1 to 110 tagged bats detected in a single box on any given day. Based on roost emergence counts, we expected the average number of bats within a box on any given day to be considerably higher due to the presence of untagged bats, particularly during July and August when juveniles are also present.

There were up to 15 consecutive days where a day roost record was noted for a single bat, although not necessarily in the same roost. We filtered our data down to 570 tagged adult female bats that had ≥ 20 records of day roost use within a single year, with an average of 38 (± SE 0.35) day records per individual per year. Of these, 394 bats had ≥ 20 observations in multiple years with 19 individuals included in each of the 7 years (Figure 3.1). Among the 570 bats, 131, 355, and 84 were originally captured in the HQ, VC and HB roosting areas respectively. Meanwhile, 34.3 % of individuals were exclusively observed day roosting in one roosting area, 50.5 % of individuals were observed day roosting in two roosting areas, and 15.1 % of individuals were observed day roosting in all three roosting areas. We found evidence that bats switched roosts frequently but there was considerable interindividual variation. Full year networks were well connected, with an average edge density of 0.60 (± SE 0.02, range 0.54 – 0.69) and mean degree ranging from 101.54 to 161.94 among years. Individual bats used a mean of 3.4 (± SE 0.04) different roost boxes in any given year and only 10.69% of bats were detected at only one box in any given year.

Figure 3.1 Number of individuals that were included in multiple years of network analysis by meeting the requirement of ≥ 20 day roost observations over a single maternity season.

3.4.1 Nonrandom patterns of association

When comparing to nonroost fidelity-corrected null models, both maternity group networks and local group networks in all years showed significant evidence ($p < 0.025$) for nonrandom patterns in association with the exception of HB in 2013 (Table 3.2). When the null models were corrected to account for roost fidelity, association strengths between dyads were more evenly distributed than expected by roost fidelity alone (CV SRI actual > 97.5% of CV SRI random networks) in all seven maternity group networks.

The results for roost fidelity-corrected comparisons within local group networks were mixed, with 12 of 20 network (i.e. in the VC network in 2013) showing CV SRI values that were significantly less than those of roost fidelity-corrected null models ($p > 0.975$), indicating that some individuals with different roost fidelities may have interacted more than expected and some individuals with similar roost fidelity may have interacted less than expected, resulting in a more even distribution of association strengths throughout the local group. Another 2 of the 20 networks showed CV SRI values significantly greater than roost fidelity-corrected null models ($p < 0.025$) indicating additional variation in association strengths that could not be accounted for by roost fidelity patterns (Table 3.2). These analyses were also conducted using the half-weight index (HWI) resulting in consistent conclusions and only slight changes in the number of communities detected (± 1) in some years and locations.

Table 3.2 Comparison of association patterns to null models that were either nonroost fidelity-corrected or roost fidelity-corrected, in each maternity group and local group network based on the coefficient of variation of the Simple Ratio Index (CV SRI). In both types of null models $p < 0.025$ indicates that the actual network CV SRI value was significantly higher than 97.5 % null values, and that association strengths were significantly more bimodal than expected by roost fidelity and nonroost fidelity-corrected null models while a $p > 0.975$ indicates that the actual CV SRI was significantly less than 97.5% of null model values. Significant results based on a two-tailed test are indicated with an asterisk.

Year	Location	No. of Individuals	CV SRI	p compared to nonroost fidelity-corrected null	p compared to roost fidelity-corrected null
2013	Maternity group	170	151.14	< 0.001*	>0.999*
	VC	108	113.266	< 0.001*	> 0.999*
	HQ	50	81.268	< 0.001*	0.994*
	HB	13	65.742	0.083	0.186
2014	Maternity group	299	153.15	< 0.001*	> 0.999*
	VC	165	113.106	< 0.001*	> 0.999*
	HQ	108	85.904	< 0.001*	< 0.001*
	HB	28	62.001	< 0.001*	0.006*
2015	Maternity group	149	121.26	< 0.001*	> 0.999*
	VC	103	87.429	< 0.001*	< 0.001*
	HQ	45	63.068	< 0.001*	> 0.999*
	HB	2	NA	NA	NA
2016	Maternity group	277	150.21	< 0.001*	> 0.999*
	VC	159	94.862	< 0.001*	> 0.999*
	HQ	82	79.248	< 0.001*	> 0.999*
	HB	37	47.688	< 0.001*	0.628
2017	Maternity group	264	154.805	< 0.001*	> 0.999*
	VC	156	94.96	< 0.001*	> 0.999*
	HQ	62	78.3	< 0.001*	> 0.999*
	HB	46	67.699	< 0.001*	0.118
2018	Maternity group	191	163.988	< 0.001*	> 0.999*
	VC	134	110.145	< 0.001*	> 0.999*
	HQ	14	56.221	0.001*	> 0.999*
	HB	43	43.128	< 0.001*	> 0.999*
2019	Maternity group	203	160.601	< 0.001*	> 0.999*
	VC	144	79.438	< 0.001*	0.806
	HQ	20	79.438	< 0.001*	0.806
	HB	39	48.869	< 0.001*	0.981*

3.4.2 Presence of communities based on modularity and community assortativity

Modularity (Q) values were significantly larger ($p < 0.025$) for all maternity group networks when compared to the nonroost fidelity-corrected null models indicating the presence of community structure within the maternity group (see Table 3.3). Within local groups, Q values indicated the presence of community structure in 15 of 20 local group networks with the exception of HB in 2013, 2016, 2018 and 2019, and HQ in 2018 (Table 3.4). Community structure was approximately related to roosting locations as those in the same community frequently used roost boxes in the same area (Figure 3.2).

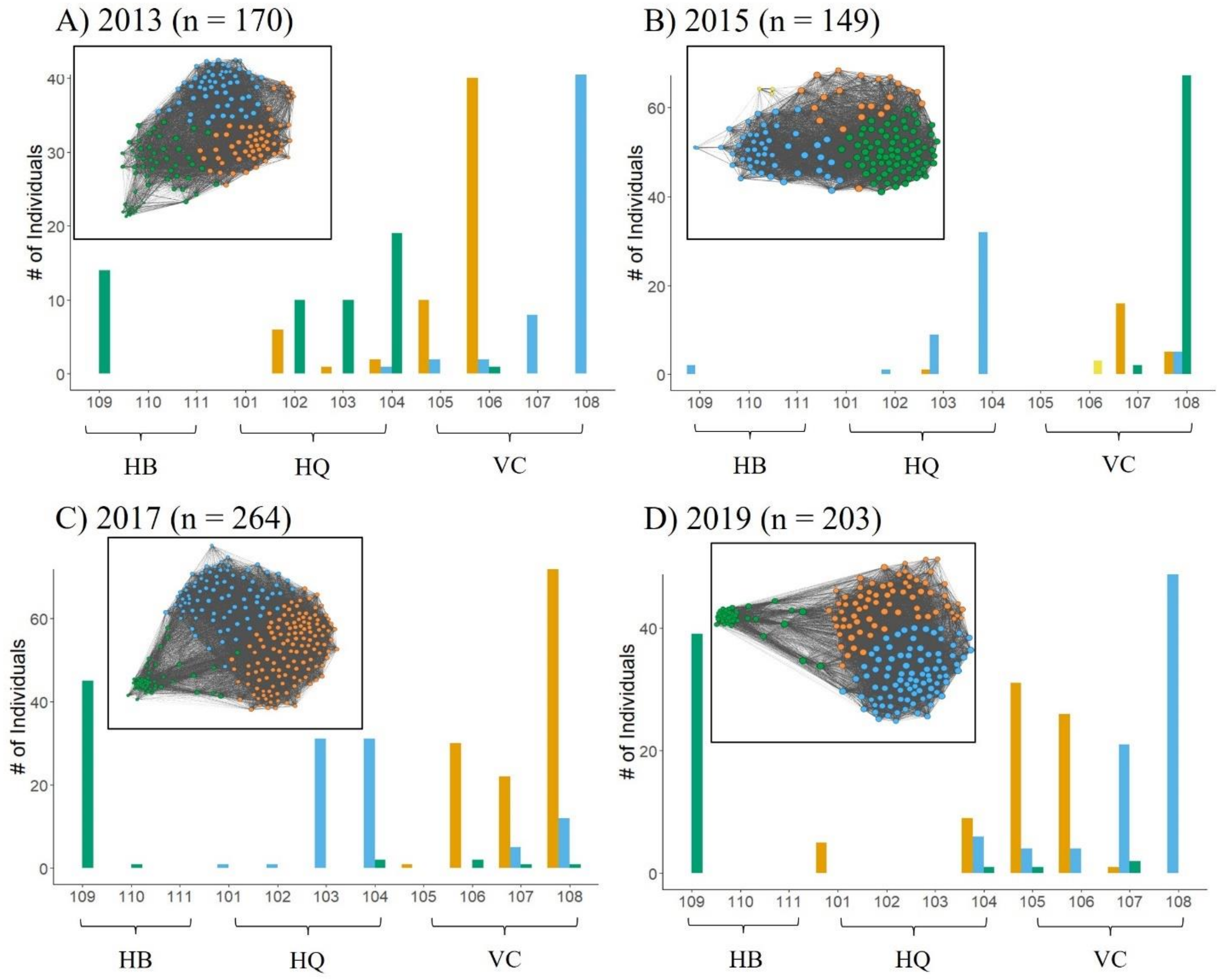
Table 3.3 Interpretation of each p-value outcome for the two tested null hypotheses. CV SRI is the coefficient of variation of the simple ratio index and Q is modularity. The p-value corresponds to the proportion of null model metrics that are higher than the actual calculated value for the network thus a low value of p indicates a high actual metric value. Both the statistical and biological interpretation are provided, where the biological interpretation is specific to the system of bat roosts under study.

Null Hypothesis	Possible Outcome	Statistical Interpretation	Biological Interpretation
Nonroost Fidelity-Corrected	$p<0.025$	Fewer than 2.5% of null models have a CV SRI and Q greater than or equal to the actual model. - Distribution of SRI may be bimodal	The network is composted of more than 1 community (high Q), resulting in high variation in dyad association strengths (CV SRI) as individuals within a community roost together more frequently and individuals in different communities roost together less frequently.
	$0.025<p<0.975$	Measure does not significantly differ from null model	It cannot be concluded that network structure significantly differs from chance and the most probable explanation is that the network comprises of one community in which individuals roost together
	$p>0.975$	More than 97.5% of null models have CV SRI and Q values greater than or equal to the actual model. - Distribution of SRI is very narrow	The network is composed of just one, highly connected community (low Q) and association strengths are consistent among pairs of individuals. This may be due to an intentional effort on the part of individuals to maintain connections with all other individuals or to roost in large groups.
Roost Fidelity-Corrected	$p<0.025$	Fewer than 2.5% of null models have a CV SRI and Q greater than or equal to the actual model. - Distribution of SRI may be bimodal	Association strengths are more unevenly distributed than expected by differences in roost fidelity thus other factors, not tested here, may explain the observed network structure. This may mean that bats with different roost preferences roost together less than expected, and/or bats with similar roost preferences roost together more than expected.
	$0.025<p<0.975$	Measure does not significantly differ from null model	It cannot be concluded that network structure significantly differs from roost fidelity and the most probable explanation is that individuals interact as a consequence of their roost preferences
	$p>0.975$	More than 97.5% of null models have CV SRI and Q values greater than or equal to the actual model. - Distribution of SRI is narrower than expected by differences in roost fidelity	Association strengths are more evenly balanced than expected by roost fidelity; thus, other factors influence bat roosting decisions. This may mean that individuals with different roost preferences roost together more than expected and/or that individuals with similar roost preferences roost together less.

Table 3.4 Modularity (Q) values and their difference from nonroost fidelity-corrected and roost fidelity-corrected null models in both whole maternity group and local group networks. $p < 0.025$ indicates significant evidence for the presence of community structure or a greater ratio of within-community connections to among-community connections than in 97.5% of the null models, while $p > 0.975$ indicates a significantly smaller ratio of within-community to among-community connections than in 97.5% of the null models, or that connections were more evenly distributed among groups. The coefficient of community assortativity (R_{com}) was also calculated where a value greater than 0.5 indicates reliable estimates of community assortment. Significant results based on a two-tailed test are indicated with an asterisk

Year	Location	Q	p compared to nonroost fidelity-corrected null	p compared to roost fidelity-corrected null	Number of Communities	R_{com}
2013	Maternity group	0.325	< 0.001*	>0.999*	3	0.82
	VC	0.277	< 0.001*	> 0.999*	2	0.857
	HQ	0.147	< 0.001*	0.62	3	0.574
	HB	0.11	0.625	0.004*	2	0.779
2014	Maternity group	0.315	< 0.001*	> 0.999*	4	0.597
	VC	0.276	< 0.001*	> 0.999*	2	0.875
	HQ	0.161	< 0.001*	0.001*	3	0.496
	HB	0.054	< 0.001*	< 0.001*	2	0.898
2015	Maternity group	0.228	< 0.001*	< 0.001*	4	0.672
	VC	0.123	< 0.001*	<0.001*	3	0.733
	HQ	0.076	< 0.001*	0.108	2	0.633
	HB					
2016	Maternity group	0.354	< 0.001*	0.459	4	0.6
	VC	0.202	< 0.001*	0.489	2	0.732
	HQ	0.137	< 0.001*	0.984*	2	0.661
	HB	0.016	0.835	0.589	3	0.168
2017	Maternity group	0.361	< 0.001*	0.995*	3	0.782
	VC	0.187	< 0.001*	< 0.001*	3	0.601
	HQ	0.188	< 0.001*	0.010*	2	0.826
	HB	0.114	< 0.001*	0.048	2	0.771
2018	Maternity group	0.388	< 0.001*	> 0.999*	2	0.964
	VC	0.256	< 0.001*	0.027	3	0.737
	HQ	0.034	0.092	0.982*	2	0.461
	HB	0.025	0.513	0.199	2	0.414
2019	Maternity group	0.417	< 0.001*	>0.999*	3	0.865
	VC	0.258	< 0.001*	0.069	3	0.683
	HQ	0.105	< 0.001*	< 0.001*	3	0.508

HB	0.03	0.071	0.021*	3	0.3



A) 2013 (n = 170)

B) 2015 (n = 149)

C) 2017 (n = 264)

D) 2019 (n = 203)

Figure 3.2 Number of individuals that were most frequently detected in each roost box in Salmonier Nature Park, Newfoundland, Canada, in a given year coloured by their assigned community for some example years. Ten of the 11 boxes were paired on the same pole (e.g. 101 and 102 were on the same pole, as were boxes 103 and 104). Box 111 was not paired and was on the side of a barn 5 m from the pole containing boxes 109 and 110. The order of presentation on the X-axis roughly corresponds to the south–north arrangement of the boxes over a 1.1km distance. Roosting areas are identified as HB – a private property, HQ – headquarters and VC – visitors centre. Inset shows a diagram of the maternity group network structure for that year with node colours corresponding to community assignment. Individuals were arranged by Force Atlas in Gephi 0.9.2. Communities were assigned based on the *cluster_fast_greedy* assignment algorithm in “igraph”.

The maternity group annual network for 2015 indicated the presence of community structuring beyond what was explainable by roost fidelity ($p < 0.025$). In other years, modularity was lower than in roost fidelity-corrected null models ($p > 0.975$) suggesting higher connectivity among potential community boundaries than expected based on roost fidelity. Within subsets of the study area, local group networks could be further subdivided into smaller communities even when accounting for roost fidelity in modularity analyses, such as VC in 2015 and 2017, HB in 2013, 2014 and 2019, and HQ in 2014, 2017, and 2019 (Table 3.4). Other local group networks had significantly lower Q values than roost fidelity-corrected null models including VC in 2013, and 2014 and HQ in 2018, indicating greater connectivity among potential communities than expected by roost fidelity. In 4 of 20 local group networks, individuals could not be reliably assorted into the identified communities ($R_{com} < 0.5$; Table 3.4) while assortment was reliable in all maternity group annual networks. Examples of network structure in local group networks are shown in Figure 3.3.

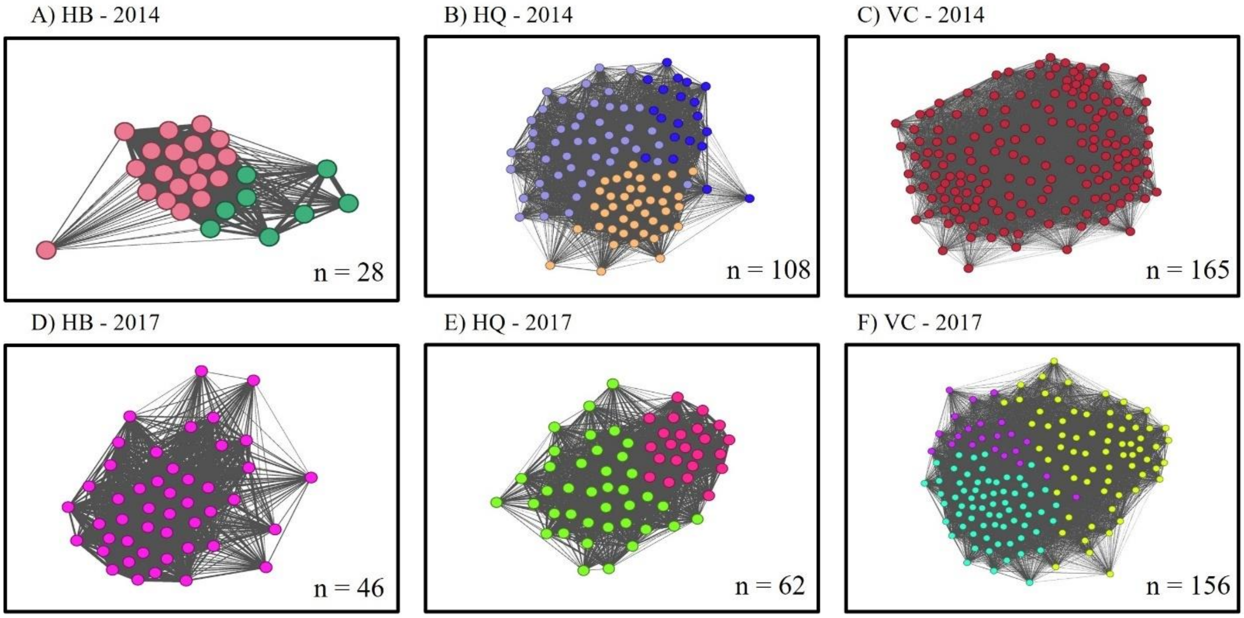


Figure 3.3 Example networks from 2014 (A-C) and 2017 (D-F) showing local group networks that varied in the number of detected communities across years. Division into communities was based on comparison of modularity to the roost fidelity-corrected null model ($p < 0.025$). The HB roosts (A, D) show bats using roosts in the area of a private property most frequently; HQ roosts (B, E) shows bats using the headquarters roosts most frequently; VC roosts (C, F) shows bats using roosts near the visitor's centre most frequently. Colouring of nodes indicates different community assignments based on the *cluster_fast_greedy* community detection algorithm in "igraph", and colours were arbitrarily assigned for each community. Edge weights are shown proportional to the Simple Ratio Index (SRI) between each dyad and positioning was assigned using the Force Atlas layout algorithm in Gephi 0.9.2.

3.4.3 Correlation between roost fidelity similarity and association strength

Similarity in roost fidelity between individuals in a dyad was significantly correlated with the dyad’s association strength in all years ($p < 0.05$). Mantel R scores were statistically significant and ranged from 0.808 to 0.852 with a mean of 0.830 (± SE 0.006) for maternity group networks. Mantel R scores ranged from 0.325 to 0.845 with a mean of 0.682 (± SE 0.029) for local group networks, and were significant ($p < 0.05$) for all local group networks with the exception of HB in 2013 ($p = 0.062$). Despite the significant correlation between roost fidelity similarity and association strength across the maternity group, the relationship between roost fidelity similarity and association strength varied considerably among dyads (Figure 3.4). In all networks, some individuals never interacted (SRI = 0) despite high similarity in roost fidelity (> 0.90; two bats used the same roosts with similar frequencies but not necessarily on the same days).

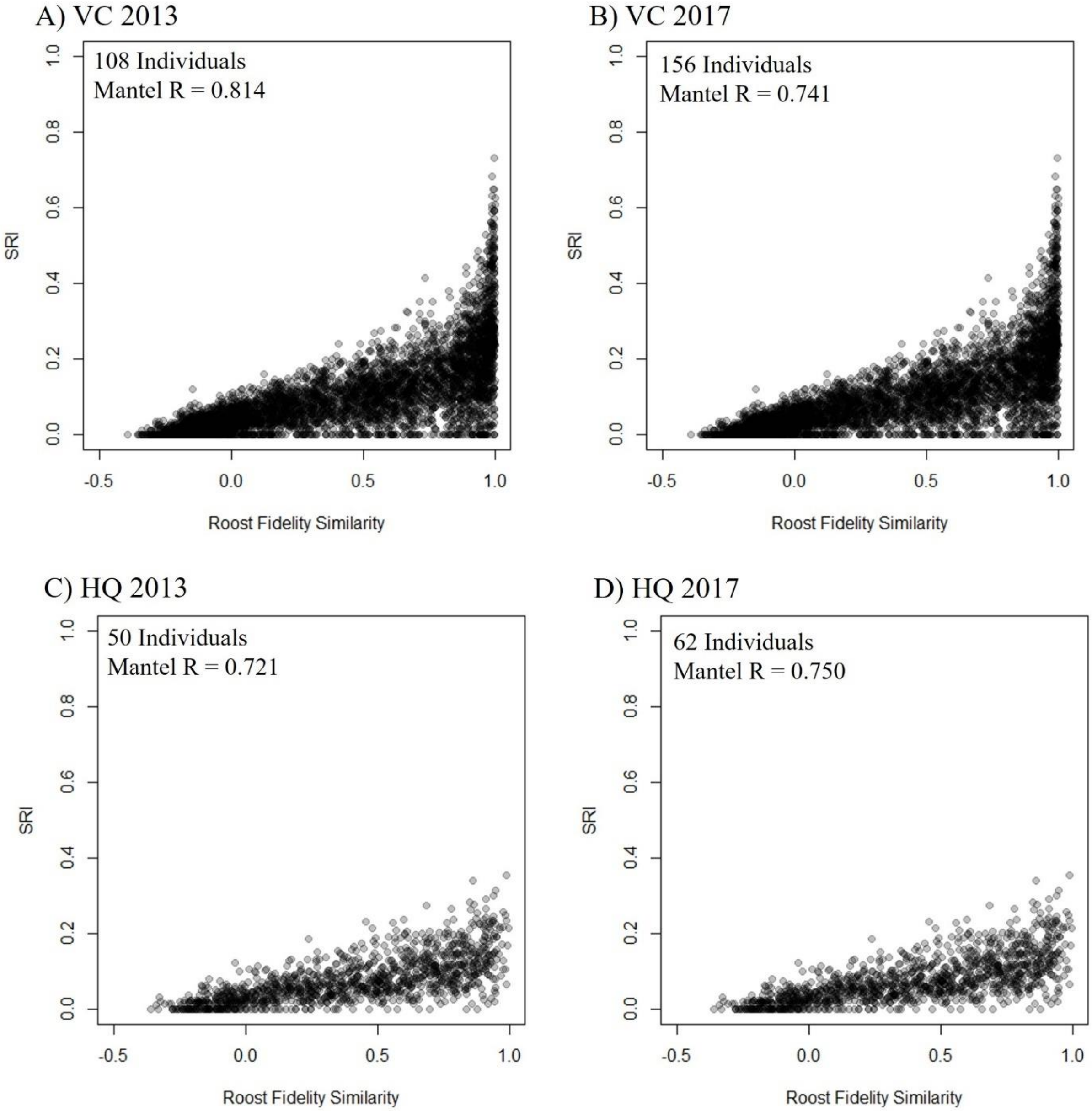


Figure 3.4 Sample figures of the correlation between roost fidelity similarity and association strength calculated as the Simple Ratio Index (SRI) for all possible dyads in A) the visitor's centre (VC) local group network in 2013, B) the VC local group network in 2017, C) the

headquarters (HQ) local group network in 2013, and D) the HQ local group network in 2017. Each dot represents one dyad.

