

**SOCIAL STRUCTURE, EMERGENCE BEHAVIOUR
AND ROOST SWITCHING IN
FEMALE LITTLE BROWN BATS (*MYOTIS LUCIFUGUS*)**

by

Alicia Irwin

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Copyright Alicia Irwin

Approved: Dr. Hugh Broders
Supervisor

Approved: Dr. Lisa Gannett
Committee member

Approved: Dr. Timothy Fraiser
Committee member

Approved: Dr. Cynthia Staicer
External examiner

Date: August 7th, 2014

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Abstract

The evolution of sociality involves trade-offs between benefits (e.g. protection from predation, information transfer) and costs (e.g. transfer of disease, competition). This study investigated the potentially social behaviour of little brown bats (*Myotis lucifugus*) at two maternity colonies in Newfoundland using passively integrated transponders. Emergence order on the busiest days of the season was examined at different roosts for patterns in the order in which bats emerged. Emergence order was significantly concordant, but bats formed only weak associations that lasted 30-80 days, based on proximity in emergence time. There was variation in day roost use by bats, with the number of switches in day roosts ranging from 0 to 37 per season. Night visits to roosts were greater for reproductive bats, especially during the lactation period. I hypothesized that bats that visited more roosts during the night would be more social, but there was no support for this, and there was no observed difference in social measures between reproductive classes. These findings suggest that female little brown bats maintain weak associations throughout a season, and reproductive status influences their night behaviour, specifically roost visitation frequency.

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Table of contents

Abstract	i
Acknowledgments	ii
Table of contents.....	iii
List of tables	iv
List of figures	v
Chapter 1: Introduction to sociality	1
Chapter 2: Emergence behaviour	23
Chapter 3: Patterns of roost use	49
Chapter 4: Conclusions	74

List of tables

Chapter 2

<u>Table 1.</u> New bat captures (not previously tagged) from 2011-2013 at Pynn’s Brook and Salmonier Nature Park, Newfoundland.....	34
<u>Table 2.</u> Concordance analysis of <i>Myotis lucifugus</i> bats emerging from busiest roosts at Salmonier Nature Park on all top 5 nights (nights with highest emergence data through each season)	36
<u>Table 3.</u> Association analysis of emergence order of <i>Myotis lucifugus</i> from multiple roosts at Salmonier.....	38
<u>Table 4.</u> Association analysis of emergence order of <i>Myotis lucifugus</i> from multiple roosts at Pynn’s Brook	39

Chapter 3

<u>Table 1.</u> Mean and maximum association values using half weight index for both sites of <i>M. lucifugus</i> over two years analyzed separately and together	59
<u>Table 2.</u> Network analysis values from associations calculated using half weight index for both sites over two years analyzed separately and together.....	60

List of figures

Chapter 2

<u>Figure 1.</u> Comparison of emergence time of adult female <i>Myotis lucifugus</i> of known reproductive status at Salmonier Nature Park, 2013	35
<u>Figure 2.</u> Kendall's coefficient of concordance of emergence order between each pair of days at Salmonier.	37
<u>Figure 3.</u> Temporal analysis associations (half-weight index) of <i>Myotis lucifugus</i> for two roost sites of one colony at Salmonier Nature Park	40
<u>Figure 4.</u> Temporal analysis for two roost sites of one colony at Pynn's Brook of <i>Myotis lucifugus</i>	41

Chapter 3

<u>Figure 1.</u> Site map of Salmonier Nature Park location site.....	54
<u>Figure 2.</u> Day roost use by <i>Myotis lucifugus</i> at Pynn's Brook (1) and Salmonier Nature Park (2) in Newfoundland.....	61
<u>Figure 3.</u> Roost use at Salmonier Nature Park (refer to site map for locations, Figure 4)	62
<u>Figure 4.</u> Number of recorded incidences of bats switching day roosts over a season.....	63
<u>Figure 5.</u> Number of roosts visited per 24 hour period during 2013 at Salmonier Nature Park (Right panel) and Pynn's Brook (left panel)	64
<u>Figure 6.</u> Left panels show association index frequency for SNP 2012, 2013, then 2012-13 combined (top to bottom).....	65

Figure 7. Left panels show association index frequency for PB 2012, 2013, then 2012-13 combined (top to bottom). Right panels show standardized lagged association rates for the above mentioned..... **66**