3.5 Discussion

Our study provides evidence that little brown myotis (*Myotis lucifugus*), like many other bat species, demonstrate nonrandom patterns of roosting associations. We hypothesized that bats make roosting decisions based on social preferences, and we predicted that roost fidelity would not entirely account for observed roosting patterns among (1) maternity groups or the smaller (2) local groups. Although patterns of co-roosting associations were largely explained by differences in roost fidelity, there was evidence of greater connectivity among detected communities and between some individuals than expected by roost fidelity alone. There was also variability in how roost fidelity similarity was related to the association strength between individuals within a dyad. With regard to our second prediction, roost fidelity also largely explained association patterns of bats that frequently used roosts within the same geographical subset of the study area (the local groups), but unexplained patterns still remained, including greater cohesion in some areas and years, and further subdivision into social communities in others. Taken together, these results support the contention that bats make decisions not only about which roosts to use but also about when to use them. Observations of nonrandom association, coordinated movements, and potential social preferences have been reported in the roosting patterns of other bat species such as Northern long-eared bats (*M. septentrionalis*; Garroway & Broders, 2007), Bechstein's bats (*M. bechsteinii*; Baigger et al., 2013; Kerth et al., 2011; Mavrodiev et al., 2021) and Spix's disc-winged bats (*Thyroptera tricolor*; Vonhof et al., 2004). These patterns are also common in other mammal species such as dolphins (i.e. Frère et al., 2010) and baboons (i.e. Silk et al., 2006), thus the formation and maintenance of bat maternity groups may function on many of the same principles. Our results showing that roost fidelity alone may not explain all observed patterns of roosting association are in agreement with Wilkinson et al. (2019), who suggested that social preferences may influence frequent roost switching in multiple bat species. Furthermore, our results are also in agreement with evidence from a study on common vampire bats (*Desmodus rotundus*) showing the presence of nonrandom association patterns even when roost preferences were accounted for (Wilkinson 1985), supporting the possibility of social preferences in bats.

It is of note that little brown myotis differed widely in their roost fidelity patterns, and therefore roost preferences likely differ between individual bats. In a maternity group of pipistrelle bats (*Pipistrellus pipistrellus*), individuals used two to three roosts (out of 17 possible roosts) more frequently, and the most frequently used roosts were not the same among all individuals (Thompson 1990). Given the similar construction of roost boxes and the close proximity of roosts within our system, the drivers of variation in roost preference for this little brown myotis maternity group are not immediately clear. In our study, the maximum distance between roosts was 1.1 km and was therefore unlikely to be a limiting factor for individual roost use, particularly as bats often travel over 5 km in a night from roosts to foraging sites (Randall et al. 2014). Prior work on bats suggests that individual bats require specific roosting characteristics based on their reproductive status (Willis and Brigham 2007; Olson and Barclay 2013) and that different reproductive periods have different energetic demands (Patriquin et al. 2010; Webber et al. 2016). These factors may lead to individuals repeatedly using a known roost that matches their required characteristics or altering roost preferences throughout the maternity season. This, in turn, can result in homophily, which is the tendency for individuals to associate more frequently with conspecifics based on similar characteristics, such as reproductive status, as found in northern long-eared bats (*M. septentrionalis*; Garroway & Broders, 2007). Further investigation is needed to determine why individual roost preferences vary, and whether these preferences vary with individual reproductive condition. It must also be considered that different social groups may be more established in different roosting locations, and thus although passive aggregation mechanisms cannot be ruled out, differences in roost fidelity may be explained by interactions between social groups, such as aggressiveness between groups as described in Bechstein's bats (Kerth et al. 2002).

Inference of social relationships from bat roosting subgroups must be done with caution, as previous studies using social network analysis have demonstrated the possibility for social relationships to be inferred simply due to sufficient spatiotemporal opportunity for individuals to interact, or "nonsocial noise", and thus, the simple frequency of interaction does not necessarily reflect the true underlying mechanisms of association between individuals (Cantor et al. 2012). It is clear from our results that accounting for roost fidelity leads to different outcomes than a naïve null model without roost fidelity. These two null models would lead to different conclusions regarding the influence social preference on bat maternity group organization. Thus, our results emphasize the importance of accounting for factors like habitat preferences when inferring the effect of social influences on constructed animal networks and support the suggestion of specifically tailoring null models to suit research questions (Farine 2017). When both active and passive mechanisms of association are suspected, altering null models to account for controllable factors such as habitat use patterns can greatly improve our ability to infer an effect of social behaviour. We demonstrate this here using frequency of roost use in a particular location, but more fine-scale movement metrics or habitat features could also be incorporated based on individual movement trajectories during foraging (Spiegel et al. 2017). By accounting for confounding habitat factors, particularly in heterogenous environments, we can better assess the decisions individual animals make daily as well as the relationship between social and spatial preferences in animal groups.

It is clear from our results that little brown myotis maternity groups demonstrate complex fission-fusion patterns in roosting behaviour. In multi-level societies, fission-fusion events consistently occur along the social boundaries of core units (Grueter et al. 2020) and thus, we would expect to detect consistent communities based on a smaller number of individuals who always roost or forage together, patterns which we did not detect in this study. In other bat species, groups break apart and rejoin regularly into roosting subgroups and do not show the strict boundaries for division across all fission and fusion events, as social communities have been shown to mix between roosting occurrences, such as in Natterer's bats (*M. nattereri*; Zeus et al., 2018). It is possible our study system, and other bat maternity groups, may constitute a "vague" (*sensu* Grueter et al., 2020) hierarchical structuring described as greater variability in core unit composition such as in reticulated giraffes (*Giraffa camelopardalis*; VanderWaal et al., 2014) and elephants (*Loxodonta africana* and *Elephas maximus*; de Silva & Wittemyer, 2012). Given the variable evidence for community structuring in local groups within our study area, the number of unmonitored roosts that may surround our study area and the number of unmonitored individuals, a “vague” multi-level component to bat maternity groups can not be completely ruled out. It is also possible that some multi-level structuring exists when considering interactions between bats during foraging and their relationship to roosting groups, or by observing interactions among bats within roosts. Although maternity roosts in trees and roost boxes tend to be smaller than those in building roosts, due to our use of the gambit-of-the-group assumption, we were also unable to rule out the possibility that bats using roost boxes in our study system only associated with certain individuals within a roost (Waag et al. 2021), thus creating smaller units than we observed here.

Unsurprisingly, similarity in roost fidelity between a pair of individuals was correlated with their association strength. However, we observed a large degree of variation, particularly among individuals with very similar roost fidelity, which suggests a strong likelihood of other factors such as social mechanisms, (i.e. homophily, information sharing), driving roost use. Because we applied the gambit-of-the-group assumption in this study, some individuals with similar roost fidelity patterns may not actually have been associating despite being in the same roost at the same time. Of particular interest, was the large number of individuals with low association strengths or no instances of shared roost use despite near identical roost fidelity. In instances of bats rarely associating despite similar roost fidelity patterns, these bats may be showing avoidance or competitive exclusion at preferred roosts, resulting in the absence of co-roosting instances. Similar instances of avoidance despite extensive habitat overlap have also been described in other taxa such as dolphins (Frère et al. 2010), a group well known for their intelligence and social complexity. Whether bats are actively avoiding certain individuals remains to be determined, although it is of interest to determine the extent to which factors such as relatedness, as seen in some other bat species (e.g., Evans et al., 2020; Kerth et al., 2000; Metheny et al., 2008) may drive social decisions.

In some cases, individual little brown myotis were more connected to members of other communities than expected by roost fidelity alone, suggesting the presence of an active effort to maintain social cohesiveness between individuals. We observed some instances of bats with fidelity to different roosts interacting more than expected by chance. Social cohesiveness may improve protection from predators (e.g., Krause & Ruxton, 2002), facilitate information exchange (e.g. Romano et al., 2018), and increase foraging success (e.g. Tanner & Jackson, 2012) in a variety of social species. Romano et al. (2018) specifically noted that the potential for information transfer (network efficiency) was highest in networks with intermediate levels of community structure, similar to the type of community structure we identified here. Connections with members of other communities in addition to regular associations among individual little brown myotis from different communities during fusion events suggests that social cohesiveness may be crucial to meeting individual needs such as ensuring adequate roosting subgroup sizes for social thermoregulation. In bats across multiple genera and geographical locations, overlap between social communities in different roosting areas has been reported, such as in northern long-eared bats (Garroway and Broders 2007) and Spix’s disc-winged bats (Vonhof et al. 2004), and is supported by findings in big brown bats (*Eptesicus fuscus*) where roost-switching behaviour is suggested to maintain associations within the larger group (Willis and Brigham

2004). Given the social cohesiveness of such a large group of bats with varied roost fidelity and across frequent fission and fusion events, bats may be balancing both environmental and social costs and benefits to make daily roosting decisions.

Despite missing a portion of the maternity group, our sample size of tagged individuals was large (N = 570), given that many studies applying social networks to bat maternity groups include fewer individuals (Johnson et al. 2013). Note however, that our results do not include all associations among all individuals as we were unable to tag all the bats in the maternity group, and some individuals were excluded due to insufficient information on their roost use and association habits (for validations see Sunga et al., 2021 [Chapter 2]). The omission of individuals less frequently observed in our study system may lead to an overestimate of the number of strong relationships within the maternity group. But, given that we observed both strong and weak relationships among individuals frequently roosting in this study system, and previous assessment of how community structure estimates are affected by missing individuals specific to this study system (Sunga et al. 2021a [Chapter 2]), we expect that our conclusions regarding the role of roost fidelity are reflective of little brown myotis behaviour. We also expect that other unmonitored structures were used as roosts by the maternity group but, given the number of roosts monitored and by limiting our study to bats observed at these roost boxes a minimum number of times, we are confident that we had sufficient observations to characterize the roost use patterns among bats who regularly used our system for maternity roosting habitat.

3.5.1 Conclusions

Our results show that roost fidelity, and therefore potentially roost preferences, account for much of the patterns of roosting associations in this bat maternity group. Among little brown myotis showing dissimilar patterns in roost fidelity, interactions between communities may explain differential roost preferences among very similar roost boxes. Meanwhile, individuals with similar roost use patterns did not always roost together frequently. Thus, other factors such as social preferences may also influence when little brown myotis use a particular roost, and therefore the overall organization of the maternity group. The strong connectivity across the maternity group in most years, and even within roosting areas, supports the contention that benefits of maternity group cohesiveness may drive the coordination of roost use between individuals. However, maternity group cohesiveness may be slightly over-estimated due to our use of the gambit-of-the-group assumption as bats within a roost may not necessarily be associating. We also emphasize the importance of controlling for nonsocial factors whenever possible, allowing greater inference into the role of social mechanisms on the organization of animal groups.

Chapter 4

Individual variation in parturition timing within and among years in a bat maternity colony

4.1 Overview

In monoestrous species, the timing of reproduction can have important impacts on offspring survival. For heterotherms in temperate areas, parturition timing is constrained by cold weather survival strategies such as hibernation and torpor. Female bats that are year-round residents of temperate regions, such as little brown myotis (*Myotis lucifugus*), invest significantly in parental care resulting in sharp changes in behavior immediately following parturition. These behaviour changes may include increases in nighttime roost revisits, which can be used to identify parturition dates for individual bats that have been PIT tagged and use monitored roosts. Using a system of tagged bats and monitored roosts in Pynn's Brook and Salmonier Nature Park Newfoundland, Canada, we identified parturition dates of 426 female *M. lucifugus* in at least one year based on changes in nighttime roost revisit patterns, and quantitatively characterized group and intraindividual variation between 2012 and 2021. Overall, we report wide variation in parturition date within years among individuals as well as year-to-year variation both across the population and within individuals. Spring weather conditions appeared to be important influencers of parturition timing. Thus, anticipated changes in spring and summer temperature and extreme weather events may impact parturition timing and therefore offspring survival of temperate bats.

4.2 Introduction

In K-strategist species characterized by energetically expensive parental care, individuals must maintain their own energy balance while investing in care of their offspring. In many mammals that exhibit parental care, particularly in temperate environments, parturition is also timed to maximize the probability of offspring survival. In some species, this may mean that offspring are born before seasons with more frequent extreme weather events (e.g., Long et al. 2016), at times of plentiful resources (e.g., Gogan et al. 2005), and/or relatively synchronously to reduce predation (e.g. Patterson et al. 2016). Phenology of parturition also may vary spatially as a result of resource availability and climate (e.g., Neumann et al. 2020). Any combination of these nonmutually exclusive factors may explain variation in timing of parturition of species, populations, and individuals.

Many bat species that are year-round residents of temperate areas undergo a seasonal reproductive cycle consisting of copulation in the fall, sperm storage over the winter, and parturition in the spring/summer months (Racey 1982). Following winter hibernation, females build up fat deposits to fuel embryonic development (Fenton and Barclay 1980; Fenton 2001). However, because spring conditions can at times still be inhospitable, bats use torpor for energy conservation, particularly during periods of increased precipitation and wind gusts (Besler and Broders 2019). Previous studies have demonstrated inter-individual variation in use of torpor, with nonreproductive females typically using longer and deeper bouts than reproductive females (Willis et al. 2006), as torpor-use may slow fetal development and delay parturition (Racey and Swift 1981; Dzal and Brigham 2013).

Although offspring born earlier in the season may have a greater chance of survival due to a longer period of fat gain before the winter (Kunz and Racey 1998; McGuire et al. 2009; Balzer et al. 2022), , the high energetic cost of lactation and low availability of food early in the season means that females must wait until conditions are suitable to support foraging for both mother and pup (Frick et al. 2010). Thus, at certain times of year, females must balance investment in their own survival with that of their offspring to maximize lifetime fitness. Therefore, factors that may explain variation in parturition timing for temperate bats include timing of emergence from hibernation (Fontaine et al. *in prep*) and spring torpor use (Racey and Swift 1981; Dzal and Brigham 2013; Linton and Macdonald 2018). Intraspecific variation among females in decisions on hibernation, torpor use, and other factors leads to parturition being asynchronous within populations. As temperate bats are long-lived (Florko et al. 2017), parturition timing may also vary among individuals of different ages. Given that many bat species produce one offspring per year, are long-lived, and often show fidelity to maternity areas, there may be changes in reproductive success and timing from year-to-year as females become more experienced.

In this study, we use a long-term monitoring system of roost use by individually marked little brown myotis (*Myotis lucifugus*) in Newfoundland, Canada and changes in nightly roost revisit behaviour to estimate parturition date. Given the high energetic investment of pregnancy (Kurta et al. 1989) and parental care responsibilities of the lactation period, it is expected that the frequency of night-time visits to maternal roosts will increase at parturition (Henry et al. 2002), and therefore a change in this behaviour can be used to estimate the timing of parturition

(Fontaine et al. *in prep*). Using these estimates, our goal was to characterize phenological inter- and intra-individual variation in parturition of little brown myotis in Newfoundland, Canada across years by estimating the parturition dates for individual bats in as many years as possible. We tested hypotheses that may explain inter- and intra-individual variation in parturition date including spring weather conditions, minimum age, and location. Given that Newfoundland is generally a wetter environment with cooler summers than parts of Quebec, we predicted that annual variation in precipitation would have an opposite impact on parturition timing than reported by Fontaine et al. (*in prep*) for little brown myotis. Additionally, as our system consists of multiple monitored roosts within a small geographical area, we describe intra-individual consistency in roosts used for parturition and possible instances of bats moving their pups between roosts to shed light on further decisions bat mothers may be making when caring for their offspring.

4.3 Methods

4.3.1 Study System

Female little brown myotis were captured in and around Salmonier Nature Park (Lat: 47.3º, Long: -53.3º) and Pynn's Brook (n = 583; Lat: 49.1º, Long: -57.5º) Newfoundland, Canada between 15 May and 19 August of most years between 2011 and 2021. Bats were captured using mist nets (Avinet, Dryden, New York, USA) and harp traps (Austbat Research Equipment, Lower Plenty, Victoria, Australia) and for each individual we recorded age, sex, and reproductive status. Age class as adult or juvenile was determined based on ossification of the metacarpal joint (Anthony 1988) and individuals first captured as an adult were assigned a minimum age of one for the year of capture while individuals first captured as juveniles were assigned an exact age of zero. Reproductive status was designated based on palpating the abdomen to detect pregnancy and expressing the nipples for lactation. An obvious bare patch around the nipple with no lactation was designated as post-lactation (Racey 1988). Only adult female bats (≥ 1 year old) were included in this study. Bats were subcutaneously implanted with passive integrated transponder tags (PIT tags; 0.09 g; EID-ID100 implantable transponders, EIDAP Inc, Brampton, Ontario, Canada and Trovan Electronic Identification Systems, UK) between the scapulae. No data was collected in either location in 2020 due to the COVID-19 pandemic.

Within Salmonier Nature Park, eleven artificial 4-chamber roost boxes within a 1.1 km^2 area were outfitted with RFID transponder antennas (LID650, Dorset Identification, Netherlands). These antennas continuously monitored the passage of tagged bats into and out of the roost and recorded data on individual ID, and time and date. In 2021, three of the monitored roost boxes were no longer available for bats to use due to degradation. Within Pynn's Brook, there were four artificial 4-chamber roost boxes paired on two trees approximately 20 meters apart. These roost boxes were also outfitted with transponder antennas. These antennas continuously monitored roost use but due to malfunctions and technical issues, there was no data collected in 2016, 2017, or 2018 or after 6 July in 2015 in Pynn's Brook. Outside of the noted exceptions, there was near continuous monitoring of the roost boxes in both Pynn's Brook and Salmonier Nature Park. However across both locations, it is expected that some observations were not recorded due to missed detections or malfunctions at individual boxes.

4.3.2 Parturition date assessment

Fontaine et al. (*in prep*) detected parturition dates by seeking a sequence of three or more nights with a single return to a roost followed by three or more nights with at least two returns. As our system contained multiple roosts, bats in our system often revisited roosts at night even early in the maternity season (Figure 4.1) and revisit behaviour was highly variable among individual bats. Given this, we instead estimated parturition dates based on a change in nighttime roost revisit patterns relative to each individual rather than a predetermined threshold. We filtered our database within each year to select individual bats for which we had at least one recording on a minimum of 40 days between 1 June and 31 July in any year (n = 426 unique individuals). These requirements were selected as the 'window' when we generally expect parturition to occur based on observations of volant juveniles, and to ensure that our analysis focused on bats that were consistently present in the monitored system. We identified parturition date based on roost revisits where parturition was estimated based on an abrupt increase in the number of nighttime roost revisits (Figure 4.1). We calculated the maximum number of nighttime (23:00 – 03:00) revisits to a single roost on each night for each individual across all days. To ensure reads at each box were independent and best represented revisit behaviour, we further limited our data such that reads at the same roost by an individual must be at least 5 minutes apart unless another roost box was visited in between. We used observations up until 4 August, approximately one week prior to when most bats departed from the maternity site. Observations after this date were removed as some little brown myotis displayed a change in roosting habits, often using the monitored roosts infrequently, as they prepared to depart towards swarming locations and thus interfering with the changepoint detection methods described below.

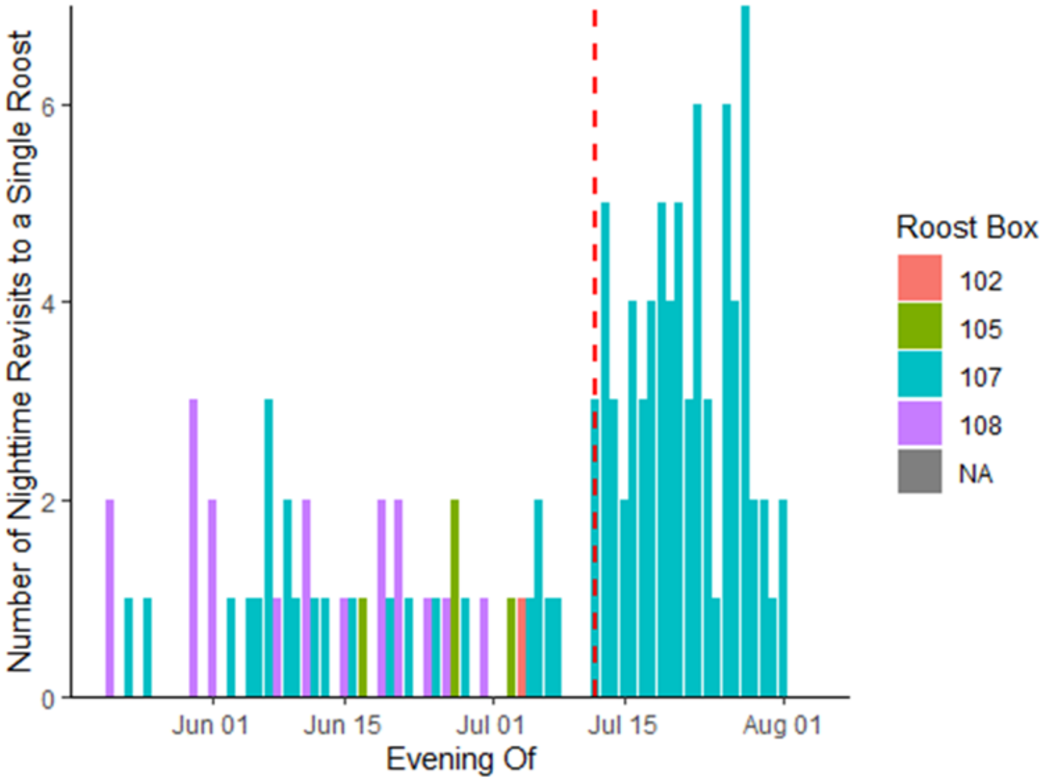


Figure 4.1 Example histogram showing the number of nighttime revisits to different roost boxes by a single female *Myotis lucifugus* (PIT ID: 00074EEFAB in 2014) throughout the maternity period in Salmonier Nature Park, Newfoundland, Canada. The red dashed line indicates the detected changepoint and therefore estimated parturition date based on a break point of the mean. Colours represent the different monitored roost boxes.

We then calculated a single change point of the mean using the AMOC (at most one changepoint) method with the *cpt.mean* function in package "changepoint" with an asymptotic penalty value of 0.05 (Killick and Eckley 2014). As this method assesses a changepoint in the mean, occasionally a single night with a large number of revisits could lead to estimates of parturition date which are likely spurious. We thus followed this analysis with visual inspection of the data and manually corrected estimates that seemed influenced by a single night to either a new parturition date, where a "clear" increase in nighttime revisits was present or removed in incidents where a changepoint was not clearly visible. Additionally, if the changepoint was influenced by the departure of the bat from the system for a long time (i.e. the changepoint occurred right before a long series of 0 nighttime revisits), the estimated parturition date was corrected if a clear increase in nighttime revisits could be detected earlier or later in the season. A "clear" increase in nighttime revisits for visually correcting parturition date was defined by displaying at least three consecutive nights with revisit frequencies all greater than the three preceding nights, a method similar to that of Fontaine et al (*in prep*) but accounting for the possibility of multiple nighttime revisits prior to parturition as a regular behaviour of the individual. If these criteria were not met and the changepoint analysis was deemed unreliable due to the influence of a single night or potential departure from the system, no parturition date was identified.

As it is not known what time of day little brown myotis give birth to their pups, our estimates of parturition date may be biased by one day before or after the true parturition date. Given that the bias would be consistent across all individuals it was not expected that this bias would have any effect on our overall conclusions.

4.3.3 Validation of reproductive status

We validate our reproductive status assignments by comparing the change point results to in-hand reproductive assessments for bats opportunistically recaptured within 10 and 20 days of the estimated parturition date. For bats whose pattern of nightly revisits did not indicate a parturition event within our system of monitored roosts, we compared this assessment to available recaptures between 5 July and 30 July, the period when bats were expected to be noticeably pregnant or subsequently lactating if reproductive.

4.3.4 Parturition location and movement

For each parturition event, we qualitatively assessed whether there was evidence that the mother had moved the pup to a different roost. To do this, we surmised location of each pup based on the most revisited box by the mother each night for up to 3-weeks following parturition, the expected length of time for pups to reach volancy (Krochmal and Sparks 2007). If there was a change in the box that was visited most frequently within a night, we detailed the number of times that this occurred and whether movements were to a box on the same pole, or a box on a different pole in the same area. For Salmonier Nature Park, we also noted whether the movement was between the two closer areas, the Visitor's Centre (VC) and Headquarters (HQ), or between one of HQ or VC locations and the more distant private property (HB). We report the minimum number of movements possible as if a bat revisited two roosts the same number of times in a night, and at least one of those roost boxes matched the box used most frequently the night before, no movement was counted. Similarly, in instances where pup movement between different distances may have been observed due to equal revisits counts at multiple roosts, the shortest possible movement distance was recorded. For bats which had a parturition date detected in multiple years (Figure 4.2), we also noted the box in which parturition is suspected to have occurred in each year.

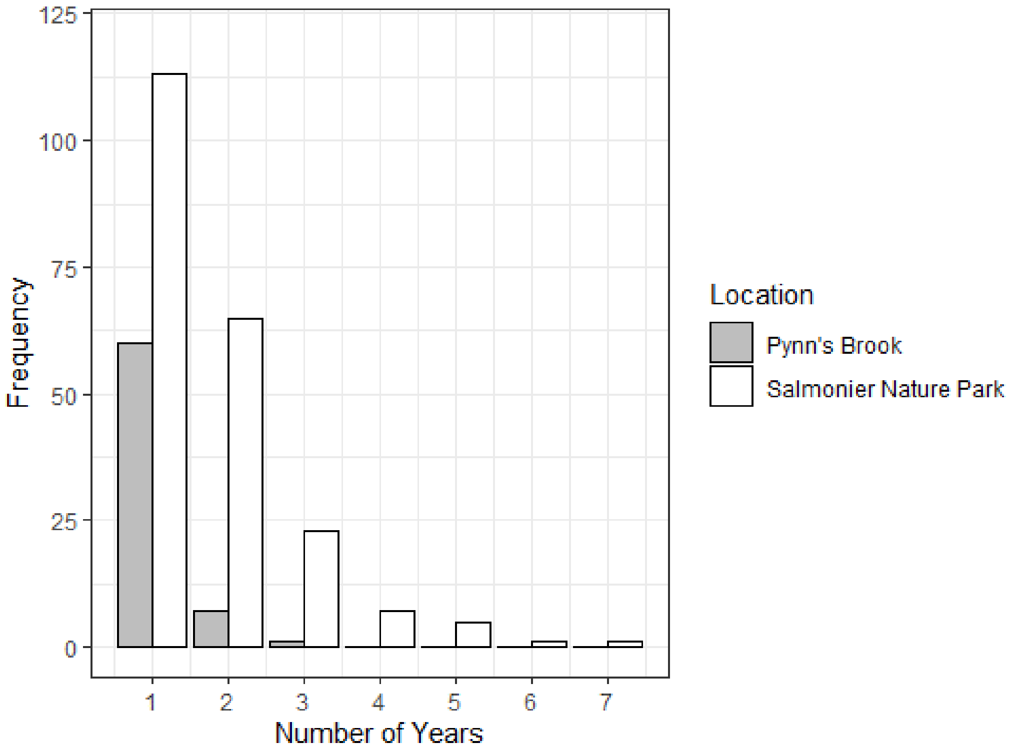


Figure 4.2 Histogram of the number of little brown myotis (*Myotis lucifugus*) that had at least 40 day roost observations between 1 June and 31 July and for which a parturition date could be estimated based on changes in nighttime roost revisit behaviour in varying numbers of years. Numbers of individuals are separated by the study location in Newfoundland, Canada.

4.3.5 Annual and individual variation in parturition dates

To assess factors that may influence parturition timing we used individuals for which a parturition date could be estimated and conducted a multi-model inference analysis using Conditional Akaike's Information Criterion (AIC_c) to rank models. We applied a mixed effects model with a numeric response of parturition day of the year to assess how environmental conditions may impact the timing of parturition. We included individual as a random effect in all models to account for the fact that individuals may be included in multiple years and to assess inter-annual variation in intra-individual parturition dates. To assess a hypothesis of individual experience influencing parturition date, we created a model with minimum age as a fixed effect. We also tested a hypothesis of study location (Pynn's Brook or Salmonier Nature Park) as the only fixed effect to determine whether differences in parturition date may be related to the maternity location.

As torpor has been observed to be used more frequently in poor conditions (Besler and Broders 2019) while also possibly delaying fetal development (Dzal and Brigham 2013), we tested a hypothesis of torpor use during pregnancy as the main determinant of parturition timing. The torpor use candidate model included the effects of mean minimum temperature from 20 April, the earliest detection of individuals in our monitored system, until the first estimated parturition date across all years, and mean daily precipitation for the same time period. These dates were selected as they represent when pregnancy may be influenced by local weather conditions. An interaction between temperature and precipitation was also included where temperature was calculated as degrees away from 25ºC so that the highest values of this interaction term would correspond to cold and wet days which were expected to have the most influence on bat behaviour (Besler and Broders 2019). The mean of this interaction term from 20 April until the first estimated parturition date was then recorded for each year and location. We also tested a more general hypothesis of spring-time weather conditions which included the above factors in the torpor hypothesis model plus the proportion of days with wind gusts over 30 km/h. No interaction terms were added for this model as our data source did not include wind speeds for days where gusts were less than 30km/h.

For both locations, weather data was collected from Environment Canada weather stations available through "weathercan" (LaZerte and Albers 2018). For Salmonier Nature Park this weather station was at St. John's International Airport (47.6212º, -52.7424º). For Pynn's Brook, weather data was obtained from the weather station at Deer Lake Regional Airport (49.2128º, -57.3943º).

4.4 Results

There were 78 and 348 unique bats that met the minimum criteria of at least one read on 40 days between 1 June and 31 July in at least one year and for which parturition date could be estimated at each of Pynn's Brook and Salmonier Nature Park, respectively. There were no bats that met the minimum criteria in Pynn's Brook in 2017. Within a site in any given year, the proportion of bats for which a parturition date could be estimated ranged from 39 % to 88 % (Table 4.1). The median parturition date was 10 July in Pynn's Brook (range 25 June to 27 July) and 15 July in Salmonier Nature Park (range 15 June to 3 August).

Table 4.1 Summary of parturition date detection success and median parturition dates in Newfoundland as measured at Pynn's Brook and Salmonier Nature Park based on changepoint analysis of nighttime roost revisit behaviour.

Year	# of bats with estimated parturition date	# of bats with no estimated parturition date	Median estimated parturition
2012	76	10	8 July
2013	58	22	12 July
2014	67	98	12 July
2015	29	27	14 July
2016	46	35	20 July
2017	65	57	20 July
2018	35	55	23 July
2019	79	42	18 July
2021	33	40	13 July

4.4.1 Parturition date assessment

The number of individuals for which parturition date could be estimated and the median parturition date varied from year-to-year (Table 4.1). The magnitude of intra-year variation in parturition date also varied among years (Figure 4.3). In Pynn’s Brook, eight bats had parturition dates detected in multiple years, while in Salmonier Nature Park, 111 bats had estimates of parturition dates in multiple years with two individuals with a detected parturition date in seven of the nine years of the study (Figure 4.2). In each year, between three and 14 parturition dates were manually corrected due to suspected spurious conclusions based on single nights with a high number of roost revisits or potential absence from the system. Upon qualitative inspection, increases in the number of nighttime revisits by individual bats was not noticeably correlated with any extreme precipitation or wind events.

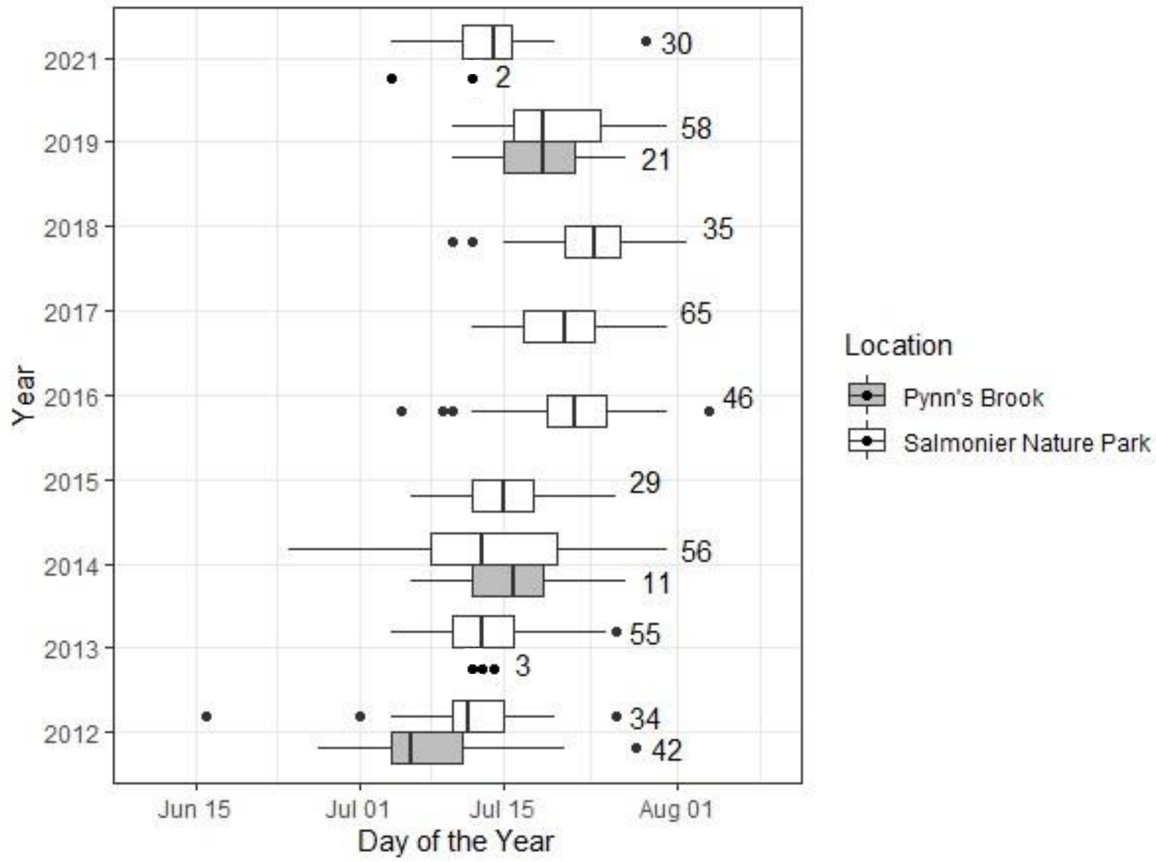


Figure 4.3 Distribution of little brown myotis (*Myotis lucifugus*) parturition dates in each year in Newfoundland, Canada as measured at Pynn's Brook and Salmonier Nature Park. Boxes represent the 50 % quantile range and whiskers represent the 95 % quantile range. There were no individuals that met the minimum criteria in Pynn's Brook in 2015, 2016, 2017, and 2018.

4.4.2 Validation of reproductive status

We report strong agreement between our parturition estimates and in-hand assignment of reproductive individuals. When a recapture occurred within 10 days before or after the estimated parturition date, there was agreement between reproductive status assigned at recapture and estimated parturition date in 15 of 16 bats (93.8 % correct). One bat was designated as pregnant during recapture processing three days after the estimated parturition date. Expanding to 20 days (Table 4.2) between recapture and parturition date, recapture reproductive status assignment agreed with estimated parturition date in 35 of 37 bats (94.6 %).

For bats where no parturition date could be estimated, we were not able to reliably designate these bats as nonreproductive. Of twenty bats where no parturition date was detected and the bat was recaptured between 5 July and 30 July of that year, only six of these bats were suspected to be nonreproductive during in-hand processing (Table 4.2).

Table 4.2. Summary of agreement between expected reproductive status based on in-hand assessment and estimated parturition date using changes in nighttime roost revisit patterns of little brown myotis (*Myotis lucifugus*) in Salmonier Nature Park and Pynn's Brook Newfoundland, Canada. For expected pregnant and expected lactating bats, agreement was assessed based on in-hand assessments within 20 days of estimated parturition date while for expected nonreproductive bats, agreement was based on in-hand assessments between 5 July and 30 July.

Agreement with in-hand assessment	Expected Pregnant	Expected Lactating	Expected Nonreproductive
Correct	13	22	6
Incorrect	1	1	14

4.4.3 Parturition location and movement

Based on the most visited box on the day of parturition, individual bats used up to five different boxes for parturition across all years they were studied. One bat used five different boxes for parturition, one bat used four different boxes, 11 bats used three different locations and 65 bats used two different locations. These numbers represent a minimum estimate as it is possible that more locations were used and that is why parturition was not detected at our monitored roost boxes.

Across all bats and years where parturition was estimated, only 17.0 % of bats did not appear to move their pups at all in the three weeks following estimated parturition. Many bats did appear to move their pups with 54.6 % of bats suspected to have moved a pup between boxes on the same pole at least once, and 46.6 % of bats suspected to have moved a pup among poles within a small zone of the study area at least once. Surprisingly, potential pup movement between poles was more frequent by total count than pup movement between boxes on the same pole in Pynn's Brook (Figure 4.4). The same pattern was not seen at Salmonier Nature Park. In Salmonier Nature Park, pup movement between boxes on the same pole was the most frequent by total count, followed by pup movement between poles within the same zone, then pup movement between the closer zones of HQ and VC (Figure 4.4). Potential pup movement to HB after parturition occurred at least once in only 3.4 % of individuals (14 of 408) while potential pup movement among HQ and VC occurred at least once in 31.4 % of individuals.

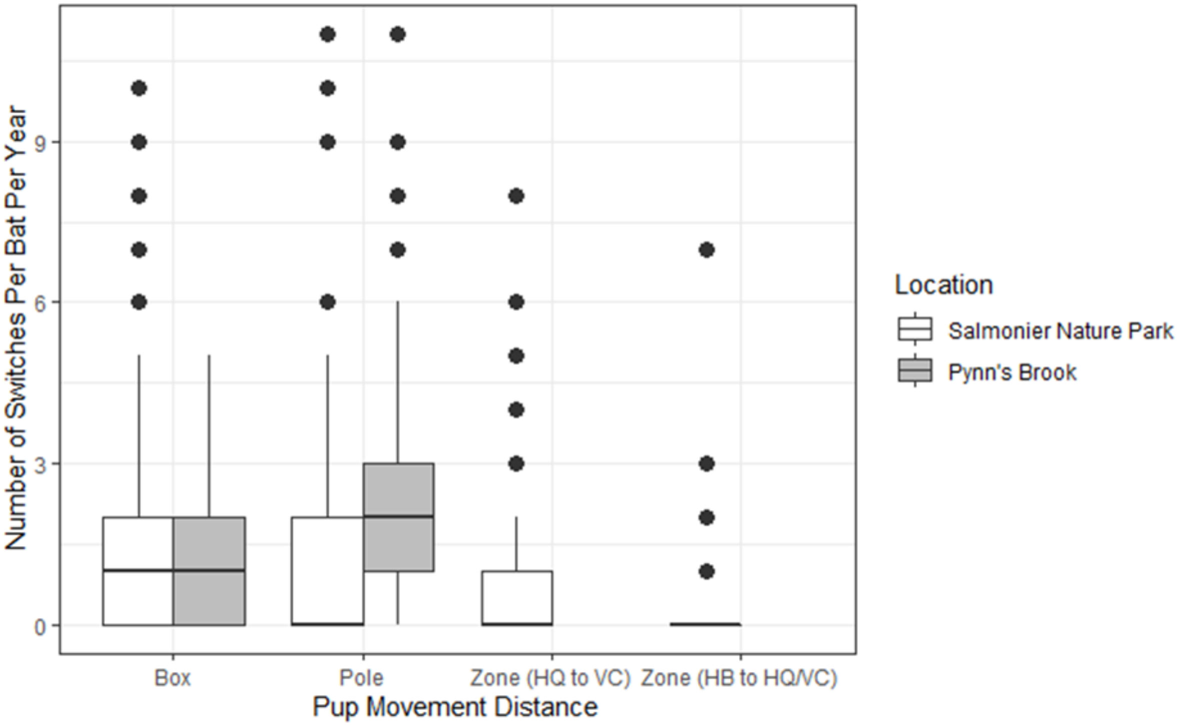


Figure 4.4 Observed frequency of suspected pup movement based on changes in the most revisited box by adult female *Myotis lucifugus* in Newfoundland Canada between 23:00 and 03:00. Counts are based on 21 nights following estimated parturition to represent when pups were expected to not yet be volant and thus have to be carried by their mothers. “Box” movements represent moves between two monitored roost boxes on the same pole, “Pole” movements represent moves between two poles within the same area of the study site (distance < 50 m) and the maximum observable movement distance in Pynn’s Brook. For Salmonier Nature Park, “Zone” movements are also included which are separated into headquarter (HQ) to visitors’ centre (VC), representing moves between zones separated by ≈ 100 m), and movements between HQ or VC and the more distant private property on the study site (HB; max distance ≈ 1 km).

4.4.4 Annual and individual variation in parturition dates

Parturition dates varied greatly among years even within individuals in both Salmonier Nature Park and Pynn’s Brook. The global model was the best model of our candidate set with an Akaike weight of 99.4 % and corrected R-squared of 0.57. This model contained effects of temperature, precipitation, an interaction of these terms, the number of days with wind gusts over 30 km/h, minimum age, and location. The weather hypothesis model, which did not include the factors of minimum age and location, was our second-best performing model (Table 4.2) with ∆AIC of 10.42, an Akaike weight of 0.5 %, and a corrected R-squared of 0.55. Greater precipitation was related to earlier parturition dates. The interaction of precipitation and minimum temperature indicated that years with combined colder and wetter conditions resulted in later parturition dates. More days with wind gusts greater than 30km/h also appeared to result in later parturition dates. Minimum age had a slight effect whereby older individuals had slightly later parturition dates while capture location did not appear to be an important factor in parturition timing between the two assessed locations (Table 4.3).

There was considerable interannual variation in parturition dates within individuals. Parturition in some individuals appeared to be consistently later or earlier than the rest of the individuals in the same location in multiple years but this trend was not seen in many individuals in this study population (Figure 4.5). The random effect of individual had a variance of 14.2 (± SD 3.4) but this was small relative to the overall residuals of the model 25.8 (± SD 5.1).

Table 4.3 Conditional Akiake's Information Criterion (AICc) values and the difference from the top-ranked models (ΔAIC), Akaike weights (w_i) for all models and the sum of Akaike weights (Σw_i) for models comprising ≥ 95% of Akaike weights explaining the parturition date of little brown myotis (*Myotis lucifugus*) in Pynn's Brook and Salmonier Nature Park Newfoundland, Canada between 2012 and 2021. All models except the null model also included individual as a random effect.

Hypothesis	K	AICc	ΔAIC	w_i	Σw_i
Global (Weather + Torpor + Experience + Location)	9	2932.61	0	0.994	0.994
Weather (Temperature + Precipitation + Temperature*Precipitation + Wind)	7	2943.04	10.42	0.005	
Torpor (Temperature + Precipitation + Temperature*Precipitation)	6	2996.01	63.40	1.71×10^{-14}	
Experience (Minimum Age)	4	3012.42	79.81	4.67×10^{-18}	
Location (Capture area)	4	3073.01	140.40	3.25×10^{-31}	
Null	2	3133.31	200.70	2.62×10^{-44}	

Table 4.4 Parameter estimates and standard errors for the top, global model explaining the parturition date of little brown myotis (*Myotis lucifugus*) in Pynn's Brook and Salmonier Nature Park Newfoundland, Canada between 2012 and 2021.