Figure 8. Comparison between reproductive classes of individual maximum number of different roosts visited in 24 hour period during 2013 compared to individual network measures at Salmonier Nature Park..... **67**

Chapter 1: Introduction to sociality

Explaining the variability of animal sociality and how it evolved has been a challenging task since social ethology began (Crook 1970). The fitness benefits of being social include protection from predation (colobus monkeys, Teichroeb et al. 2012; prairie dogs, Hoogland 1981; sperm whales, Arnborn & Whitehead 1989; bats, Fenton et al. 1994), information transfer (African striped mice, Rymer et al. 2008; evening bats, Wilkinson 1992a; Bechstein's bat, Kerth & van Schaik 2012; chimpanzees, Crockford et al. 2012; Pallas' Mastiff bat, Dechmann et al. 2010), social warming (mole-rats, Boyles et al. 2012; Sichuan snub-nosed monkeys, Zhang et al. 2011; Townsend's big-ear bats, Betts 2010), kin selection and cooperative breeding (Asian elephants, de Silva et al. 2011; *Dromiciops gliroides* (marsupial), Franco et al. 2011; orcas, Foster et al. 2012; giant noctule bat, Popa-Lisseanu et al. 2008; greater sac-winged bat, Nagy et al. 2007; red wolves, Sparkman et al. 2012; warthogs, White & Cameron 2011; vampire bats, Wilkinson 1984). Along with these benefits come associated costs, such as transfer of disease and parasites (raccoons, Cote et al. 2012; zebras, Fugazzola & Stancampiano 2012, white-nose syndrome in temperate cave-roosting bats of North America, Dzal et al. 2011), competition (male reindeer, Djakovic et al. 2012; male bats, Safi 2007) and infanticide (cougars, Ruth et al. 2011; greater spear-nosed bat, Bohn et al. 2009). In mammals, specifically, exists the possible costs of milk theft and vertical transfer of pathogens in scenarios with allonursing (Hayes 2000). Given these potential costs, the common occurrence of sociality in many different groups of animals (Wilson 1975) is impressive.

The variability in sociality is wide-ranging, from aggregations of animals around a resource (i.e., marten groups, Newman et al. 2011) to highly complex societies (i.e., open fission-fusion network in dolphins, Randic et al. 2012). An aggregation is a group of

individuals who do not necessarily recognize each other and simply co-occur in an area to exploit a resource (Kerth 2010). To the other extreme, complex societies exist that involve individual recognition, long-term associations, and intimate interactions such as allogrooming or allonursing. The vast majority of bats are social (Kerth 2008) and the full spectrum of societies can be found, from solitary (hoary bat, Klug et al. 2012), to unstable groups (harems in the greater sac-winged bat, Nagy et al. 2007), to complex fission fusion groups (Bechstein's bats, Kerth & van Schaik 2012; *Nycticeius humeralis*, Wilkinson 1992b; greater spear-nosed bat, Wilkinson & Boughman 1998).

The social system of any species has three parts: the organization, the structure and the mating system (Kappeler & van Schaik 2002). Social organization involves the number of individuals present, composition of the group and its cohesiveness. The social structure consists the relations and interactions between individuals, and how that may form an overlying pattern or structure. Finally, the mating system, which describes how males and females interact during the reproductive period, is another critical component of the social system, since this social aspect heavily influences the genetics of the group and thus the connectivity of populations (Kappeler & van Schaik 2002, Kerth 2008).

The first step to cooperative breeding is the existence of small social groups, which consist of families and extended family relations (Emlen 1982). The evolution of the family unit has historically had two main explanations as outlined by Emlen (1995) explaining why young remain with their family instead of dispersing to breed. The first explanation involves the ecological constraint model, which states that there are no viable options for the young to disperse to for reproduction, generally occurring when the suitable surrounding area is already inhabited to saturation with breeding pairs which the young cannot outcompete. Alternatively, the benefits-of-philopatry model is based on there being benefits to staying in

the natal area where the animal was born or hatched, and this may include protection by parents, increased experience and maturity, and the possibility of inheriting the parental territory (Emlen 1995). In both models, the young leave home only when the costs of leaving incurs a higher inclusive fitness. These models explain why young may be philopatric, but to explain why they would help their parents raising other young is more complicated (Emlen 1992).