Parameter	Estimate	Standard Error
Proportion of Days with maximum windspeed > 30 km/h	23.36	6.05
Precipitation	-17.07	3.95
Temperature*Precipitation	0.75	0.17
Minimum Age	0.72	0.19
Temperature	-0.45	0.54
Capture Location (Salmonier)	0.43	1.26

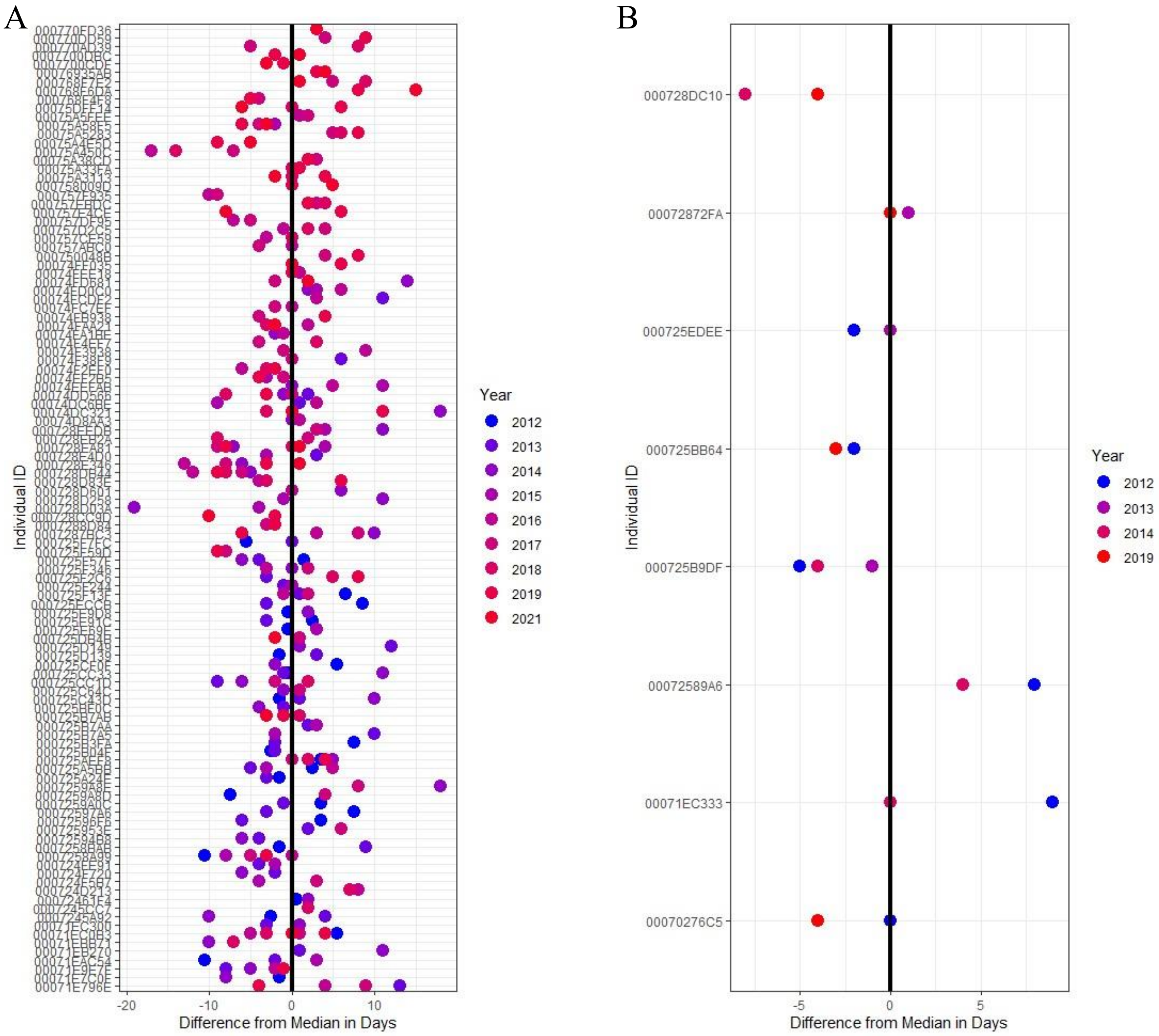


Figure 4.5 Difference in individual parturition dates from the population median, represented as a solid black line, in A) Salmonier Nature Park and B) Pynn's Brook in each year for little brown myotis (*Myotis lucifugus*) where parturition date was estimated in at least two years using a breakpoint in the mean of nighttime roost revisit. Each point represents the difference in estimated parturition date from the population median in the corresponding year and the colour of the dot represents the year. Individuals are ordered bottom to top based on their earliest parturition date across all years.

4.5 Discussion

By using changes in nighttime roost revisit behaviour, we were able to estimate parturition dates for 426 individuals across two locations and multiple years. As expected, parturition was asynchronous among individuals within sites and varied within individuals between years at each of Salmonier Nature Park and Pynn’s Brook, Newfoundland. Among years, spring-time weather conditions and minimum age explained 57.4 % of the variation in timing of parturition. The apparent variation in parturition date in response to spring-time weather conditions means that parturition timing, and thus reproductive success may be susceptible to anticipated changes in weather patterns due to global climate change.

For individuals where parturition dates were estimated, the parturition date and assignment of the individual agreed in 93.8 % of cases when in-hand assessments occurred within 20 days of the estimated parturition date. Although this sample size was small, this provides us with confidence that the changepoint method can reliably designate reproductive individuals and the correct reproductive period. Further work with recaptures closer to estimated parturition dates and captures of juveniles at the onset of volancy would help to solidify this method. Meanwhile, bats for which a parturition date could not be detected could not be reliably designated as nonreproductive. To make these sorts of conclusions, we would require greater coverage of potential roosting sites within each study location. An evaluation of nighttime roosting behaviour in known, nonreproductive individuals based on capture assessments would also assist in eventually identifying nonreproductive individuals from roost use data alone.

For individuals for which parturition date could be estimated, parturition dates varied greatly from year to year. The interaction of temperature and precipitation from mid-April until the beginning of parturition had an expected influence such that colder and wetter springs resulted in later parturition. These conditions favour torpor use in bats therefore delaying parturition (Dzal and Brigham 2013) as demonstrated in little brown myotis (Burles et al. 2009). Spring conditions also may affect departure from hibernacula and therefore parturition timing as demonstrated in Daubenton's bats (*M. daubentoniid;* Lučan et al. 2013). In our system, greater precipitation alone resulted in earlier parturition. This may be due to an increase in insect abundance with greater levels of precipitation, which has also previously been associated with higher adult survival (Frick et al. 2010). Cumming and Bernard (1997) found that African bat species timed parturition such that juveniles were weaned right before maximum insect abundance. Given that there may be a delay between increased precipitation and peak insect abundance, bats may be timing parturition to improve survival outcomes for their young. However, given the large amount of precipitation in Newfoundland, this effect may be limited such that eventually additional precipitation would be detrimental to insect abundance and bat survival, therefore delaying parturition or reducing parturition success as reported by Burles et al. (2009). Finally, an increase in the proportion of days with winds over 30 km/h appeared to delay parturition. This effect may be due to high winds and storm events influencing one or both of torpor use and insect availability as well as the ability of bats to fly and therefore forage in these conditions.

As climate change predictions call for an increase in global mean temperature, there is the potential for a decrease in cold and wet spring conditions and thus for parturition timing to become progressively earlier which may improve survival outcomes for juvenile little brown myotis in Newfoundland. This shift was not seen in our 10-year study although this time period may simply be too short to demonstrate these effects directly. This expected shift was found over a 40-year period in bats in the Czech Republic where warming temperatures were correlated with a shift to earlier parturition timing in Daubenton's bats (Lučan et al. 2013). These projected future changes in temperature may change which roosts are most suitable for having pups. Conversely, climate projections currently predict an increase in extreme precipitation events in the next 50 years (Abbasnezhadi et al. 2020). Given the large amount of precipitation already occurring on the island of Newfoundland, an increase in precipitation, particular extreme precipitation events may be detrimental to insect availability and thermoregulation, and therefore little brown myotis reproduction. Previous study has shown a decrease in little brown myotis reproductive success with increased precipitation (Burles et al. 2009) possibly attributable to fewer insects flying during rain events (Anthony et al. 1981) and interference with echolocation abilities (Griffin 1971; Grindal et al. 1992). These extreme weather events may also include stronger wind gusts, which we find here to delay parturition, or even impact the immediate survival of adult females. It is unclear why some bats use certain roosts for parturition, or move pups between roosting locations, but it remains that these patterns suggest that a community of roost are advantageous for population viability. Roosting options in the face of changing environmental conditions will allow a behavioural buffer for animals to adjust to variable climate conditions.

Parturition timing in Pynn's Brook, Newfoundland was on average six days earlier than in Salmonier Nature Park, however, based on our analysis, location did not appear to be an influential factor in predicting parturition timing. Despite that Pynn's Brook is farther north than Salmonier Nature Park with lower minimum temperatures, there is generally lower precipitation in Pynn's Brook than Salmonier Nature Park. It is uncertain whether differences in climatic conditions between the two locations are biologically meaningful to cause differences in parturition timing and success, and what other environmental differences between the two locations may impact little brown myotis reproductive patterns. As in moose, the success of bats in these different locations may be aided by their site fidelity (Neumann et al. 2020), as they return to the same maternity locations and are familiar with both available roosts and weather and insect abundance patterns.

Minimum age did appear to have a slight effect on timing of reproduction where individuals with a higher minimum age had later parturition dates, warranting greater future study into the effects of age on reproductive timing and success. Given that we do not know the exact age of the individuals assessed here, it is uncertain whether our study truly reflects a relationship between parturition timing among different aged individuals rather than a change in parturition timing within individuals as they age. Further, given that parturition dates were progressively later from 2012-2019, this observed minimum age effect may be due to other changes in the environment over the study period that aren't currently accounted for with our models. In relation to exact age, it is additionally possible that there is a nonlinear effect of age on parturition timing and success, such that there is an optimal age range where females are best able to give birth to offspring early in the year after a few years of experience but before any detrimental effects of older age as seen in pinnipeds (Hastings and Jemison 2016). We are not able to assess these long-term effects here due to only having a few years of estimated parturition dates for most individuals compared to the decades-long life expectancy of the species (Florko et al. 2017).

Within years and within locations, parturition was expectedly asynchronous with some years more variable than others. Whether an individual was consistent between years also varied by individual. Many individuals changed their parturition timing greatly between years although there were a few individuals that were consistently among the earliest or latest parturition dates each year relative to the rest of the population. This variation in the consistency of individual parturition timing was reflected in our mixed effects model as although the random effect of individual had a low standard deviation relative to the predicted value, the variance attributed to individual was small compared to the remaining overall unexplained variance in our models. Thus, there are likely other factors that better explain why individual parturition timing varies within and between years that we have not included in this study. Additional factors that could influence the timing of parturition on an individual basis include previous reproductive success, the fat stores accumulated in the previous year, winter weather conditions, and spring foraging efficiency as these would influence the energy stores females have available for pregnancy and lactation (Racey and Swift 1981; Kurta et al. 1989). As we do not know where the bats in our study system hibernate, we are unable to assess many of these factors. Similarly, variation in the timing of parturition will influence when bats leave for hibernation as the lactation period cannot be shortened but only extended in response to food scarcity (Racey 1982).

Although synchronicity of parturition has been shown to correlate with better reproductive success both in bats (Burles et al. 2009) and other mammal species such as bison (Jones et al. 2010), variation in the above factors and parturition timing within the population may assist in ensuring population persistence through changing climate conditions and increasing frequency of extreme weather events. Just as varied individual behaviours in reproductive timing will provide resiliency for the population against changing climatic effects, it is also important to provide variation in habitat, particularly roosts for parturition and lactation as weather conditions continue to change. These habitat options will provide opportunities for behavioural compensation to weather conditions. Thus, on the island of Newfoundland, the continued protection of natural habitat, particularly forests with dead-standing trees and anthropogenic roosting structures, is imperative. Better information is needed on population reproductive success in both study locations, including information on the proportion of reproductive individuals, survival of offspring through winter hibernation, and how offspring survival is related to the parturition timing and roosting decisions of the mother. These efforts and this information would greatly assist both in understanding the reproductive ecology of little brown myotis in Newfoundland, and in best directing efforts to maintain stable populations.

Chapter 5

Changes in roosting decisions and group structure following parturition in little brown myotis (*Myotis lucifugus*)

5.1 Overview

In many temperate animals, reproductive cycles coincide with seasonal weather changes and cause changes in behaviours such as movement and habitat selection. In social species, these changes in physiological and environmental conditions can alter the costs and benefits of social interactions, impacting the structure of animal groups. In little brown myotis (*Myotis lucifugus*), a gregarious bat occupying much of North America, the pregnancy and lactation phases of the reproductive cycle present different challenges to energy balance and have been shown to result in changes in maternal movement patterns including reduced foraging distances. As such, we hypothesized that differences between reproductive phases alter the roost switching decisions of individual bats and therefore the overall group structure of little brown myotis maternity colonies. We observed that adult females were less likely to switch roosts during the lactation period even when accounting for changing weather conditions. This shift in roost switching behaviour may be the source of observed differences in group structure between reproductive periods. We reported a decline in network cohesiveness, but no meaningful variation in individual roost fidelity and association strengths of dyads between reproductive phases. These results support the contention that females prioritize investment in reproduction over maintaining roosting patterns and social needs may change during lactation.

5.2 Introduction

Animals modify their behaviour in response to seasonal changes in both the environment (e.g. weather) and their physiology (e.g. reproductive condition). For many taxa, behavioural patterns change at parturition as time invested in parental care and promoting offspring survival increases while strategies to reduce parent mortality may decrease. Strategies to maximize fitness vary interspecifically and may include selecting areas of lower predation risk when offspring are most vulnerable at the expense of forage quality for the mother (*Alces alces;* Severud et al. 2019), prioritizing forage quality over predation risk to meet the energetic demands of lactation (*Cervus elaphus;* Berg et al. 2021), or a reduced home range size during pup-rearing (*Canis rufus;* Hinton and Chamberlain 2010).

The benefits of social relationships and group living change with physiological requirements such that the interactions between individuals, group size and composition, and social behaviours may also vary with an individual's changing reproductive status (e.g. Rose and Croft 2020, Shizuka et al. 2014). In addition to decisions about habitat use, animals may make decisions about their social environment to improve the probability of offspring survival. For example, ungulates often socially isolate prior to parturition (e.g. Karsch et al. 2016; Berg et al. 2021) while similarly in Scottish blackface sheep (*Ovis aries*), individuals with offspring take a more peripheral position in a flock (Pérez-Barbería and Walker 2018). The nature of interactions between individuals may also vary with breeding season, breeding status, and sex. For instance, females may increase agonistic interactions to protect offspring while males increase affiliative interactions to improve access to breeding opportunities (Kusch and Lane 2021) or, mothers may increase their distance from conspecifics while nonmothers in the same group do not (Pérez-Barbería and Walker 2018).

Temperate bats have distinct seasonal cycles of movement and reproduction which includes a spring-summer season where females aggregate in large maternity groups (Fenton 1997; McCracken and Wilkinson 2000). At least some females switch roosts frequently throughout this period, resulting in changes in the composition of roosting subgroups each day (Fenton and Barclay 1980; Willis and Brigham 2004). While meeting the energetic demands of pregnancy and lactation, bats balance energy conservation via torpor with its impact on the timing of parturition and offspring survival (Racey and Swift 1981; Frick et al. 2010; Dzal and Brigham 2013), and regularly employ social thermoregulation to minimize torpor use (Willis and Brigham 2007; Webber and Willis 2018). Accordingly, female bats select roosts with warmer microclimates or, in the case of roosts with cooler microclimates, may select roosts that are used by a greater number of conspecifics to facilitate social thermoregulation. Lactation represents a period of higher energetic demand for adult females than pregnancy (Kurta et al. 1989), but as ambient temperature is also typically higher during lactation compared to pregnancy, it is not clear how energetic demands of different reproductive periods may influence bat roost selection. Not only are roosting conditions influenced by thermoregulatory needs, but bats also need to balance foraging and parental care after parturition. Females travel shorter distances during foraging following parturition as females frequently return to roosts to nurse their pups (Henry et al. 2002). Changes in foraging behaviour, along with the limited mobility of pre-volant young may impact the ability of females to move to the most optimal roost each day.

Bat roosting decisions also influence, and are influenced by, social relationships (e.g., Wilkinson 1985; Chaverri et al. 2007; Kerth 2008; Wilkinson et al. 2019; Mavrodiev et al. 2021). Individuals may select roosts based on the presence of certain conspecifics and thereby influence their social environment by the information they bring, or physically by their effect on space and roost temperature. Social grouping may confer additional benefits, such as energy conservation, cooperation during foraging, or by reducing inter-individual conflict (Carter and Wilkinson 2013). The benefits and effects of group behaviour, and thus the structure of bat groups may also change between seasons. Variation in network structure and subsequently social relationships between seasons and reproductive periods has been shown in other social mammal species including Tasmanian devil (*Sarcophilus harrissi*; Hamede et al. 2009), rhesus macaques (Brent et al. 2013), and black-tailed prairie dogs (*Cynomus ludovicianus*; Kusch and Lane 2021) however these studies focused on differences between mating and nonmating seasons in both male and female individuals rather than relationships between only females. Previous study in female bats has shown greater aggregation of individuals at roosts during pregnancy compared to lactation in some species (i.e., *Myotis lucifugus*; Willis and Brigham 2004; Webber et al. 2016), but smaller roosting groups during pregnancy in others (*M. septentrionalis*; Patriquin et al. 2010).

Little brown myotis (*Myotis lucifugus*) colonies are typically comprised of interconnected and sympatric social communities, where individuals do not interact with frequencies entirely explained by roost fidelity (Sunga et al. 2022 [Chapter 3]) . As bats return to the same roosts within and between years, there is the potential for social familiarity and preferences to form among individuals. We hypothesized that changes in the physiological requirements of female little brown myotis due to reproductive condition will affect the roosting decisions and social structure of a maternity colony. Based on this hypothesis, we tested the prediction that (1) the likelihood of adult female bats using the same roost on consecutive days would be highest during lactation, when females have nonvolant offspring, even when accounting for weather variation between days. We also predicted (2) that roost fidelity, the frequency with which individuals used each roost in the study area, would change between pregnancy and lactation as individuals become more selective about which roosts to use and thus use fewer monitored roosts during lactation. Finally (3), we predicted that the network-level patterns of co-roosting associations in the maternity colony would change between the pregnancy and lactation periods.

5.3 Methods

5.3.1 Data collection

Using mist nets (Avinet, Dryden, New York, USA) and harp traps (Austbat Research Equipment, Lower Plenty, Victoria, Australia) little brown myotis were captured in and around Salmonier Nature Park (n = 1604; Lat: 47.3º, Long: -53.3º) Newfoundland, Canada from 2012-2021 between May 15th and August 19th of each year. Reproductive status (Racey 1988) and age (Anthony 1988) were determined for each individual and then a passive integrative transponder (PIT) tag (0.09 g; EID-ID100 implantable transponders, EIDAPInc, Sherwood Park, Alberta, Canada and Trovan Electronic Identification Systems, North Ferriby, UK) was subcutaneously implanted between the scapula. Transponder antennas (LID650, Dorset Identification, The

Netherlands) were deployed at eleven roost boxes within a 1.1 km^2 area from April to September each year to collect data on roost use. One roost box was placed on a building while the other ten were paired on five poles throughout the study area. The last detection before sunset, but after sunrise of the same day, was used to infer the roost box in which an individual spent the day and represents an ‘observation’. Due to potential errors in PIT-tag recording, an unknown number of unmonitored roosts, and an unknown proportion of the population being untagged, it is expected that many instances of roost use remain unrecorded.

Males were not included in these analyses as they were rarely detected at maternity roosts and do not have the same variation in energy requirements as females throughout the maternity season (Kurta et al. 1989). Juveniles were excluded as it is uncertain whether juvenile movements are independent from their mothers (Wilkinson 1992; Ripperger et al. 2019), and juveniles would only be present for the second portion of the maternity season. Data were constrained to include detections between 15 May and 15 August of each year and only individuals that were observed >10 times in each of the pregnancy and lactation reproductive periods in a single year were included. For each year, the population parturition date was the date when at least 25 % of females in which parturition could be detected were expected to have had their pups (Table 5.1; Sunga et al. *in prep* [Chapter 4]). As parturition is relatively asynchronous, this cutoff was chosen to reduce the number of individuals already lactating included in the parturition period while also ensuring that there were not many still pregnant individuals for a significant portion of the lactation period. Individuals were included in each year in which they met these criteria, and so some individuals were included in multiple years of analysis.

Table 5.1 The number of individuals included in each year of analysis by meeting the criteria of at least 10 observations at monitored day roosts both before and after the parturition cut-off date (25th percentile of population parturition dates; Sunga et al *in prep* [Chapter 4]).

Year	Parturition Cut-off Date	Number of Individuals
2012	July 2nd	56
2013	July 9th	99
2014	July 7th	228
2015	July 11th	74
2016	July 17th	145
2017	July 16th	166
2018	July 20th	117
2019	July 14th	138
2021	July 10th	97

5.3.2 Variation in daily roost switching behaviour

To assess the extent to which reproductive period may influence daily roosting decisions in bats, we applied an information theoretic approach using Conditional Akaike's Information Criterion (AIC_c; Burnham and Anderson 2002) to explain variation in the likelihood of reusing the same roost on consecutive days based on logistic models. We quantified the probability of individual bats reusing the same roost on consecutive days in each reproductive period and in response to daily weather conditions between 15 May and 15 August. This analysis included information for all individuals for which we observed day roosting in our monitored boxes on consecutive days on at least one instance. As hourly precipitation data was not available for the entire study period, this analysis included data only to 2017, with dates included in the analysis only if precipitation data was available on consecutive days.

Each bat on each day was assigned a 0 or 1 based on its location on the consecutive day where a 1 indicated a bat that was in the same roost on day one and day two while a 0 indicated that a bat was in a different, monitored roost on day one than on day two. Any bats that were recorded on day one, but not recorded on day two were not included in the analysis due to the possibility that the disappearance may actually be a missed read at the same roost, creating contamination of our dataset. Although it is expected that the number of bats that reuse a roost between consecutive days may be underestimated due to missed observations, it is expected that these observations were missed randomly and do not covary with our independent variables.