Group stability may range from being completely cohesive (moving together as a unit all of the time) to a dynamic fission-fusion group (Kerth 2010). Fission-fusion groups will regularly split apart (fissure) and then come back together (fuse), and there are many ways and different levels in which this can occur. The term “fission-fusion” was first used in 1971 to describe several non-human primate species which display this pattern of group stability as a result of resource availability (Kummer 1971, Aureli et al. 2008). Since then, there has been much debate about fission-fusion groups and whether they are adaptive or not (Kerth 2005). It has been hypothesized that since cohesive groups most likely make a consensus decision, they gain the most group benefits since all have agreed. In a fission-fusion structure, subgroups may split off instead of potentially having made a common decision, and it has been thought that this is not beneficial because not all of the group benefits are obtained (Conradt & Roper 2003). In response, Kerth (2005) claims that different species are under different constraints, and fission-fusion may be a coping mechanism for this, and thus provide the most individual benefits for these species. If species have different life histories, such as the number of breeders in their social group, this will impact the ability of the group to undergo fission-fusion dynamics. For example, in honey bees, where there is one breeding female queen (McGlynn 2012), if a female were to leave the group, she would not be able to start a colony on her own, and thus leaving would not be beneficial for her. In Asian

elephants there is frequent splitting and merging of female groups yet there are also multiple breeders (de Silva et al. 2011) and thus leaving the group is not detrimental to the one leaving – she is still able to reproduce. Kerth (2005) notes that one consensus decision may not always be best for all, and thus breaking off into smaller groups temporarily may have the best overall benefit. For example, certain individuals may have specific food preferences and thus can split up to forage for their favourite foods but later on join back together and still receive group benefits such as social warming.

Only a handful of in-depth studies have looked at fission-fusion in bats (e.g. Bechstein's bats *Myotis bechsteinii*, Kerth & Van Schaik 2012, big brown bats *Eptesicus fuscus*, Metheny et al 2008). Research on fission-fusion dynamics have been mostly focused on primates, and it is unclear whether this social system requires higher cognitive skills, decision-making abilities or advanced communication (Aureli et al. 2008). By including a variety of bat species, which are known to have a wide range of cognitive skills and communication, the uncertainty of the requirements for a fission-fusion society may be answered. It is known that mating systems are correlated with brain size (and perhaps cognition) in bat species (Pitnick et al. 2006). Bat species with promiscuous females tend to have smaller brains than those with monogamous mating (Pitnick et al. 2006). Thus by completing studies on the social behaviour of these species, uncovering their social structures could reveal the brain size or cognitive abilities required to live in certain social systems (although these factors may be correlated and/or caused by additional ecological factors).

II. Intrinsic and extrinsic factors

The factors influencing social structure can be classified into two categories: intrinsic and extrinsic. Intrinsic factors are inherent to the group under study, such as the individuals and their roles within the group, the interactions between pairs, the mating system, and the

culture (Whitehead 2008). Extrinsic factors are those outside the animal, such as the environment, and this can include not only climate, but also prey, predators, parasites, etc. (Ebensperger et al. 2012). Intrinsic and extrinsic factors can function at an evolutionary time scale, shaping sociality over vast periods of time, but I will focus on the more immediate proximate response of animals to these factors (Kappeler et al. 2013) in the following chapters.

Intrinsic factors

One of the main hypotheses about intrinsic factors used to explain and predict how sociality affects individual fitness is Silk's hypothesis (Silk 2007). This hypothesis seeks to explain the continuum of breeding strategies, from singular breeding species to plural breeding species without communal care, to plural breeding species with communal care. Silk predicted that the singular breeding species would have the highest direct fitness consequences, and this would decrease as continuing along the continuum to plural breeding species with communal care. In singularly breeding species, where parents are the sole care givers, there will be a higher survival of offspring since the parents are not relying on non-breeders to care for the young (as would be the case in communal raising of young). There is support for Silk's hypothesis across mammal species (Ebensperger et al. 2012), and thus it should be considered for any model of mammal social structure.