Our candidate model set consisted of multiple, nonmutually exclusive explanations for the roosting decisions of female bats. A candidate model of thermoregulatory effects driving roost use included change in mean nightly temperature between consecutive days (ºC), change in mean nightly absolute humidity between consecutive days (g/m^3), and an interaction between these terms as it is expected that a night that is both cold and humid would pose a different thermoregulatory challenge than a night that is cold and dry (Frick et al. 2010). Both temperature and absolute humidity were calculated based on the average of hourly recordings taken between 02:00 and 07:00 on each day, when we expected bats would make their day roosting decisions. The change in temperature (ΔCº) and change in absolute humidity (ΔAH) was then calculated as the absolute difference between the mean on each day, with the expectation that a greater change in either of these variables would decrease the likelihood of a bat reusing the same roost. This is because roosts may have different microclimates and therefore if weather drives, at least in part, roost selection decisions, individuals are less likely to reuse the same roost as weather conditions show greater variability one day to the next. A candidate model of flight conditions included maximum nightly windspeed and total precipitation, as it was expected that very high winds or heavy precipitation would result in more energetically expensive flight and increase the likelihood of bats reusing a roost. The maximum nightly windspeed was calculated based on the maximum reported wind gust between 02:00 and 07:00 on each day, and total precipitation as the sum of all precipitation also between 02:00 and 07:00. Finally, a candidate model of maternal care was tested broadly with a binary variable of whether the date was before (0) or after (1) the population parturition date estimate, separating the pregnancy and lactation periods for this study (Table 5.1), where bats were predicted to more frequently reuse a roost on consecutive days during the lactation period, when more females are expected to be nursing young. The random effect of year was included to account for annual changes between years based on factors such as spring climate conditions and timing of emergence from hibernation (Willis et al. 2006; Frick et al. 2010; Lučan et al. 2013), and it is unknown whether roost preferences vary annually.

A random effect of individual was also included to account for the fact that some individuals may be included in this analysis more than others. All weather data with the exception of hourly precipitation information were obtained from the Environment Canada weather station at St. John’s International Airport, approximately 57 km northeast of Salmonier Nature Park, through “weathercan” (LaZerte and Albers 2018). Precipitation data was provided from the Pippy Park weather station (Government of Newfoundland and Labrador, Department of Environment and Climate Change, Water Resources Management Division (WRMD), approximately 54 km northeast of Salmonier Nature Park. Combinations of each of these candidate models were also tested. Additional two-way interaction terms were not included to avoid overfitting of models without clear biological precedent. Further, due to a correlation between variables, ΔAH and precipitation were never included in the same model and precipitation was omitted from the global model and the combined model of maternal care and flight condition model. We then selected the 95 % confidence set of models, and applied multi-model averaging of variable estimates (Burnham and Anderson 2002).

5.3.3 Variation in roost fidelity and dyadic roosting relationships with reproductive period

To assess possible changes in roost preferences between reproductive periods in each year, we generated matrices of roost fidelity, the proportion of days in which individuals roosted in each monitored roost box. For each reproductive period-year combination, we generated an individual-by-roost matrix populated with the proportion of days an individual bat was observed in each monitored calculated against the total number of days that bat was observed. We then compared these roost fidelity matrices between reproductive periods for each year using a Spearman Rank Correlation to quantify the extent to which roost preferences during pregnancy may be indicative of roost preferences during lactation.

Next we calculated the association strength between pairs of individuals (dyads) based on the simple ratio index (SRI) which is a proportion of the number of instances a dyad were found to be associating compared to the proportion of instances dyads were not associating (Cairns and Schwager 1987; Whitehead 2008). We applied the gambit-of-the-group assumption (Whitehead 2008) such that dyads were assumed to be associating if they were recorded in the same roost on the same day. To assess associate preferences, we generated an individual-by-individual matrix with values corresponding to the SRI between each dyad using the function *get_network* in the package “asnipe” (Farine 2013). In each year, we conducted a Mantel test using the function *mantel* in the package “ecodist” (Goslee and Urban 2007) with 10,000 permutations to test the similarity of associate preferences before and after parturition. Mantel R was calculated using the Spearman Rank Correlation to account for skew in the distribution of SRI values.

We then performed a simple linear regression to determine if the correlation in roost use by individuals before and after parturition was predictive of the correlation in SRI between reproductive periods. This allowed us to make inference on how a change in roost preferences may impact changes in social relationships and vice versa.

5.3.4 Variation in network structure among reproductive periods

For each reproductive period-year network based on co-roosting associations, we calculated several metrics. The coefficient of variation of the SRI (CV SRI) was calculated by computing the standard deviation of all SRI values over the mean of all SRI values then multiplying by 100. Graph density, a proportional measure of the number of connections present in the network versus the number of potential connections, was calculated using the function *edge_density*. Clustering coefficient, the probability that individuals with a common associate are also themselves connected (Wey et al. 2008) was calculated with the function *transitivity* in the package “igraph” (Csárdi ands Nepusz 2006). We also calculated community assortativity (R_{com}) a measure of the reliability of the assortment of individuals between potential social communities (Shizuka and Farine 2016). For each year, we conducted a paired t-test for each of graph density, clustering coefficient, and CV SRI to determine if there was a significant difference before and after parturition.

All analyses were conducted in R version 4.0.0 (R Core Team 2020).

5.4 Results

Four hundred and sixty adult female little brown myotis met the criteria of having at least ten observations before and after the 25th percentile of parturition dates in a single year (Table 5.1). Of the 460, 291 were included in multiple years and one individual was included in all nine years. Numbers of tagged individuals who we suspect entered or left our monitored system following parturition, individuals for which there were at least ten day roost observations in one reproductive period but zero observations in the other reproductive period in a single year, did not appear to correlate with the timing of the parturition cut-off date.

5.4.1 Variation in daily roost switching behaviour

Results of the model selection analysis suggested the candidate model that included maternal care and thermoregulation best explained the probability of bats reusing the same roost on consecutive days (AIC_c = 21530.8, model weight = 0.64), and the global model which also included flight conditions was the second best (AIC_c= 21532.0, model weight = 0.36) and only other model included in the 95 % confidence set (Table 5.2). Our results showed that changes in absolute humidity between consecutive days and reproductive period were significant parameters for predicting the probability of bats using the same roost (Table 5.3). Our results specifically showed that a greater change in absolute humidity between consecutive days reduced the likelihood that a bat would reuse a roost (Figure 5.1A). Also, as predicted, bats were more likely to reuse a roost on consecutive days following parturition (Figure 5.1). Model-averaged parameter estimates revealed temperature, maximum wind gust speed, and the interaction between temperature and humidity were not significant parameters for predicting the probability of using the same roost on consecutive days as model estimates and standard errors overlapped zero (Table 5.3). However, it must be noted that there are likely many unaccounted for factors that also explain at roost switching behaviour as model fit was low, with a corrected R^2 of 0.24 for both the global model and the model including thermoregulation and maternal care.

Table 5.2 Results of Akaike's Information Criterion (AIC_c) analysis of candidate models explaining the probability of female *Myotis lucifugus* reusing the same roost on consecutive days in Newfoundland Canada. The difference from the top-ranked models (ΔAIC), Akaike weights (w_i) for all models and the sum of Akaike weights (Σw_i) for models comprising ≥ 95 % are also calculated. The maternal care model includes reproductive period (pregnancy or lactation) and a random effect of year, the thermoregulation model includes change in temperature, change in humidity, and an interaction between changes in temperature and humidity, and the flight conditions model includes maximum wind gust and total precipitation. Change in temperature was recorded in degrees Celsius, change in humidity was calculated as absolute humidity, maximum wind gust was measured in kilometers per hour, and precipitation was measured in millimeters between 2:00 and 7:00. Total precipitation and change in absolute humidity were not included in models together due to a correlation between these variables. All models also included a random effect of individual.

Candidate Model	K	AICc	ΔAIC	w_i	Σw_i
Maternal Care + Thermoregulation	7	21530.8	0	0.64	0.64
Global Model (Maternal Care + Thermoregulation + Flight Conditions)	8	21532.0	1.2	0.36	1
Maternal Care	4	21576.9	46.0	< 0.001	
Maternal Care + Flight Conditions	6	21579.3	48.5	< 0.001	

Flight Conditions + Thermoregulation	6	21808.2	277.4	< 0.001
Thermoregulation	5	21810.6	279.7	< 0.001
Flight Conditions	4	21868.3	337.4	< 0.001
Null	1	23048.1	1517.3	0

Table 5.3 Model-averaged parameter estimates and standard errors to predict the probability of female *Myotis lucifugus* reusing the same roost on consecutive days in Newfoundland, Canada. Parameters are averaged from all models included in the 95 % confidence set which included a model of thermoregulation (changes in absolute humidity and temperature) and the global model.

Parameter	**Estimate**	**Standard Error**
Reproductive Period (Pregnancy)	-0.57	0.04
ΔHumidity	-53.52	19.31
ΔTemperature	-0.003	0.02
Maximum Wind Gust	6.33×10^{-4}	7.04×10^{-4}
ΔTemperature *ΔHumidity	-2.92	3.49

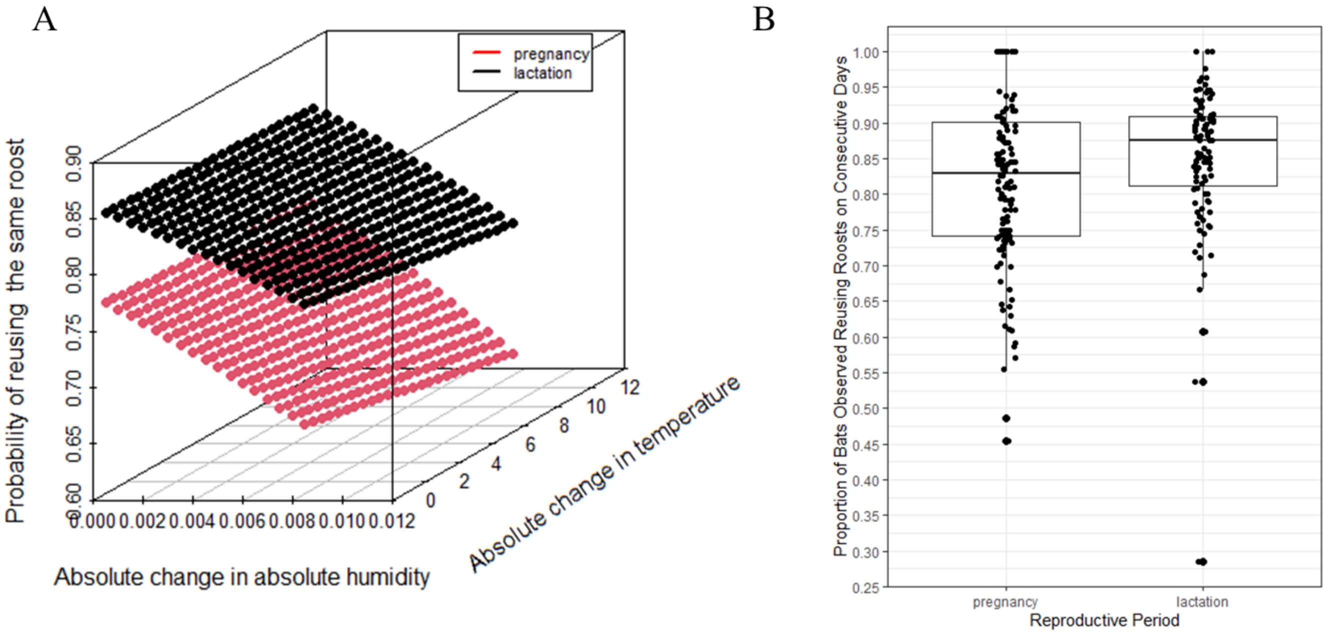


Figure 5.1 A) Predicted probability of bats reusing the same roost on consecutive days as a function of change in absolute humidity from one day to the next, change in temperature from one day to the next, and reproductive period. Changes in temperature had little effect on the probability of roost reuse while change in absolute humidity was highly influential. B) The proportion of observed bats that reused a roost on consecutive days across all dates and weather conditions in the pregnancy and lactation periods from 2012-2017, the period when hourly weather data was available. Each point represents the proportion of bats that reused the same roost on any given consecutive day period.

5.4.2 Variation in roost fidelity and dyadic roosting relationships with reproductive period

On average, roost fidelity for individuals were significantly correlated (average = 0.71, SE = 0.01, range: 0.65—0.78) before and after parturition based on Spearman rank correlation ($p < 0.001$). This means that there was moderate correlation in the frequency that individual bats used each monitored roost before and after parturition, although roost use patterns of some individuals changed between reproductive periods.

Association strengths (SRI) between dyads during the pregnancy period were significantly correlated with association strengths during the lactation period ($p < 0.001$), indicating that, on average, relationships between females were also consistent throughout the maternity season. However, there was considerable variability among dyads as some individuals that associated frequently prior to during the pregnancy period never associated during lactation and vice versa. The average Mantel R score based on a Spearman Rank Correlation of SRI between reproductive periods was 0.56 (Range = 0.49-0.65; SE = 0.02) indicating that while some dyads showed consistent association patterns throughout the entire maternity period, others experienced changes in association patterns between pregnancy and lactation. These changes in association patterns may be weakly related to changes in individual roost use patterns, as years with greater stability in roost use patterns between reproductive periods weakly showed greater stability association patterns between dyads based on a linear regression analysis (Figure 5.2; $\beta = 0.90$, SE = 0.36, $p = 0.04$). Analyses were also run using the half weight index (HWI) and yielded comparable results.

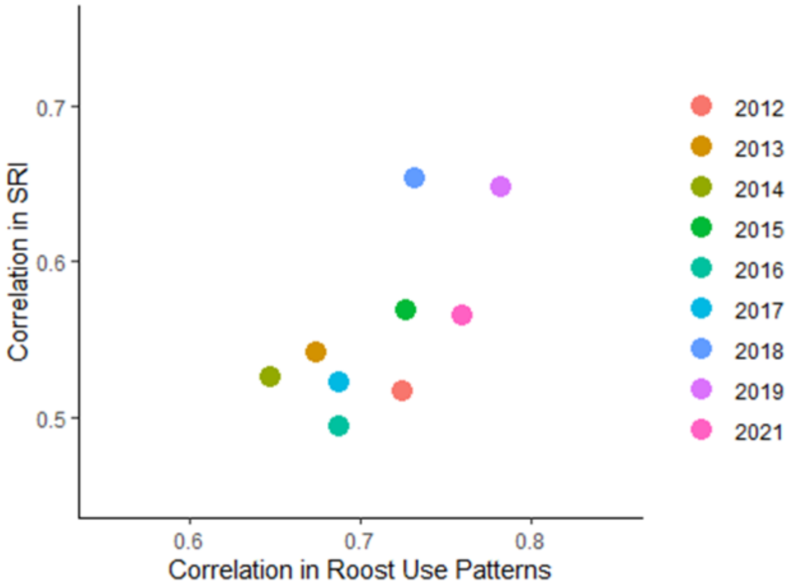


Figure 5.2 Relationship between correlation in roost use patterns and correlation in association strengths (Simple Ratio Index; SRI) between the pregnancy and lactation periods of each year. Linear regression revealed a significant but weak effect of correlation in roost use patterns between reproductive periods on the similarity in association strengths (SRI; $\beta = 0.90$, SE = 0.36, $p = 0.04$, $R^2 = 0.39$).

5.4.3 Variation in network structure among reproductive periods

Each of the CV SRI, graph density, and clustering coefficient changed significantly between reproductive periods (all $p < 0.001$). The CV SRI increased during lactation while graph density and clustering coefficient each decreased (Figure 5.3). Analyses using HWI and the CV HWI yielded comparable results.

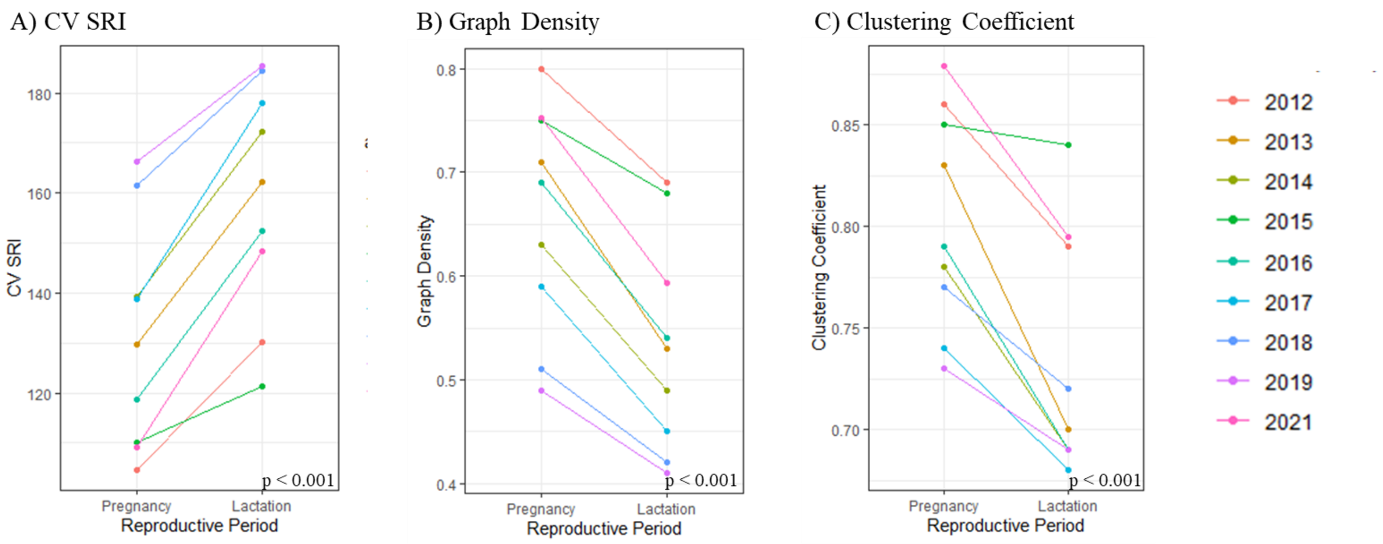


Figure 5.3 The change in A) coefficient of variation of the simple ratio index (CV SRI), B) graph density, and C) clustering coefficient between pregnancy and lactation periods. Each line connects points relating to a single year. P-values are reported based on a paired t-test comparing values between reproductive periods. CV SRI showed a significant increase following parturition while graph density and clustering coefficient showed a significant decrease.

5.5 Discussion

Animals that give birth in temperate climates experience inherently different physiological and environmental conditions while pregnant compared to during lactation. Once female little brown myotis have their pups, our study demonstrated that females generally maintained similar roost preferences as during the pregnancy period (prediction 2) but were less likely to switch roosts in response to changing weather conditions (prediction 1). Roosting association strengths between individuals during pregnancy were also predictive of these relationships during lactation, and our results suggested that although individual needs may change once pups are present in the system, individual variation in selection for both associates and roosts were generally maintained throughout the maternity season (prediction 3). However, just as bats may be limited in their ability to switch roosts during the lactation period, bats also appeared limited in their ability to maintain all social connections that existed prior to parturition. Overall, our findings suggest that reproductive period may be an important factor in the patterns of co-roosting associations of female little brown myotis and impacts the wider structure of the maternity network.

In support of our first prediction, regardless of weather conditions, bats were more likely to reuse a roost on consecutive days following parturition. These results may indicate that the energetic costs of moving offspring are high and/or the survival of the pup is maximized by returning to the same roost on consecutive days, and thus the ability of the mother to select roosts based on her own thermoregulatory needs may be limited. Importantly, changes in weather conditions did have an impact on the probability of switching roosts across both reproductive periods, and we found changes in absolute humidity to be the most influential environmental factor in determining whether female bats switched roosts between consecutive days, with no significant effect of changes in temperature. The influence of absolute humidity is also supported by findings demonstrating absolute ambient moisture as the most important factor in determining evaporative water loss and the surface temperature of animals (Kurta 2014). However, given that female Bechstein's bats (*M. bechsteinii*) were shown to prefer warmer roosts during the lactation period (Kerth et al. 2001), it is surprising that temperature did not have a significant effect on roost switching patterns in little brown myotis in our study, and that the effect of temperature appeared similar in both reproductive periods. These results may be due to the similar construction of the monitored roost boxes along with the presence of other bats, therefore making social thermoregulation more influential on the temperature of the roost. Wind gust and precipitation also did not appear to be influential in affecting daily roost switching of bats in this study. Therefore, conditions outside the roost may not be important determinants of roost selection and strong winds or heavy rains not limiting to mobility, particularly given the close proximity of the monitored roosts in our system. However, our results also suggest that there are many unaccounted-for factors influencing the roost switching decisions of female little brow myotis. Factors such as changes in foraging sites and other social mechanisms may represent other, unmeasured factors in roosting decisions. Roost type has also been shown to affect roost switching in response to precipitation in other temperate bat species in Atlantic Canada (Patriquin et al. 2016), and therefore the use of artificial roost boxes may also have impacted our results. The distance between our study site and the nearest weather station at Pippy Park (≈ 54km) and the variable nature of precipitation and wind across a landscape compared to temperature and humidity may also have limited our ability to make inference on precipitation and wind as factors influencing roost switching decisions.

In contrast to our second prediction, we reported a strong correlation in roost use patterns, specifically the fidelity of individuals to certain roosts, between the pregnancy and lactation periods, however, in agreement with our second prediction, bats did vary in their roost use patterns between the two reproductive periods. It is unsurprising that roost use patterns differed slightly between reproductive periods given previous study of differential roost preference (Kerth et al. 2001), reduced mobility and roost switching during lactation (Henry et al. 2002), and that seasonal changes in body composition and hormone status, such as those experienced throughout a reproductive cycle, can impact an individual's thermoregulatory needs (Terrien et al. 2011). It is additionally possible that during the pregnancy period, bats regularly use a few additional roosts, and then reduce to a "core" set during lactation to which they have high fidelity. As we do not know how many unmonitored roosts are used by the bats in this study area, further study would be needed to quantify the number of different roosts used by reproductive females in both pregnancy and lactation periods, and how females may be selecting the roosts that they use the most frequently. However, given the similarity in construction of monitored roost boxes and lack of information on prey availability, we could only speculate why bats differed from each other in their potential roost preferences.