Intrinsic factors, such as the role or status of an individual, can play a key part in social structure. In macaque monkeys, certain individuals keep order within the group (Flack et al. 2006). When these policing individuals were removed, aggression increased by 30%, which had a significant effect on the interactions between individuals and thus the social structure. In Bechstein's bats, some colonies consist of multiple communities held together by older females (Kerth & van Schaik 2012). These older females may also transfer

information between groups. In African elephants, the age of the matriarch (the leader of the family group) has a significant effect on group cohesiveness (McComb et al. 2001). If a matriarch is young, and a call from a neighbouring family is heard, the entire group will huddle together in close proximity. If the matriarch is older, the group does not huddle after hearing a neighbouring family, and this may indicate that they are more relaxed with a leader who has more experience (McComb et al. 2001). Therefore, in multiple species of mammals, the roles of individuals as well as their age can affect group behaviour and consequently the social structure of their groups.

Physiological constraints can also influence social structure. Martens and badgers are from the same family and share many similar traits (life history, foraging, ecology) but can differ greatly in social structure (Newman et al. 2011). Badgers may be either social or not social, whereas martens are always solitary. Newman et al. (2011) suggested that the difference in social structure was due to their anatomy, because although they consume the same resources, badgers can store fat and use torpor whereas martens have to keep slender to successfully hunt and cannot use torpor. Therefore, martens have stronger physical constraints placed on them, and lack the ability to cope with periods of restricted food, which the authors claim to be a fundamental precursor to living in social groups. Badgers, being able to store fat and use torpor are able to go for periods without food, which may mean that intracompetition (competition between those in the species) is not as severe and being part of a social group may not be as stressful for them. Similarly, Bechstein's and Daubenton's bats are both small temperate bats that are insectivorous and roost in similar tree cavities, yet the males of these groups have different social behaviours (Kerth & Morf 2004, Senior et al. 2005). In Bechstein's bats, males are solitary and roost alone, whereas in Daubenton's bats, males form social groups similar to those of females (up to 20

individuals). It is not clear why this difference exists between the male social structure of the two species given their similar roost and food constraints, as well as the ability of both species to use torpor. The above studies suggest that many intrinsic factors can influence sociality, including both traits of the individual (role/experience) as well as physiological constraints (metabolic limitations).

Extrinsic factors

Extrinsic factors may also play a role in shaping social structure of mammals. Emlen (1992) hypothesized that stable environments that were saturated with breeding individuals or unstable environments with occasional harsh breeding seasons would lead to young staying with their family for longer periods, creating persistent family groups. Female Asian elephants group together more during the dry season, creating multifamily units which band together to defend territories which include their water sources (de Silva et al. 2011). On the other hand, female Thornicroft's giraffes have larger herds during the wet season and smaller herds in the dry season (Bercovitch & Berry 2010). The opposite behaviours of elephants and giraffes is unclear, but could be due to some intrinsic trait, such as the hierarchical structure of elephant groups, the communal raising of young (see Silk's hypothesis above) or the behaviour of defending a water source which is not displayed by giraffes. Not only does water limit sociality, but food can also play a role. During years of low Chinook salmon abundance (the food of choice), orcas will be less social, forming fewer associations (Foster et al. 2012). Therefore, the orcas are less social in harsh environments, similar to the giraffes. These examples suggest that the environment may influence social behaviour, however at the same time there may be interactions with intrinsic factors such as inherent social structuring (e.g. elephant matriarchal society).

In bats, especially those in temperate regions, maternity colonies are often formed during the reproductive period of gestation and lactation (Kerth 2008). These maternity colonies consist of female bats living in close proximity, raising their young together. Whether the reproductive period would be considered a harsher time and/or a more social time of year for the bats is not apparent. During the winter, little brown bats lose up to 25% of their body weight (Fenton & Barclay 1980). For juveniles survival is even more difficult, because despite being able to intake the same amount of nutrients before hibernating, they lose weight while adults are gaining and it is not known why (McGuire et al. 2009). While the energetic demands are high during this time, and no food is available in their northern range, they do often form clusters and arouse from torpor synchronously (Czenze et al. 2013). Even though females will require more energy for pregnancy at the onset of spring, they use the same amount of energy as males during hibernation (Jonasson & Willis 2012). In the summer, little brown bats use torpor, although females use it less when pregnant, and both pregnant and lactating females entered torpor for shorter periods than non-reproductive females (Dzal & Brigham 2013). Despite using torpor less and for shorter periods, both reproductive and non-reproductive females had similar foraging behaviour, which suggests that even small shallow bouts of torpor helped to conserve energy. Which season is harsher for females in temperate zones is unclear. In the summer they have to raise their young, which would be energetically demanding, but they do have access to food and the use of torpor at least in some capacity. In the winter, with no food, cold temperatures and thus a loss in body weight, it is more likely that winter is a harsher time than the summer season for temperate bats.