It is important to note that in social animals, not only do behavioural decisions influence the environment an individual uses, but that these decisions can also alter the environment itself, a concept now known as social niche construction (Flack et al. 2006; Stamps and Groothuis

2010). Based on the relationship between individuals and their social environment, decisions made by parents about site selection and social association with conspecifics throughout their reproductive cycle can also influence the wider population and therefore the behaviour of conspecifics. The observed changes in roosting decisions here, in turn resulted in changes in the social structure of the animal group, specifically a decline in network connectivity, and it is unknown whether this reduction in connectivity is directly beneficial to the wider population during lactation. We reported a weak relationship in which years with higher correlation in roost use patterns between reproductive patterns also displayed a higher correlation in association patterns. Given this, we cannot rule out our third prediction, that in addition to limitations in roosting decisions imposed by parental care, the social needs and preferences of mothers may change once pups are present. In this study, we noted an overall decline in network connectivity, an expected result given the less frequent roost switching of lactating females. The higher network connectivity during pregnancy may also facilitate information transfer as in rhesus macaques (*Macaca mulatta*), females played an important role in information transfer during the mating season Brent et al. (2013). Our results were also consistent with other network studies on bats that report little brown myotis roosting groups are larger prior to parturition (Willis and Brigham 2004; Webber et al. 2016). However, as we were only focused on individuals which met minimum criteria over the study period and did not have information on the number of pups in the system or the number of untagged bats, it remains uncertain whether changes in roosting group size, as reported by Olson and Barclay (2013), also occur in this system.

Across all of our measures, and particularly the change in association strengths between reproductive periods, not all pairs of individuals changed in the same way. Homophily is the preferential association of individuals with similar characteristics (Newman 2002), and mammals have been previously shown to preferentially associate with those of similar reproductive status (Godde et al. 2015), including in big brown bats (Willis and Brigham 2004). The relationship between reproductive and nonreproductive individuals may change once pups are present and the individuals are making decisions based on very different selective pressures such as the energetic demands of nursing (Barclay 1989; Henry et al. 2002; Dzal and Brigham 2013). Given the different selective pressures, we expect that in future studies, nonreproductive individuals would not show the same change in behaviour and therefore social relationships as reproductive individuals around parturition as demonstrated in other mammals (Pérez-Barbería and Walker 2018). These differences in selection pressures and therefore behavioural decisions may explain the individuals that entered or left the system following parturition, and the observation of strong relationships between dyads that appear or completely disappear following parturition.

We cannot rule out however, that some of the observed changes in roost use patterns are attributable to seasonal differences independent of reproductive needs. That said, given the consistency of these changes with our expectation based on reproductive pressures, and the importance of reproductive period when assessing roost switching behaviour even when environmental factors are controlled for, it is reasonable to infer that the reproductive cycle is an important influence of network structure. As the reproductive status of many individuals is uncertain, we could not yet determine how a shift in reproductive condition may affect roosting decisions at an individual level. Moving forward, this information will be important as parturition in little brown myotis and other temperate bat species is largely asynchronous (Fenton and Barclay 1980; Krochmal and Sparks 2007) and thus our data represents an approximation of when behavioural shifts are expected and individual bats may change their habitat or social needs at different times. As our analysis represents a broad overview of what may be occurring in the population at an average parturition date, it is expected that changes would be even more pronounced when analyses are refined to the level of the individual. As changes in roosting patterns are expected to occur at the time of parturition, the association patterns between individuals may be based on similarity in reproductive timing. Other limitations of our study include that our study focused on individuals present throughout the study period and transient individuals may be influencing network structure and interacting at unmonitored locations. We do not know how the inclusion of nearby, unmonitored roosts would affect these results but expect that patterns of association and roost-use of our included bats are reflective of their general behaviour patterns given that we required a minimum number of observations for inclusion in network analysis. Finally, we assumed that years were sufficiently independent from each other due to the large number of individuals that entered or left the study system between years, but the consistency in individual roosting decisions and social relationships between years remains to be determined.

Overall, our data support the contention that female little brown myotis roosting decisions may be influenced by changing social needs in addition to changing roosting needs and roost switching limitations following parturition. We lend further evidence that between the pregnancy and lactation periods, female little brown myotis experience a changing trade-off as they balance the energetic costs of caring for their offspring while ensuring their own survival and future reproductive success.   Consistent with studies in other mammal species (Hinton and Chamberlain 2010; Pitman et al. 2014; Karsch et al. 2016; Severud et al. 2019), these findings lend additional support to the contention that in animals demonstrating maternal care, the presence of offspring has a strong influence on decisions mothers make and may require flexibility in responses to their environment throughout a reproductive cycle. species.

Chapter 6

Consistency in individual relationships across years in a bat maternity group

6.1 Overview

Long-lived, group living animals have the potential to form multiyear relationships. In some temperate bat species maternity groups break apart and rejoin both daily, as females select day roosts to use, and annually, as bats leave for and return from hibernation. Characterization of the daily and interannual variation in bat roosting association patterns is necessary to identify hypotheses to explain patterns and test predictions. Here, we investigated whether bats have persistent social preferences by testing predictions about inter-year association patterns, specifically that relationships between dyads in one year could be predicted by previous years. We also hypothesized that experience influences social preferences and predicted that an individual's age would influence its network position while familiarity with bats of the same cohort would drive persistent social preferences. We quantified instances of roost co-occurrence in little brown myotis (*Myotis lucifugus*) in Salmonier Nature Park, Newfoundland, Canada both within and among maternity periods. We found that roost use frequencies were strongly predictive of roost co-occurrence, yet roost co-occurrence patterns of previous years still had predictive value. However, we found no evidence that cohort familiarity or age explained any of the variation. Overall, we reported long-term patterns of association that suggest levels of social complexity akin to other large mammal species in this temperate bat species.

6.2 Introduction

Long-lived, group living animals have the potential to form social bonds that persist for many years and span generations. The persistence of group behaviour requires that individuals continually interact through mechanisms such as social attraction or aggregation around common resources (Krause and Ruxton 2002; Croft et al. 2008), while long-term social bonds require factors such as spatial memory to return to the same locations (Emlen 1994; Kappeler 2019) and/or social memory to recognize associates over time (Gheusi et al. 1994; Barrett and Henzi 2005; Emery et al. 2007). Understanding which factors explain the persistence of group behaviour and social relationships among individuals is an ongoing challenge in behavioural ecology, and the answer may differ greatly within and among species.

Fission-fusion social systems describe animal groups where one or more individuals break away from and rejoin subgroups in changing conformations over various periods of time (Aureli et al. 2008; Sueur and Maire 2014). As groups break apart and rejoin, there is the opportunity for social relationships to exist at different temporal and spatial scales and therefore different strengths of relationships between individuals. Individuals may separate simply between different times of day to forage, or at a much larger temporal and spatial scale, gather during certain times of year such as during the breeding season (Francesiaz et al. 2017). Thus, both transient and long-term relationships may exist within an animal group that displays fission-fusion dynamics. In species that further demonstrate social preferences between individuals and community structuring, such that some dyads interact more than others, animals may possess the ability to recognize conspecifics across varying periods of absence.

Network analysis is a useful way of visualizing and quantifying the relationships between individuals and its application in animal groups has expanded greatly in recent years (Webber and Vander Wal 2018). In many applications, networks represent an aggregate of interactions that occur over a finite period of time (Haddadi et al. 2011; Blonder et al. 2012; Zhao et al. 2018). Comparing time-aggregated networks across intervals may reveal persistent relationships between individuals and possible mechanisms driving the maintenance of group structure. When using time-aggregated networks, one significant challenge is determining the most informative time step length for the species under study or the research question at hand, as these decisions can have profound implications on estimated network structure and strength of ties between individuals (Cantor et al. 2012; Pinter-Wollman et al. 2014; Farine and Whitehead 2015). Despite these difficulties, rigorous analysis of such datasets is crucial to understanding consistent factors that may shape relationships in social networks.

Time-aggregated networks are particularly useful when animals only exist together or in a study area during certain times of year separated by long (multi-week or multi-month) periods of absence, either from each other or a particular geographic region. Throughout the spring and summer, female temperate bats of some species use multiple roosts within a maternity area, and are dependent on social thermoregulation for rearing their young (Fenton 1997; Willis and Brigham 2004). Previously, it has been demonstrated that temperate female bats interact nonrandomly at maternity roost sites suggesting a role of social preferences in shaping maternity groups (Garroway and Broders 2007; Sunga et al. 2022 [Chapter 3]). It has also been shown that not all patterns of co-roosting can be accounted for by roost fidelity, thus further implicating a role of social preferences in shaping temperate bat groups (Sunga et al. 2022 [Chapter 3]). During the maternity period, females return from hibernation sites, gestate, give birth to their young, then nurse their young for approximately 3-weeks until the pups reach volancy, after which point they depart for swarming and hibernation sites (Fenton 1997; Krochmal and Sparks 2007; Slough and Jung 2020). As females progress through these different reproductive phases, roost use patterns and relationship strengths also change, and thus the overall social structure of the maternity group changes accordingly (Sunga et al. *in prep* [Chapter 5]).

Temperate bats have been regularly recorded to live over ten years, with a record of a little brown myotis (*Myotis lucifugus*) of at least 28 years old in Saskatchewan, Canada (Christiansen et al. 2022),and it is known that in multiple temperate bat species, at least some females are philopatric (Willis and Brigham 2004; Kerth and Petit 2005; Arnold 2007; Metheny et al. 2008; McLeod et al. 2015). As individuals enter or leave the population between maternity periods due to factors such as mortality or dispersal, and as bats return to maternity sites from possibly extended periods apart, or at least away from maternity sites, during swarming and hibernation, it is of interest to understand how the relationships among those that return may change or remain consistent. In long-lived species, social preferences and relationships may also change with age. Exactly how age affects individual habitat use and social preferences is uncertain however, as results vary between taxa. In male African elephants (*Loxodonto Africana*), older individuals had more stable network centrality, while younger males were far more variable (Murphy et al. 2020). Meanwhile in Northern long-eared bats (*Myotis septentrionalis*) there is evidence supporting that juveniles play an important role in maintaining connections across the population (Patriquin et al. 2010) and thus hold a more central position in modelled networks.

In this study we hypothesized that female bats select daily roosts based, at least in part, on social preferences that persist across years. Specifically, we predicted that given their long-lived nature, social relationships between bats in maternity groups will persist across years above a rate expected by random chance interactions. As roost fidelity is related to roost co-occurrence patterns, we also predicted that roost association patterns in previous years would be predictive of patterns in the focal year, even when roost use frequencies are accounted for. Subsequently, we hypothesized that persistent social preferences may be informed by experience in the system and familiarity with conspecifics. As such, we predicted that a bat's age and therefore its experience in a system influences the social preferences and network position of an individual. Specifically, that older individuals will be more selective of their associates and therefore interact with fewer conspecifics, while younger individuals will have higher centrality as demonstrated by Patriquin et al. (2010). We also predicted that bats of the same cohort would be most familiar with each other and, as such, roost most frequently with each other.

6.3 Methods

6.3.1 Data collection

Little brown myotis were captured in Salmonier Nature Park (Lat: 47.3º, Long: -53.3º) Newfoundland, Canada using mist nets (Avinet, Dryden, New York, USA) and harp traps (Austbat Research Equipment, Lower Plenty, Victoria, Australia) from 2012 to 2021 between 15 May and 19 August of each year. Age (Anthony 1988), sex, and reproductive status (Racey

1988) were recorded for each individual. Bats were marked with passive integrated transponder (PIT) tags (0.09 g; EID-ID100 implantable transponders, EIDAPInc, Sherwood Park, Alberta, Canada and Trovan Electronic Identification Systems, UK) implanted subcutaneously between the scapulae. Transponder antennas (LID650, Dorset Identification, Netherlands) were deployed from April to September each year to collect data on roost entry and exit at eleven roost boxes within a 1.1 km^2 area. Ten of the eleven roost boxes were positioned in pairs on five poles, and one box was placed on the side of a barn. As many bats were detected in multiple boxes on any one night, it was assumed that the last detection before sunset represented the roost where an individual had spent the day. The last detection before sunset was the same roost as the last detection prior to sunrise the previous morning in 96.9 % of all assigned day roost records, and thus we expect our day roost assignments are reliable. Due to missed detections during PIT-tag monitoring, it is expected that some proportion of roost use was unrecorded. Although not part of the experimental design, due to degradation one roost box was no longer available for bats to use from 2018 onwards. Two other boxes were not monitored during the parturition period in 2018 due to a malfunction but were monitored again in 2019 and 2021. Further, there were three unavailable boxes in 2021 due to degradation, and one available box was not monitored due to malfunction. Data were limited to adult females detected on at least ten days between 28 April and the parturition cut-off in each year as determined by a previous assessment of parturition timing (Sunga et al. *in prep* [Chapter 4]). This cut-off was used to ensure that we had a reasonable amount of information on each individual to properly infer their relationships with other included bats and their position in the wider network (Frantz et al. 2009; Sunga et al. 2021a [Chapter 2]).

All social network and statistical analyses were conducted in R version 4.0.0 (R Core Team 2020).

6.3.2 Social association patterns across years

To quantify the longevity of social relationships based on co-occurrence at a day roost, we computed lagged association rates (LARs), the probability that two individuals re-associate a given number of days from their first observed instance of association (Whitehead 2008). LARs were computed using the function *LAR* in “asnipe” (Farine 2013). LAR values were compared to the expected rate if all associations in the network were random (i.e. the null), which was equal to the average number of connections per individual divided by the total number of individuals minus one (Whitehead 2008). We calculated these values based on the gambit-of-the-group assumption (Whitehead 2008), such that bats detected in the same roost on the same day were assumed to be associating through co-roosting.

To assess whether annual roost use and social interaction patterns were consistent among years, we created a matrix of association strengths based on the Simple Ratio Index (SRI) of co-roosting occurrences, whereby we compared the instances of co-roosting to instances of bats roosting separately or when only one bat of a dyad was detected (Cairns and Schwager 1987). The SRI was calculated using the function *get_network* in the package “asnipe” (Farine 2013). For individual × individual association matrices, we performed Mantel tests for all possible pairwise year combinations to assess the inter-year correlation. Mantel tests were calculated using the function *mantel* in the package “ecodist” (Goslee and Urban 2007). These comparisons included individuals that were present and had at least ten observations prior to parturition in both years, and thus sample sizes varied between comparisons. We then visualized the Mantel test correlation score (*r*) on the number of years difference between years to investigate whether years closer together in time were generally more similar.

6.3.3 Influence of persistent social relationships when accounting for roost use patterns

We tested whether the association strength among dyads in previous years was predictive of current association strengths even when roost use patterns were accounted for by using multiple regression quadratic assignment procedure (MRQAP). In this analysis, we regressed the dependent matrix of the individual × individual association strengths in the focal year (2013 to 2021) against the individual × individual association strengths in each previous year representing social influence, and individual × individual co-occurrence probability in the focal year (Shizuka et al. 2014). Co-occurrence probability was based on the probability of overlap at each box based on the product of the % of days each individual spent in each box, summed across all boxes. This approximation of probabilities does not account for days where neither individual was detected as it is possible that individuals still associated at unmonitored roosts or were not recorded in monitored roosts, but we assumed that these observations were missed randomly. These analyses for each year were thus limited to individuals present in both the focal and previous years being compared. The MRQAP procedure was performed using the function *mrqap.dsp* in the package “asnipe” (Farine 2013). We then calculated the fold-difference in scaled effect sizes of roost use patterns and previous year association patterns, to investigate whether previous year association strengths were more predictive when compared years were closer together in time.

6.3.4 Effect of cohort on association strength

For each individual of known age that had at least ten observations prior to parturition in at any year (n = 42), an assessment of the number of associates and strengths of associations with other individuals with at least ten observations prior to parturition in each year, regardless of whether their age was known was conducted. To assess the effect of cohort on association patterns, we performed a paired t-test of known aged individuals to assess the average SRI of within and among cohort associations. This analysis began in 2014 as there were no known aged adults in 2012 and only one known aged adult in 2013. For each individual, we averaged the SRI of within and among cohort dyads across all years to ensure that individuals present in more years or with more associates did not have a greater influence on the analysis than those meeting observation requirements in only a single year. Further, this ensured that the presence of more individuals of different ages than of the same age did not impact the statistical analysis.

6.3.5 Influence of age on distribution of social relationships and network position

For each individual of known age that had at least ten observations prior to parturition in any year (n = 42) we recorded the coefficient of variation of the simple ratio index (CV SRI), node degree, and betweenness centrality within networks containing all other individuals with at least ten observations prior to parturition in each year, regardless of age status. Although the possible associates could have changed, including as many individuals as possible with sufficient numbers of observations, should provide a better characterization of the overall network structure and therefore the known-aged individual’s position in it (Frantz et al. 2009). CV SRI and node degree were selected as we predicted that individuals would become more selective in their associates with age and experience in the system thus the lowest CV SRI values and highest node degree values would be found in the youngest individuals. Node degree, a measure of the number of connections an individual has (Wey et al. 2008), was calculated using the function *degree* in the package “igraph” (Csárdi and Nepusz 2006). A measure of centrality was included as it has been shown to vary with age in other social systems (Patriquin et al. 2010; Murphy et al. 2020). Betweenness centrality is a measure of the number of times an individual is a component of the shortest path between two other individuals (Wey et al. 2008), and was calculated using the function *centr_betw* in the package “igraph” (Csárdi and Nepusz 2006). We then performed a linear regression for each of these factors with age as the independent factor.

6.4 Results

6.4.1 Social association patterns across years

Lagged association rates across the entire study period declined considerably over the first 60-70 days (1 season), likely related to transient interactions among some dyads with some stable relationships each pregnancy season. This was followed by a slight decline in LAR across years but remained above the null prediction for the entirety of the study period (2012 - 2021) following the first interaction (Figure 6.1). A drop in LAR was seen right before the limit of data selection, the expected parturition cutoff, in many years. This is likely due to the fact that not all individuals were observed on all days, thus causing an artificial decrease in the probability of observing associations right before the parturition cut-off in each year. At the beginning of each season LAR appeared to spike briefly as bats returned from swarming sites in the first six years, but this pattern dissipated beyond this point. This pattern may be related to the fewer number of roosts used on average early in the maternity season causing a greater number of individuals to use each roost box due to social thermoregulatory needs, and thus increasing the probability of association at used roost boxes (Figure 6.1 inset).

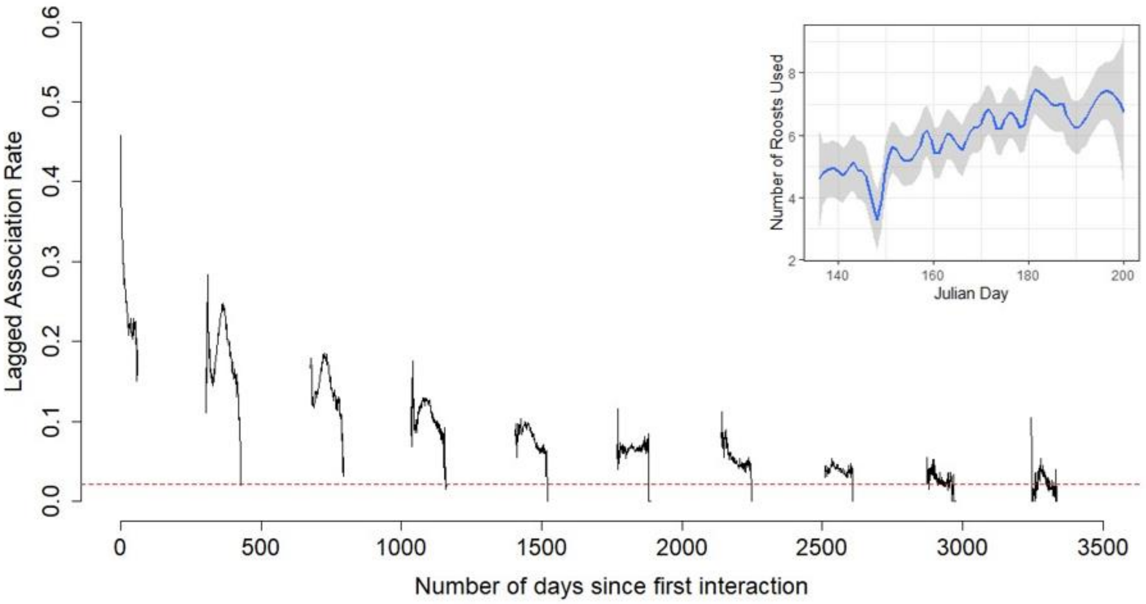


Figure 6.1 Lagged association rates for female little brown myotis with at least ten day roost observations during the pregnancy period from 2012-2021 in Salmonier Nature Park demonstrating the probability that an association persists on the i-th day after it first occurs. Red dashed line denotes the null rate of association calculated based on Whitehead (2008). Periods of no data that occur at yearly intervals correspond to fall-winter (swarming and hibernation period) and no data was collected in 2020. The inset shows the averaged number of roosts used by day of the year (Julian Day) for all individuals across all years of the study where the line represents the smoothed value based on a smoothed loess fit and the shaded area shows the standard error. Fewer roosts used early in each year may correspond to the increased lagged association rate peaks seen at the start of each maternity period.

Consistency in association strengths varied greatly between dyads, but overall, networks were significantly correlated ($p < 0.05$) between years in all comparisons except for association patterns in 2012 compared to association patterns in 2021 ($p = 0.40$) indicating that relationships between dyads were relatively consistent between years. Mean Mantel R score was 0.46 (SE: 0.03; range: 0.15-0.72). Although it appeared that strong relationships (SRI > 0.5) in one year were generally predictive of strong relationships in later years, some dyads lost or gained relationships between compared years. Further, whether relationships of moderate strength (SRI 0.2 - 0.5) became stronger or weaker in subsequent years was highly variable (Figure 6.2A). As predicted, Mantel R scores decreased over time and there may be a slight plateau when there are more than four or five years of difference between years being compared (Figure 6.2B). All analyses were also conducted using the half weight index (HWI) and yielded comparable results.

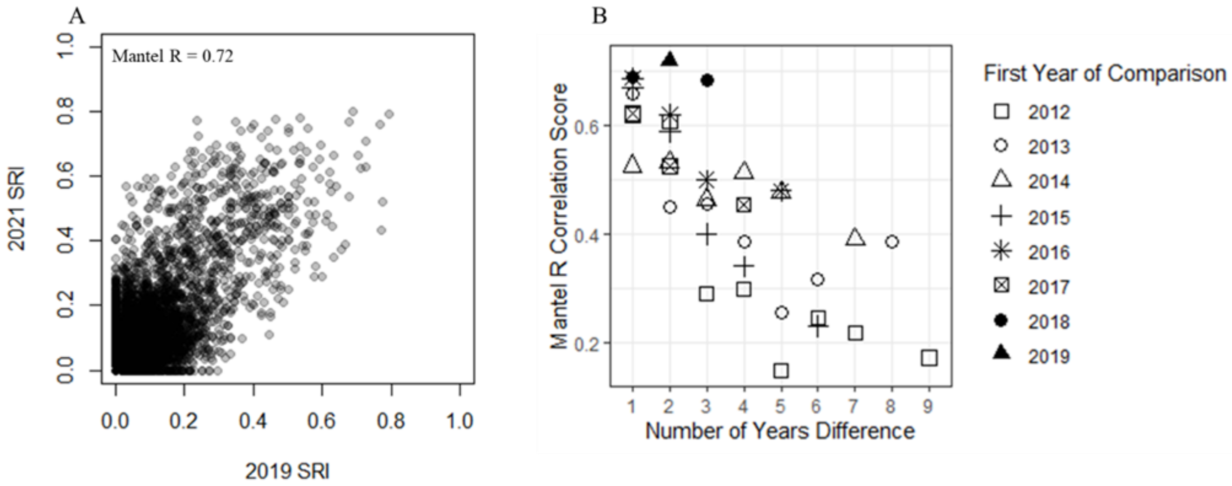


Figure 6.2 The correlation of association strength (SRI; Simple Ratio Index) between female little brown myotis dyads in Salmonier Nature Park, Newfoundland, Canada, calculated between different combinations of years. Panel A shows the SRI in 2019 compared to the SRI in 2021 for all dyads that were present in both years where each point represents one dyad that was present in both years. Panel B shows the Mantel R correlation scores for matrices of association strengths in different years, based on the number of years difference between the matrices being compared.

6.4.2 Influence of roost fidelity and associate familiarity on network structure

Both the matrix of probability of roost co-occurrence for all individuals in the focal year and the matrix containing association strengths (SRI) between all individuals in the immediately previous year were predictive of the focal year association strengths ($p < 0.001$). The scaled effect size of the roost co-occurrence matrix was 4- to 65- fold greater than the scaled effect size of the previous year association strengths (Table 6.1) suggesting a strong predictive ability of roost fidelity. Fold difference could not be calculated for the comparison of 2017 to 2012 as the scaled effect size of the previous year association strengths was zero. The fold difference generally increased with a greater difference between the focal year and comparison year indicating that the predictive ability of previous year association strengths declined when there was more time between the networks being compared (Figure 6.3). Association matrices from 2012 were not predictive ($p > 0.05$) of association matrices in 2016, 2017, 2018, 2019, and 2021 when roost use patterns were accounted for and the association matrices of 2013, 2014, and 2015 were similarly not predictive of association matrices in 2021 (Supplementary Table 6.1). All analyses were also conducted using the half weight index (HWI) and yielded comparable results.

Table 6.1 Scaled effect sizes of the immediately previous year association strengths and roost co-occurrence probability on the association strengths between adult female little brown myotis in the focal year based on a Multiple Regression Quadratic Assignment Procedure (MRQAP). Estimates of effect size can then be compared to determine which factor was more influential, and to what magnitude, on observed roosting association patterns in the focal year. Results for MRQAP of all pairwise comparisons of years are available in Supplementary Table 6.1.

		Previous year association		Roost co-occurrence probability		
Focal Year	n	Estimate	p	Estimate	p	R^2
2013	64	0.139	< 0.001*	0.791	< 0.001*	0.778
2014	133	0.086	< 0.001*	0.823	< 0.001*	0.770
2015	132	0.091	< 0.001*	0.755	< 0.001*	0.653
2016	126	0.157	< 0.001*	0.715	< 0.001*	0.692
2017	203	0.144	< 0.001*	0.756	< 0.001*	0.695
2018	151	0.069	< 0.001*	0.814	< 0.001*	0.724
2019	152	0.095	< 0.001*	0.779	< 0.001*	0.727

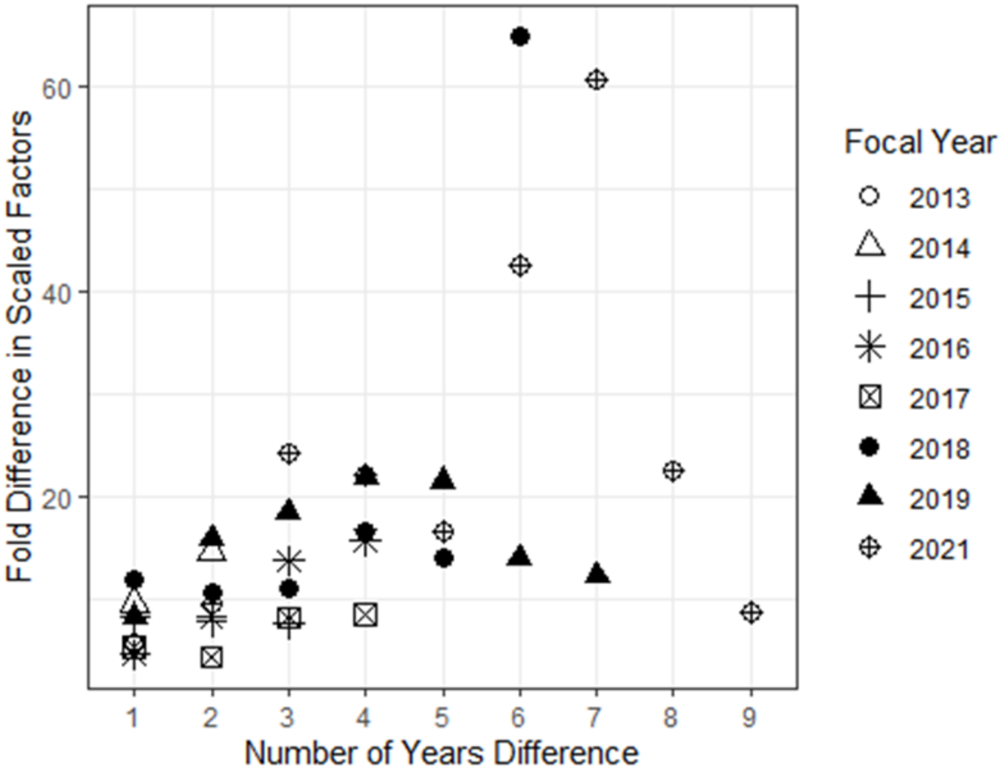


Figure 6.3 The change in predictive ability of previous year association strengths on co-roosting association networks of little brown myotis in Salmonier Nature Park, Newfoundland, Canada. Fold-difference, calculated as the scaled effect size of focal year probability of roost co-occurrence divided by the scaled effect size of association strengths in the comparison year, was plotted against the number of years difference between the comparison year and the focal year. The fold difference generally increased, indicating a decrease in the predictive ability of comparison year association strengths with a greater amount of time between focal and comparison years. The comparison of 2017 (focal year) to 2012 (comparison year) is not shown as the effect size of the comparison year was 0, and thus a fold difference could not be calculated.

6.4.3 Effect of cohort on association strength

The strengths of associations between bats in the same cohort were not significantly different from association strengths between bats of different cohorts ($t = 0.26$, $df = 41$, $p = 0.80$). On average, there were 6.4× as many bats outside of an individual's cohort than there were from the same cohort within the sample in any given year. Meanwhile, bats on average had 2.5× as many associates outside of their cohort than within their cohort, within the sample. Some individuals had little to no association with many of the other known aged individuals despite being present in the system in the same year.

6.4.4 Influence of age on distribution of social relationships and network position

Individual network metrics did not vary with age in a consistent manner across the tested known-aged individuals. Node degree was relatively consistent across all ages (Figure 6.4A). A slight increase in median betweenness centrality was noted between ages 3 and 5 but, due to largely unequal sample sizes, this difference might not be biologically significant (Figure 6.4B). There was no evidence that there was a difference in CV SRI across the different ages (Figure 6.4C). Some individuals were included in multiple exact age categories if they met minimum requirements in multiple years, but the change in network metrics within an individual as they aged was not explored here.

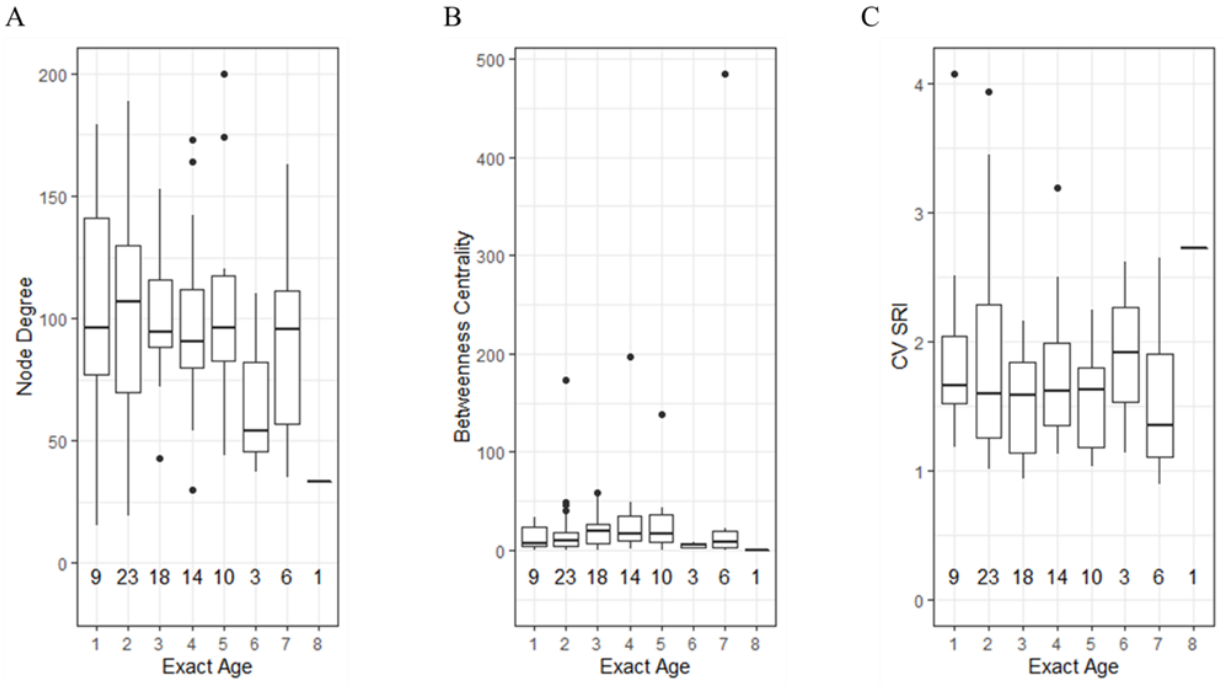


Figure 6.4 Distribution of network metrics for female little brown myotis in Salmonier Nature Park, Newfoundland, Canada in networks of bats containing at least ten observations at a day roost prior to parturition in a year. Box plots show the different individual network metrics of A) node degree, B) betweenness centrality and C) the coefficient of variation of the simple ratio index (CV SRI) at different known ages. Networks were constructed to include individuals of unknown age, but metrics were only calculated for known-aged individuals. Individuals were assigned an age of 0 in the year they were captured as a juvenile, and thus an exact age of 1 corresponds to the summer a year after birth. The number of known aged individuals for which the metrics could be calculated in each age category are shown along the bottom of each plot.

6.5 Discussion

In this study, our findings indicated that we cannot reject the hypothesis that bats have persistent social preferences with conspecifics that influence roost-use decisions across years. We presented evidence that patterns of roost co-occurrence between adult female little brown myotis persisted over time at a greater rate than what is expected by random chance. We also showthat the association strengths between bats in any given year were correlated with association strengths in subsequent years, even when accounting for roost use frequencies, however the predictive ability of previous year associations is small in comparison. By maintaining consistent relationships at maternity sites, bats may accrue benefits such as reduced competition among neighbours and improved information sharing (van Noordwijk et al. 2012), benefits which may in turn be drivers of long-term relationships. We did not find evidence that, among known-aged individuals, familiarity or experience influenced relationships or network position from year-to-year. Although the exact cause for the maintenance of relationships over time remains unknown, our data cannot dispute the suggestion that bats may act on long-term social preferences.

In mammals, it is common for females to display philopatry and maintain relationships with matrilineal relatives (Clutton-Brock and Lukas 2012). Although we do not know the relatedness among individuals in this system, or which of the individuals of unknown age are philopatric, it is clear that some bats were returning to this maternity site for at least nine years after we first observed them (including individuals caught at the site as young-of-the-year) and continuing to share roosts with at least some of the same associates. For up to eight years following first observations of shared roost use, the rate of association between many pairs of bats were, on average, greater than expected by chance and association patterns across all dyads were significantly correlated in 35 of 36 year combinations. Unsurprisingly, roost use patterns in a focal year were far more predictive of association patterns than previous year association patterns, further suggesting an important role of roost fidelity in shaping association patterns. We also observed that previous year association patterns were still predictive even when accounting for roost fidelity, often for up to a five year difference between years being compared, it is clear that previous association patterns between bats may be indicative of future patterns. The large difference in scaled effect sizes between factors merits caution, as it is possible that roost use patterns of previous years, and thus multi-year roost fidelity, could be an important factor in multi-year relationships between co-roosting bats. However, given that roost use patterns do not entirely explain association patterns for little brown myotis within years (Sunga et al. 2022 [Chapter 3]) , and that even when accounting for roost use patterns, previous year association patterns were predictive of co-roosting relationship between bats, it is reasonable to posit that social preferences could persist across years. Previous study of little brown myotis in Minnesota showed a mix of philopatric and dispersal behaviours among females (Dixon 2011) and thus our study may include a mix of philopatric females with dispersing individuals from other maternity groups.

Other studies of temporal stability in social networks in other species have made similar conclusions, but also encountered similar challenges in teasing apart habitat and social mechanisms (Shizuka et al. 2014). It must be noted that the lagged association rate persisting above the null expectation hypothesis could also indicate fidelity to specific roost boxes within the maternity site, rather than persistent social preferences. In a pipistrelle bat colony

(*Pipistrellus pipistrellus*), it was shown that among 17 roost sites, each bat had two to three roosts that it used most frequently (Thompson 1990) and thus it is possible that little brown myotis in our study are demonstrating similar roost use patterns. Interestingly however, Mantel R correlation scores and scaled effect sizes in MRQAP appeared similar even in years where the availability of roosts changed (i.e., the degradation of one roost box in 2018 and two more in 2021). Temporal heterogeneity in habitat availability can lead to alternate resource selection decisions (Webber and Vander Wal 2018) and for this reason, it is interesting that association patterns remained consistent in the face of roost availability changes. It is possible that the loss of these roosts does not present a biologically significant change to habitat availability, and that other unmonitored roosts in the area may have allowed the maternity group to maintain its structure. These observations make it more difficult to reject the contention that social mechanisms are driving roosting decisions across time and lend greater support for the role of social preference in shaping bat groups across long time periods.

We did not observe a cohort-related or potential cohort familiarity effect, whereby bats in the same age cohort would associate more strongly with each other than with bats of different cohorts. Firstly, it is possible that the pattern of preferential assortment among cohorts exists at a finer scale than we are able to observe. As we apply the gambit-of-the-group assumption here (Whitehead 2008), we cannot be certain that assortment does not occur within roosts as shown previously in other bat maternity groups in buildings (Waag et al. 2021). However, when applying the gambit-of-the-group assumption, artificially high assortativity, the tendency to observe individuals associating with those similar to themselves, has been reported when sampling is limited (Franks et al. 2010) and so it is equally possible that bats simply do not select associates based on those born in the same year as themselves.

It is additionally possible that bats assort based on other factors such as reproductive condition, personality (Webber and Willis 2020), or relatedness. If bats associate with those most closely related to themselves, then a cohort related pattern of association would not be expected. Instead, much like what has been reported in cetaceans such as sperm whales (*Physeter macrocephalus*; Gero et al. 2015), maternity groups could be organized into matrilines, whereby closely related individuals stick together, then join with other matrilines creating larger groups of mixed relatedness and generally low relatedness across those in a geographic area. These patterns would also potentially explain the persistence of some, but not all, relationships across time as matrilines stick closer together but have more transient relationships with other matrilines. Across studies of social networks in bat groups, the role of relatedness in shaping network structure and influencing individual relationships has been mixed, with matriline patterns shown in Spix's disc winged bats (*Thyroptera tricolor*; Buchalski et al. 2014), but many other examples of kinship not appearing to drive bat social structure. In brown long-eared bats (*Plecotus auratus*), females rarely move between maternity sites but kin selection did not account for colony stability across years (Burland et al. 2001). Similarly in Natterer's bats (*Myotis nattereri*), overall relatedness within the colony was low despite high female philopatry (Scott et al. 2018). Work on common vampire bats (*Desmodus rotundus*) have shown that familiarity and reciprocity are the main drivers of relationships between bats rather than relatedness (Wilkinson 1984, 1985; Wilkinson et al. 2016).

We did not find an effect of age on any of the network metrics observed and thus within the age variation of our dataset, there is no evidence that experience influences an individual's network position. This result is unlike the findings of Patriquin et al. (2010), who noted greater centrality in younger individuals, identified based on the wear of canines in northern long-eared bats (*Myotis septentrionalis*). Keeping in mind the long lifespans of little brown myotis, it is possible that division of adult bats into single-year age classes or the range of ages for which we had sufficient data were not biologically relevant. In addition, considering the hypothesis of social niche construction, whereby the presence of individuals in a group in turn alters their social environment (Flack et al. 2006; Stamps and Groothuis 2010), it is difficult to discern whether the changes or consistencies in network position are due to age and experience, or changes in group composition among years, as bats are regularly observed to join or leave the system between years. Along the same vein, individual bats may maintain similar network positions throughout their lives. Little brown myotis may be specialized to a "social niche" within the larger maternity group, determined by factors such as their individual personality (Montiglio et al. 2013), resulting in no detectable difference in network position between ages when assessed at the population level. It is of interest to investigate the relationship between personality and network position, and how network position may change or remain constant across time at the level of individuals.

In Slender-billed gulls (*Chroicocephalus genei*) relationships between individuals remained consistent despite the breeding colony changing location from year to year. The degradation of roosts in 2018, and 2021 have allowed a glimpse into how social relationships may change or remain the same when roost preference cannot be used as an explanation. An understanding of how a change in group composition of individuals changes roost use patterns and therefore network position may further lend support to the role of social preferences in shaping bat groups. White-nose syndrome (WNS), a fungal disease caused by *Pseudogymnoascus destructans* continues to decimate bat populations across North America and is expected to impact this study population in Salmonier Nature Park, Newfoundland, Canada within the next five years. Although an unfortunate set of circumstances, a change in the composition of maternity groups may shed light on the role of social preferences in shaping bat roost use patterns and maternity groups. If roost use patterns remain the same despite the losses of many individuals, habitat mechanisms may be more influential than social preferences in shaping bat groups. Meanwhile, changes in roost use patterns and consistent relationships despite the loss of many individuals would suggest an important role for social bonds. These effects have been found previously in other species such as flamingos (Phoenicopteridae) where it has been described that long-standing partnerships are important to improve population resilience to environmental fluctuations (Rose and Croft 2020). Alternatively, strong philopatry or fidelity driving maternity group organization and therefore reduced behavioural flexibility, may reduce the likelihood that this site will be re-colonized following a population decline due to WNS, as shown following population stressors to common warthogs (*Phacochoerus africanus*; Muwanika et al. 2007). Understanding the social and habitat selection factors that are influencing maternity group stability will improve our ability to predict how this population will respond to WNS, and what may be needed to assist the recovery of little brown myotis.

Overall, our data supported the contention that roost use patterns and social relationships may be changing slightly year to year, but at least a subset of relationships remain consistent for many years. We provide evidence for long-term relationships in bat maternity groups and our data did not support rejecting the hypothesis that social mechanisms may be responsible for the observed consistency. We also suggest that persistent preferences for specific roosts may also be an additional contributing factor. Together, by testing the changes and consistencies in association patterns in a bat maternity network, we provide support for the possible presence of persistent social preferences in long-lived temperate bats. Future study should investigate attributes of the individual bats showing consistent relationships, including relatedness and personality measures, to better understand assortment within the maternity group.

Chapter 7

Synthesis and Discussion

Through detailed descriptions of the social organization of bat maternity groups, I have provided evidence supporting a role of social preference in shaping roosting association patterns between adult female little brown myotis (*Myotis lucifugus*). By quantifying roosting association patterns across different time periods and comparing these patterns both to random chance and to roost use frequencies, I find that other factors influence the organization of little brown myotis maternity colonies (Chapter 3, 5, and 6). I suggest that social preferences may be the missing piece in explaining the daily roosting decisions of adult female bats, driving individuals to maintain associations with large numbers of conspecifics despite different roost use patterns (Chapter 3), through transitions in reproductive phases (Chapter 5), and across multiple years (Chapter 6). To support these insights, I also investigated the robustness of population level measures of social network structure in the face of missing individuals and missing observations (Chapter 2) and applied these findings to my investigations of bat maternity groups in Newfoundland, Canada. I also used roosting behaviours to estimate parturition date to both understand how reproductive timing may relate to environmental and individual factors (Chapter 4), and to inform my analyses of changes in social network structure across reproductive periods (Chapter 5). These dynamics highlight the possibility that little brown myotis, and potentially bats in general, could retain information about dozens or hundreds of conspecifics, and therefore have social complexity comparable to other gregarious mammal species.

In chapter 3, I described a fission-fusion type structure in a bat maternity colony in Salmonier Nature Park, Newfoundland, with overlapping communities roughly related to different roosting areas within the study site. I also identified patterns of co-roosting associations that could not be accounted for by individual patterns of roost use frequency. More specifically, I found evidence that individual bats may be coordinating when roosts are used to avoid certain conspecifics while maintaining social cohesiveness with others who frequent different roosts. Communities of little brown myotis observed here, even within a single local group, often consisted of over one hundred individuals and associations were not necessarily predicted by similarities in roost fidelity. However, Kerth et al. (2011) and Zeus et al. (2018) have suggested there may be a maximum threshold of ≈ 50 individuals in a bat community, above which it is unlikely that individuals can maintain associations evenly among community members due to limitations in cognitive ability. In other taxa including social fish, the upper limit of group size is determined by the social conflict within the group, where those with less conflict can maintain larger group sizes (Wong 2011). It is unknown whether little brown myotis possess greater cognitive abilities for maintaining larger numbers of associations and/or a reduced incidence of social conflict compared to other studied bat species. Further, it remains to be determined whether social preferences are the determining factor in shaping co-roosting association patterns or if other external factors may be impacting individual bats differently, resulting in both different roost preferences and variable patterns of roost switching.

I present here that within a maternity season, population cohesiveness decreased once pups were estimated to be present (Chapter 5), likely due to the reduced roost switching flexibility resultant of maternal care responsibilities. This suggestion was supported by my findings that adult female bats were less likely to switch roosts following estimated parturition across all weather conditions and the work of Henry et al. (2002) who reported reduced foraging distances and increased numbers of nighttime revisits to the same roost once pups were present. However, despite these changes, many co-roosting relationships between dyads remained consistent throughout the maternity season, further suggesting the possibility of social preferences in shaping bat maternity groups. This hypothesis of social preferences is further corroborated by Chapter 6, where I report consistent association patterns between dyads over up to nine years (2012-2021), where maternity seasons are interspersed with swarming and hibernation when bats leave the study site entirely and their association patterns are unknown. These patterns support the possibility of social preferences as a factor in roost use decisions of adult female bat in maternity groups.