Generally, the above studies show that harsh environments (resource poor) can affect groups differently, despite the fact that all are female mammals living in fission-fusion

societies (although it should be noted that the elephant, bat and giraffe study compared seasons within a year, whereas the orca study compared the productive season between years).

Confounding the problem further are the interactions among extrinsic factors that influence social structure. For example, arctic foxes show great flexibility in their social structure, from the female breeding singly, or within a small group, to females communally caring for young (Norén et al. 2012). The study compared the effect of two extrinsic factors, food and predation, on social structure. Food was the most limiting, with groups forming when the food supply was sufficient to support multiple individuals. An abundance of food did not guarantee a complex grouping though; to achieve a group of females which communally cared for young, there needed to be heavy predation pressure, which likely increased the need for communal pup guarding. Therefore food was the most limiting factor, followed by predation, in shaping social structure in the arctic fox. This outcome in arctic foxes supports Silk's hypothesis (Silk 2007), since when enough food is present, foxes prefer to care for their own young, and only when the additional pressure of predation is added do they communally care for young.

Temperature can also affect social structure. In Sichuan snub-nosed monkeys, temperature had a greater influence on clustering behaviour than predation (Zhang et al. 2011). All monkeys slept in trees at night to avoid predation (during the day some slept on the ground), but the groups were most cohesive during the coldest nights. Therefore temperature, instead of food or predation, was the main factor driving close associations between individual monkeys.

For bats that live in areas with high raptor abundances, it has been found that predation is a key factor influencing their grouping behaviour (Fenton et al. 1994). For

example, when group size was <100 bats, emergence time was more scattered and they switched roosts often. For groups of more than 100, there were fewer attacks on each individual, yet individuals would still emerge earlier than other colonies despite the increased predation during that time.

From the above studies on extrinsic factors, it seems that there are multiple factors that significantly influence social structure, and these factors sometimes interact to create complicating factors. In a recent meta-analysis on the benefits of sociality in mammals, Ebensperger et al. (2012) found that although the literature showed conflicting results of positive, neutral, and negative impacts of sociality, there were still some overall trends. First, if offspring were cared for by their own parents rather than communally, then they had a higher survival rate, which supports Silk's hypothesis. Secondly, most studies showed an increased advantage (potentially adaptive) of being social in the tropics as opposed to temperate zones, but with no common explanation. This study also pointed out some gaps in the literature, stating that a large number of studies were on large carnivores, with data on large marine and small volant mammals (i.e., bats) lacking. Further, their finding that sociality was more beneficial in the tropics could be a correlation of species present instead of an effect of the environment. For example, most primates are found in the tropics, and thus the tropic data may be biased towards primates. Finally, classifying environments as harsh or mild is not fine scale enough and other factors such as amount of parasites present must be incorporated. Additionally, if an animal evolved in that harsh environment, it may not be important or influential on the behaviour of that animal. Expanding the types of species studied may help give a better picture of trends in sociality, although it seems that parental care and environment are key to understanding the causes of sociality in mammals.

Additional factors affect females specifically, such as the general trend for most female mammals to group together and remain in their natal area (Clutton-Brock 1989). For example, female prairie dogs remain in their natal area and generally do not disperse (Hoogland 1981). This holds true for most bat species, having females displaying natal philopatry (Kerth 2008). Female grouping allows for multiple interactions between individuals, which gives opportunity for a social structure to develop (Wilson 1975). It is important to note that there are examples of mammals, such as dolphins and raccoons, which live in fission-fusion societies but do not show the typical female bonding behaviour (Randic et al. 2012; Prange et al. 2011). Females may make temporary bonds with other females, but these break down frequently. Instead, the males of these groups form lasting bonds, even though the mother is the main caregiver for the offspring. Overall, female bonding is quite typical in mammals and females usually do not disperse (e.g. Bechstein's bats, Kerth 2005; Asian elephants, de Silva et al. 2011; lions, Arsznov & Sakai 2012; warthogs, White & Cameron 2011).

Female mammals, often being the caregiver of offspring (Rheingold 1963), have many demands placed on them since they must physically produce and care for the young (i.e., gestation and lactation). Since producing and raising young can be very demanding, there are different ways females interact to meet these demands. During times of limited food resources, females of yellow baboons and hoary marmots will suppress other females from reproducing, in turn freeing more resources for them and their own young (Wasser & Barash 1983). Some females instead work together cooperatively to meet the demands of young. During parturition, warthog females form more cohesive groups and these groups involve reproductively aged non-breeding individuals which both babysit and even adopt the offspring of others (White & Cameron 2011). In Sichuan snub-nosed monkeys, lactating

females formed closer bonds than other females, indicating that there may be cooperation between the lactating females, although they did not rely on non-breeding individuals like the warthogs (Zhang et al. 2012). It is important to understand the impact of young on females since the social structure of females can affect the male social structure as well (Galapagos sea lion, Wolf et al. 2007). Also, adding young to the group increases the group size, and increases in group size have been known to increase the number of splitting-up and merging-together events of fission-fusion societies (goat antelope, Pepin & Gerard 2008). Thus it seems that the demands of young can either draw together females, prompting for cooperation and close interactions, or cause negative interactions, such as having some females stopping others from reproducing.

The demands of young are not the only factor shaping female social structure. Thornicroft's giraffe females do not seem to be greatly affected by the demands of young yet still show seasonality in their social interactions. The giraffes do not have a breeding season, with no birth synchrony in the females, yet females are more social in wet seasons than dry (Bercovitch & Berry 2010). This may indicate a confounding factor in other mammal studies, where parturition often overlaps seasons of high abundance of food or resources in general, making it hard to distinguish the cause of social structure in these groups.

III. Bat sociality

Bats are underrepresented in the animal behaviour literature (Kerth 2005), yet they comprise about 25% of all mammal species and the vast majority of them are social (Kerth 2008). In meta-analyses on aspects of sociality in mammals, bats are often excluded or detailed information is not available for use in the analysis (e.g. Clutton-block 2009, Ebensperger et al. 2012). Like other mammals, social behaviour of bats is influenced by the benefits of protection from predation (safety in numbers) as well as cooperation with familiar

individuals (Fenton et al. 1994, Kerth & van Schaik 2012, Kerth 2008). Kerth (2008) outlined three main factors that are thought to specifically influence bat social behaviour: (i) ecological constraints (roosts), (ii) physiological constraints (social thermoregulation), and (iii) demographic traits (longevity). These three factors partially explain social behaviour in a few species, but none fully explain the vast diversity of sociality observed in bats (Kerth 2008).

The vast diversity of social behaviours in bats includes but is not limited to food sharing (Wilkinson 1984), communal nursing (Wilkinson 1992b), pup guarding (Bohn et al. 2009), and group hunting (Dechmann et al. 2010). Additionally, the difference between sociality of males and females in some groups is not clear. Males and females of little brown bats (Fenton & Barclay 1980), Bechstein's bats (Kerth 2012), as well as most of the other bats of *Microchiroptera*, have social females and solitary males despite using the same types of roosts (Kerth 2008).

One unique constraint is that bats fly unlike any other mammals, and the cost of flight is very high (Voigt et al. 2012), so being able to use torpor can save a significant amount of energy. For females, there are additional constraints, since entering torpor causes the development of young to take longer, meaning they are pregnant for longer which is costly as well (Fenton & Barclay 1980). It has been observed that in colder regions, female bats almost always form maternity colonies (Kerth 2008) with the exception of some long distance migratory bats (i.e. hoary bat, Klug et al. 2012). Thus it may seem that these social groups are created to gain social thermoregulation benefits while raising young in the cold, yet the majority of bat species in the warm tropics are also social (Kerth 2008).

Finally, bats are unique in their longevity, with megabats (larger, old world bats) living for 5-10 years and microbats (smaller, new world bats) living for over 30 years (Barclay & Harder 2003). Like most mammals, bats often have at least one sex (usually females) which

display natal philopatry (return to their birth area; Burland & Wilmer 2001). Having bats return to the same area and living for multiple years creates groups that contain multiple generations, making a stable composition. With stable group structure, individuals are continuously exposed to familiar individuals, which is the ideal scenario for cooperation (Emlen 1994). These demographic factors may explain why females are social, but it does not explain the sociality observed in males of some species (e.g. Daubenton's bats, Senior et al. 2005). Thus neither roost constraints, temperature constraints nor demography explain the vast diversity of bat sociality. Given that bats are so widespread through different environments, this finding is expected, since social behaviour should be context specific – influenced by different factors in different environments