These dynamics also highlight the possibility that female little brown myotis, and potentially bats in general, could retain information about dozens or hundreds of conspecifics, and therefore have cognitive abilities comparable to other gregarious mammal species. It is clear that active association for social thermoregulation is highly important for female little brown myotis while less so for the solitary roosting males of the species, and our results suggest that there may also be a fitness benefit for females to act on further social preferences for specific conspecifics during the maternity season. The flexibility of bat maternity groups to break apart (fission) and rejoin (fusion) provides benefits such as reduced competition during foraging, as demonstrated in spider monkeys (*Ateles geoffroyi yucatenensis*) in response to food scarcity (i.e., Schaffner et al., 2012), while still allowing benefits of social thermoregulation. The detection of potential social communities based on fission and fusion events that are not explained by potential habitat preferences has been seen previously in species classically considered to be social, such as dolphins (Frère et al. 2010; Cantor et al. 2012), as well as species less often considered social such as the slender-billed gull (*Chroicocephalus genei*; Francesiaz et al. 2017) and sleepy lizards (*Tiliqua rugosa*; Spiegel et al. 2016). Consistency in same-sex relationships across multiple years have been documented in other social mammal species such as Assamese macaques (*Macaca assamensis*; Kalbitz et al. 2016) and Bornean orangutans (*Pongo pygmaeus*; van Noordwijk et al. 2012). These patterns, combined with their long lifespans continue to prove bats distinct from other small-bodied mammals while showing more and more similarities to other ‘intelligent’, large-bodied mammals such as cetaceans and primates.

As demonstrated in chapter 2, it is expected that I have sufficient numbers of individuals and observations per individual to reliably assess the presence of social communities and their relationship to roosting patterns. However, there are still many caveats to the work I present here as it is unknown how many individuals and how many roosts remain unmonitored. Some number of detections may also be missed due to equipment error and thus I reserve my conclusions to the broader, maternity group-wide scale whenever possible. Despite these limitations, throughout my research, I demonstrate how the use of informed null models can allow for the characterization of social structure patterns in a bat maternity colony despite missing information. As I apply the gambit-of-the group assumption (Whitehead 2008) when inferring associations between bats at roosts, it is additionally possible that finer scale interactions and relationships are occurring within a roost box, as described inside building roosts in another study of little brown myotis (Waag et al. 2021). At the same time, artificial roost boxes, particularly when many are placed in a small area as is the case in Salmonier Nature Park, may provide the opportunity for larger roosting subgroups more consistently and in a smaller geographic space than would be possible if only natural tree roosts were available. Our system may therefore consist of larger roosting subgroups and social communities than would occur in an area of only natural roosts. In addition, Newfoundland is near the Northeastern limit of the little brown myotis range, and regularly experiences harsh conditions for thermoregulation including cold, wind, and rain, which may also necessitate larger roosting subgroup sizes. Social thermoregulation may be less important in southern parts of the range, and thus group and community sizes may be smaller. Although little brown myotis social behaviour has been studied in other parts of the species' range (i.e. Olson and Barclay 2013; Waag et al. 2021), there are not yet studies that would allow direct comparison to ours, either in using a similar distribution of artificial roosts in a different part of the species’ range, or assessing social structure in entirely natural roosts in a nearby area. These studies would provide further insight into how social systems may change across habitat types, or with habitat supplementation through the installation of artificial roosts.

As social structure has been described as the sum of all dyadic relationships in all contexts (Kappeler et al. 2013), I provide only a glimpse into the social structure of temperate bats, based on roosting associations during a specific time of year. Understanding how the relationships described here compare to relationships at foraging sites during the maternity season, or to relationships during swarming and hibernation, may have important implications for how we think about bat social needs, and in turn, the conservation of bat habitat. This is particularly important given that the social relationships themselves may be an essential component of a bat’s habitat. For example, in highly social species, simply protecting a few high-quality foraging patches may not be sufficient to maintain stable group structure. Other locations may be important for connectivity among individuals or behaviours that facilitate the formation of social bonds (He et al. 2019), and/or a minimum number of individuals may be needed for group stability (Cantor et al. 2020). Further, as demonstrated by the incredible travel distances that little brown myotis are capable of even during the maternity season (Sunga et al. 2021b), observations of bats moving > 4km during the peak of maternity season (unpublished observations in Pinery Provincial Park, Ontario), and conflicting results on the relatedness of bats within and between maternity groups (i.e., Burland et al. 2001; Wilkinson et al. 2016; Scott et al. 2018), it remains to be determined what constitutes a distinct social unit with regards to bat groups and therefore the scale at which any habitat conservation efforts should be directed.

Gathering further knowledge to inform conservation efforts and understand potential impacts on bat maternity colonies and social systems is particularly important in the face of ongoing climate change effects. In chapter 4, I estimated parturition timing from nighttime roost revisit patterns which allows for estimation over more individuals with less capture effort compared to the usual method of capturing juveniles and assuming parturition to be 21 days prior to first capture (Krochmal and Sparks 2007). By estimating parturition for many individuals and relating this timing back to the mothers rather than to the offspring, I was able to assess how parturition timing was affected by changes in environmental conditions. Continued rising temperature may lead to parturition dates shifting earlier, as observed in Daubenton's bats (*M. daubentonii*) in the Czech Republic (Lučan et al. 2013). Meanwhile, projected increases in extreme precipitation events (Abbasnezhadi et al. 2020) may delay parturition while also decreasing reproductive success (Burles et al. 2009). The success of temperate bats in raising their young may be aided by their fidelity to specific sites or roosts such as in moose (*Alces alces*; Neumann et al. 2020) or by greater synchronicity within the population as seen in other bat species (Burles et al. 2009) and bison (*Bison bison*; Jones et al. 2010).

Alternatively, changing sites or the timing of parturition in response to changing climatic conditions may allow bat populations to better meet individual needs as parturition timing has been shown to vary by populations and across latitudinal gradients in other mammals (Gogan et al. 2005; Neumann et al. 2020). Thus, whether the site fidelity as evidenced by my results in Chapter 6 will prove advantageous for little brown myotis in Newfoundland remains to be determined. The impact of site fidelity on the future success of temperate bat species will also be strongly related to the impacts of white-nose syndrome (WNS), a disease caused by the fungus *Pseudogymnoascus destructans*, on the social structure of bat populations. WNS is responsible for dramatic declines in many North American bat species (COSEWIC 2013), including in the study population in Pynn's Brook, Newfoundland (unpublished results) but has not yet appeared to have caused declines in the study population in Salmonier Nature Park, Newfoundland. As evidenced by my work in Chapter 6, the social structure of bat maternity groups changes year-to-year, likely influenced in part by the departure of some individuals and the addition of others. It is unknown how declines of over 90 %, as seen in other temperate bat populations across

Canada, will impact the social structure of bat maternity groups and how site fidelity may aid or inhibit species recovery. In the common warthog (*Phacochoerus africanus*), disturbance led to a breakdown of social structure while strong philopatry reduced the likelihood of re-colonization (Muwanika et al. 2007). Additionally, given the social nature of temperate bats and their dependence on social thermoregulation, Allee affects become of increasing concern when discussing WNS-related population declines. Allee effects are broadly described as a decrease in population growth rate with fewer individuals, and it is expected that in social species this may be exacerbated by fewer or less efficient beneficial interactions between conspecifics (Angulo et al. 2018). It is therefore of great concern to understand how population declines may impact bat populations both in their initial mortality and decline and their ability to recover social dynamics among surviving individuals. By understanding social habitat needs, practitioners can better understand how populations may adapt to changing conditions and more effectively target conservation efforts to maintain appropriate complexity and/or cohesiveness in these groups.

There is certainly more work needed to fully quantify the role that social preference plays in shaping bat maternity groups and determine how an understanding of social structure can improve conservation of social species. For temperate bats specifically, there is opportunity to characterize social structure in maternity populations that have already undergone population declines, and thus to understand how social structure may change or rebuild. It is also of interest to understand whether the association patterns and possible role of social preference, as demonstrated here, are consistent in other contexts including at foraging, swarming, and hibernation sites. Such study will provide a clearer picture of the relationships between individual bats and the potential evolutionary mechanisms that drive group behaviour in temperate bats.

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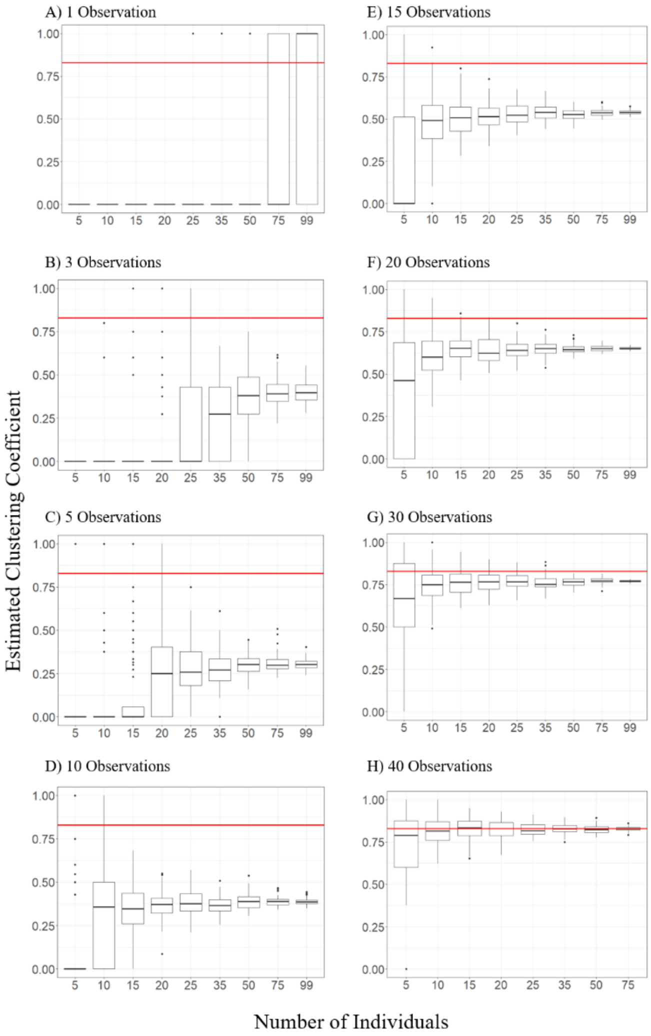
Appendices

Appendix A
Manuscript Waivers

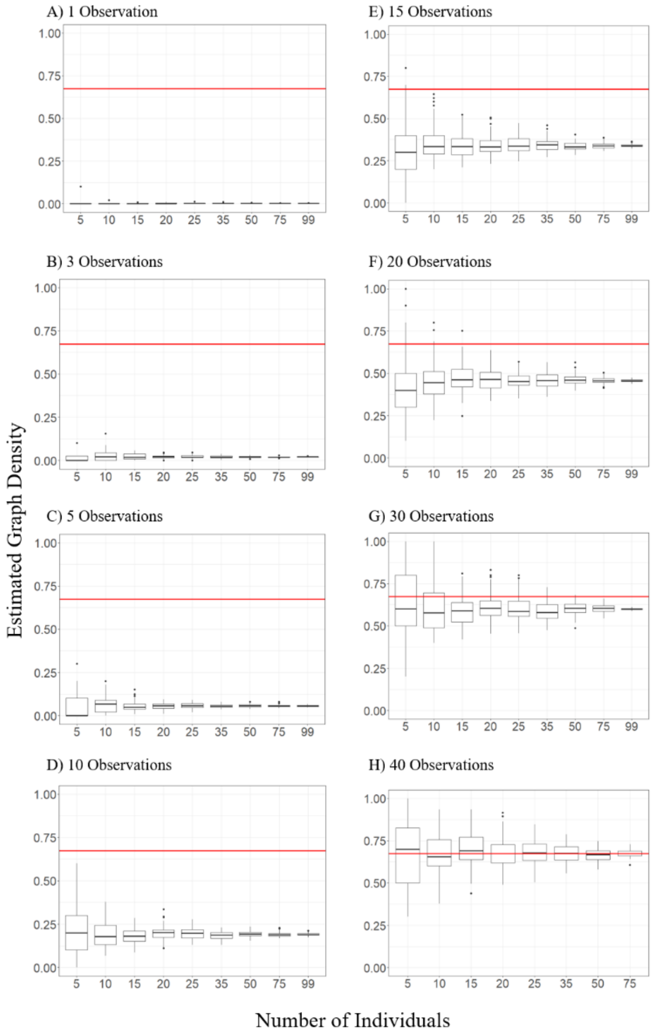
I have received permission to present all manuscripts that have been published or are currently in press that are enclosed within this thesis by way of written email consent from the respective journal editors. This includes PLOS ONE for Chapter 2 andAnimal Behaviour for Chapter 3.

Appendix B

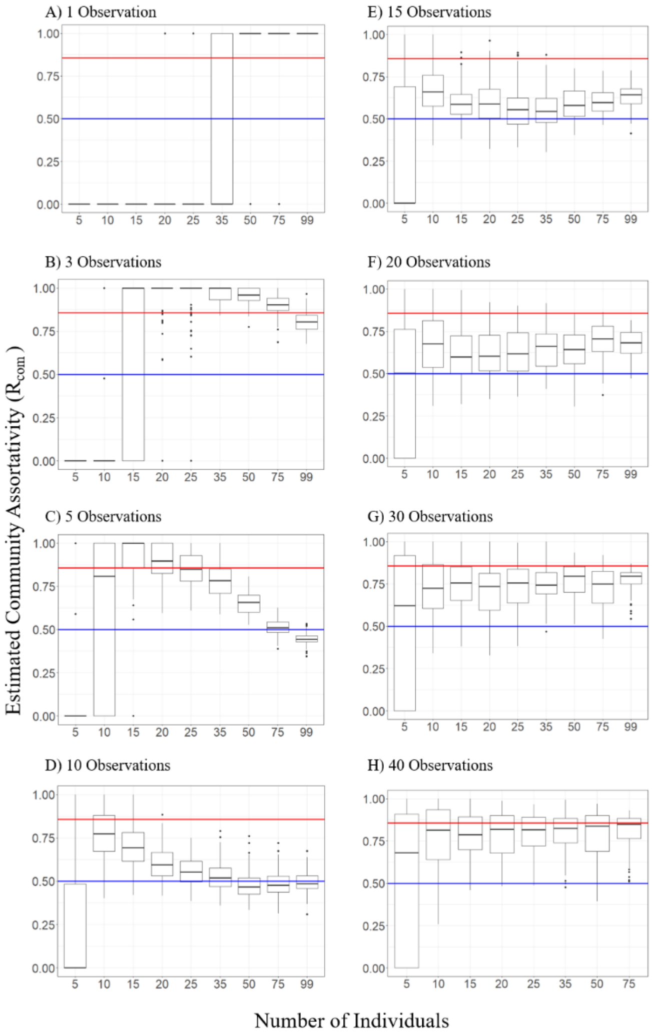
Chapter 2 Supplementary Figures



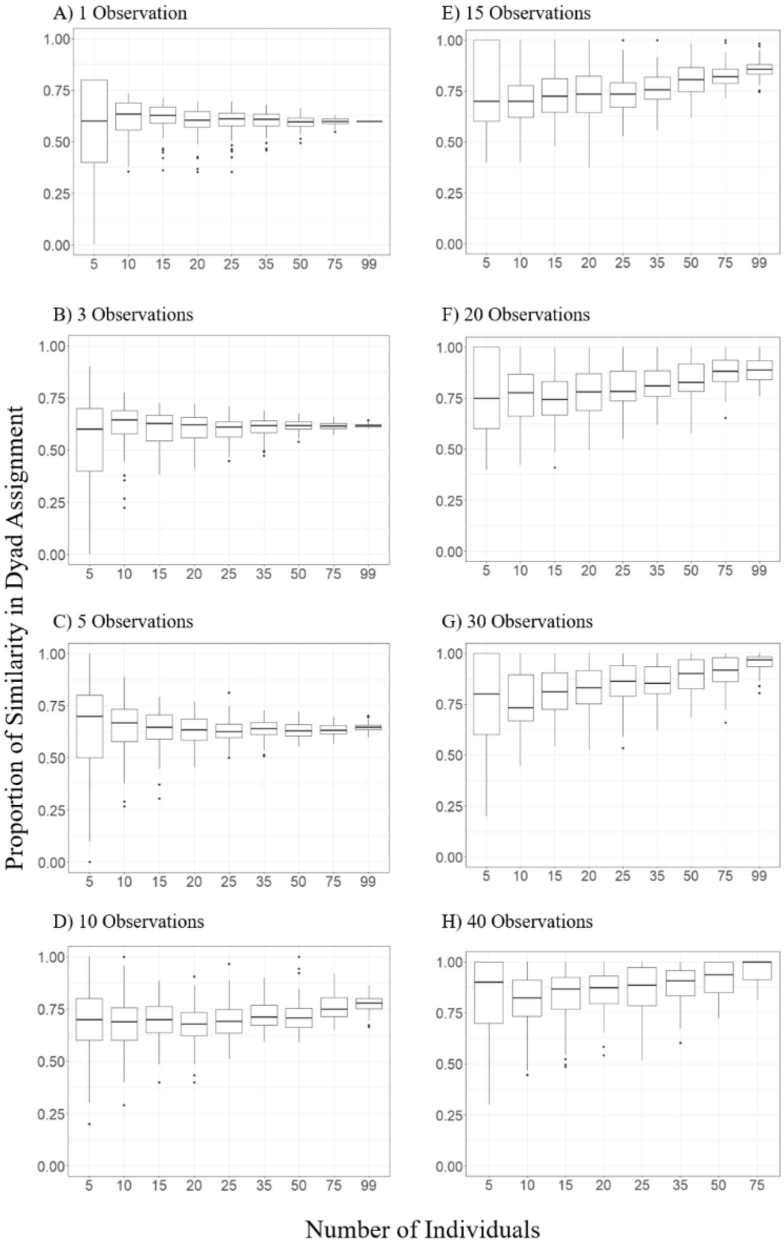
Supplementary 4.1 Influence of number of individuals and number of observations per individual on estimates of clustering coefficient (all observation levels). Horizonal red line represents the value of the ‘observed’ network at 0.828.



Supplementary 4.2 Influence of number of individuals and number of observations per individual on estimates of graph density (all observation levels). Horizontal red line represents the value of the ‘observed’ network at 0.675.



Supplementary 4.3 Influence of number of individuals and number of observations per individual on estimates of community assortativity (R_{com}; all observation levels). Horizontal blue line represents the threshold value of 0.5 and the horizontal red line indicates the actual R_{com}.



Supplementary 4.4 Influence of number of individuals and number of observations per individual on the proportion of similarity in dyad assignment (all observation levels).

Appendix C

Chapter 6 Supplementary Table

Supplementary 6.1 Results of Multiple Regression Quadratic Assignment estimating the ability of previous years and current roost use patterns to predict association strengths between female little brown myotis in Newfoundland, Canada. Only individuals present in both the focal year and comparison year are included in each analysis, and the number of individuals is presented below. Presented are the scaled effect sizes of both roost co-occurrence probability in the focal year (Roost Scaled Effect), the association strengths between dyads in the comparison year, associated P values for each factor, and the Adjusted R^2 value for each model. Comparisons where the previous year association strength is not a significant predictor are indicated in *italics*.

Focal Year	Comparison Year	n	Roost Scaled Effect	Roost P	Comparison Year Scaled Effect	Previous Year P	Adjusted R^2
2013	2012	64	0.781	< 0.001	0.146	< 0.001	0.779
2014	2013	133	0.816	< 0.001	0.107	< 0.001	0.781
2014	2012	61	0.839	< 0.001	0.073	< 0.001	0.749
2015	2014	132	0.756	< 0.001	0.1	< 0.001	0.661
2015	2013	73	0.75	< 0.001	0.107	< 0.001	0.657
2015	2012	37	0.736	< 0.001	0.101	< 0.001	0.538
2016	2015	126	0.709	< 0.001	0.174	< 0.001	0.703
2016	2014	151	0.785	< 0.001	0.101	< 0.001	0.722
2016	2013	85	0.797	< 0.001	0.071	< 0.001	0.714
2016	*2012*	*32*	*0.739*	*< 0.001*	*0.051*	*0.072*	*0.601*
2017	2016	203	0.746	< 0.001	0.161	< 0.001	0.693
2017	2015	95	0.683	< 0.001	0.177	< 0.001	0.6
2017	2014	119	0.781	< 0.001	0.104	< 0.001	0.655
2017	2013	64	0.778	< 0.001	0.098	< 0.001	0.648
2017	*2012*	*25*	*0.751*	*< 0.001*	*-0.002*	*0.515*	*0.524*
2018	2017	151	0.811	< 0.001	0.079	< 0.001	0.735
2018	2016	128	0.796	< 0.001	0.085	< 0.001	0.734
2018	2015	57	0.718	< 0.001	0.077	< 0.001	0.633
2018	2014	71	0.818	< 0.001	0.057	< 0.001	0.721
2018	2013	40	0.816	< 0.001	0.056	0.005	0.733
2018	*2012*	*16*	*0.777*	*< 0.001*	*0.032*	*0.255*	*0.66*
2019	2018	152	0.774	< 0.001	0.11	< 0.001	0.741

2019	2017	127	0.817	< 0.001	0.061	< 0.001	0.73
2019	2016	112	0.826	< 0.001	0.052	< 0.001	0.724
2019	2015	60	0.764	< 0.001	0.043	< 0.001	0.623
2019	2014	71	0.824	< 0.001	0.048	< 0.001	0.69
2019	2013	37	0.821	< 0.001	0.06	0.005	0.69
2019	*2012*	*14*	*0.707*	*< 0.001*	*0.076*	*0.334*	*0.5*
2021	2019	116	0.828	< 0.001	0.101	< 0.001	0.823
2021	2018	101	0.864	< 0.001	0.054	< 0.001	0.811
2021	2017	90	0.846	< 0.001	0.047	< 0.001	0.761
2021	2016	80	0.848	< 0.001	0.06	< 0.001	0.777
2021	*2015*	*48*	*0.767*	*< 0.001*	*0.022*	*0.123*	*0.655*
2021	2014	49	0.862	< 0.001	0.025	0.04	0.792
2021	*2013*	*26*	*0.866*	*< 0.001*	*0.041*	*0.083*	*0.781*
2021	*2012*	*8*	*0.434*	*0.003*	*0.028*	*0.403*	*0.229*