IV. Methodology of studying sociality

To continue the investigation of bat sociality, I will consider different variables that can be used to measure sociality. To assess and compare sociality between groups, Wilson (1975) described 10 characteristics of sociality. One of those characteristics, compartmentalization, has changed immensely in the last decade. In 2003, network analysis methods were first applied to animal societies, which allowed for a new way of comparing and analyzing societies (Whitehead 2008). Network analysis utilizes basic interaction data to expose hierarchies, clusters and key individuals which may keep the individuals and groups connected. This method was used in the more comprehensive studies on bat sociality mentioned above (Kerth & van Schaik 2012, Metheny et al. 2008). For most social analysis on animal behaviour, the program SocProg has been widely used (Whitehead 2009). SocProg can analyze data of over 1000 individuals, and produce association matrices in the form of sociograms (showing interconnectedness of individuals), principle component analysis (grouping factors together), and cluster analysis (which can reveal hierarchies and

communities). It is then possible to investigate preferences or avoidances of individuals and perform temporal analyses, to see how associations change over time (measured by lagged association rates). For example, temporal analysis was used to assess the order in which bats emerge each night as well as throughout the season. Gillam et al. (2011) found that the order of emergence of big brown bats is quite consistent over a short period of time, but this degrades as the season progresses. This shows that the bats can form short-term relationships, but they do not maintain them over the season, which is very informative for assessing how strongly associated individuals are with one another.

V. Objectives

My objective was to provide insight into questions surrounding the factors that may influence sociality in female mammals, specifically to continue to search for proximate causes. More specifically, what are the ways in which female mammals are social during the reproductive season and if there are factors that influence this behaviour to change? Understanding female social behaviour is important for making conservation decisions in terms of habitat and resource use (Kerth 2005). To begin to tackle these questions, I first have to address some basic questions about my species, such as: how are female little brown bats social? What is the social structure or patterning of social relationships? Is it a high fission-fusion dynamic or a constant coherent group? Does it change over the season, through the different reproductive periods? During the time when the demands are highest from the young, when they are first born and require frequent feedings, females may depend more on each other for help raising the young, and thus one would see high association rates between the breeding females during lactation, and lower associations during pregnancy and post-lactation. On the other hand, during the highly demanding lactation period, females may rarely associate with other females because they only have time and energy to focus on their

young. Thus I would expect high association rates during pregnancy and post-lactation, and low association rates when lactating.

From the basic question of understanding the way in which the females are social, I can begin to ask how this varies within a day, within a season and from year to year. Does their social structure persist over time? One way to look at this is to analyze the order in which they leave the roost in the evening, which may reveal if individuals are following each other and if they continue to do this throughout the season. Further, why do they switch roosts during the night? Are they looking for particular individuals? Are there dominant individuals kicking them out? So far, there have not been any recordings of dominance in female bats (Kerth 2008); if dominance was found in these females it would be quite influential on the way researchers think of bat sociality. Additionally, transitioning between roosts may also be seen as exploratory behaviour, and it would be interesting to see if the bats that like to explore are also bats with strong associations with others, or instead maybe they do not form strong bonds and thus move through the boxes, having no reason to stay in one area to be close to certain other individuals. At a larger time scale, bats also switch their day roosts from day to day, and although this has been recorded in many species, there has been no investigation into the pattern of day roost switching. This would be another interesting method for looking at social relationships, by looking to see if bats switch roosts in a similar order.

By tackling investigations of social structure, emergence order, and roost transitions, I aim to achieve a better understanding of little brown bat social behaviour. I expect that they will display fission-fusion dynamics as most well studied bats do, but I do not know what level of fission-fusion they will display. In terms of emergence order, a study on big brown bats found that there was some consistency between emergence order from day to day, but

this disintegrated over the season (Gillam et al. 2011). There has been no work done on characterizing patterns of roost transitions, so this will be an exploratory analysis.

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Chapter 2: Emergence behaviour

Abstract

Patterns in the behaviour of animals can reveal intricacies about their social structure, especially if the behaviour is in relation to others. To evaluate the social behaviour of little brown bats (*Myotis lucifugus*) in Newfoundland, I examined their behaviour during emergence from their day roosts both absolutely (concordance) and in relation to one another (relatively). Kendall's coefficient of concordance revealed significant concordance between bats emergence order throughout the season, meaning that the order in which a select few bats emerged from their day roost was consistent over multiple days through the season. When bats were considered associated if emerging in close proximity to one another (within 15 seconds), association indices had shown weak bonds between individuals. It is not clear why the bats emerge in a similar absolute order but not relative to one another, but this could be due to factors such as body condition or individual needs.

Introduction

Sociality amongst animals has historically been a challenging phenomenon to explain in terms of both proximate and ultimate causes (Crook 1970, Smith & Szathmáry 1995, Wilson & Wilson 2007). Alexander (1974) stated that sociality is universally detrimental due to increased competition for resources and risk of parasites and disease transmission. Others have argued the opposite, suggesting that sociality has many benefits, such as protection from predation (e.g., sperm whales, Arnbohm & Whitehead 1989; bats, Fenton et al. 1994), information transfer (e.g. African striped mice, Rymer et al. 2008; evening bats, Wilkinson 1992a; Bechstein's bat, Kerth & van Schaik 2012), and social warming (e.g. Sichuan snub-nosed monkeys, Zhang et al. 2011; Townsend's big-ear bats, Betts 2010). Whether sociality is beneficial or detrimental is context-specific, and the environment necessary to have initially

caused or maintained selection pressures on certain social behaviours remains to be understood in many cases. Ebensperger et al. (2012) reviewed the literature on female mammal sociality and noted that there was no consensus on whether it is beneficial, neutral, or detrimental to individuals. Two main trends observed in that study suggested that offspring cared for directly by their own parents had a higher survival rate, and sociality had greater benefits in the tropics than temperate zones. The researchers also noted that there was a disproportionately large number of studies on large carnivores, and lack of studies on large marine and small volant mammals (i.e., bats). Further, there was a bias towards studying certain species, specifically primates, in the tropics.

Bats stand out amongst other social animals, since they comprise 25% of all mammal species and the majority are social (Kerth 2008). The ubiquitous presence of sociality across chiroptera, combined with the diversity of life histories within this group, make them ideal for examining the factors mediating sociality. One aspect of bat sociality that has been focused on is information transfer, particularly information about resources, such as roost condition (Kerth 2005) or location of prey (Dechmann et al. 2010). For example, in *Molossus molossus*, a species that relies on ephemeral insects for food, bats from the same colony forage together (Dechmann et al. 2010). In another species that also forages on ephemeral insects, the evening bat *Nycticeius humeralis*, unsuccessful foragers follow more successful bats on subsequent foraging bouts. The followers were more successful than those that foraged alone following an unsuccessful night (Wilkinson 1992a). If the bat being followed also obtains some benefit from being followed, such as individual recognition by that individual which may result in reciprocity later on, then information transfer at roosts may be one benefit of group living that is important to certain bat species under specific or limiting environmental constraints.

Understanding how information is transferred at roosts is challenging. Kerth (2005) blocked the entrance of new roosts and observed attempts of Bechstein's bats to enter them. After an attempt by a bat to enter a blocked-off roost, subsequently arriving bats would not attempt to enter, which suggests that the bats were sharing information about roosts. In the same species, it has also been observed that relatives share the same general foraging site, although they do not forage together, but use different areas within the site at different times (Melber et al. 2013). Relatedness in colonies of *Molossus molossus* is not known (Dechmann et al. 2010), but their behaviour was opposite to that of related Bechstein's bat groups, where individuals follow and forage together. If bats forage together, then it may be expected that there would be a pattern in the order of emergence from roosts at dusk. Further, even if bats do leave the roost together and travel to the same area, they may not forage together, but their groupings can still inform us about the social structure of that species.

Studies that have examined clustering at emergence have found that temperature, light intensity, large colony size, presence of pups and drought can affect emergence behaviour and timing which may not be social in nature (greater horseshoe bat, Maltagliati et al. 2013; Brazilian free-tailed bats, Frick et al. 2012). Gillam et al. (2011) examined clustering patterns at a higher resolution - the individual level. By evaluating individual patterns of emergence, insight may be gained into interactions occurring between individuals within bat roosting groups. Perhaps it is not a reflection of social interactions but rather an action for individual gain, where individuals that emerge earlier may have access to more or better prey, but may be more susceptible to predation (Frick et al. 2012). For *Myotis lucifugus*, the early evening feeding bout is when the most food is obtained and when insect availability is highest (as compared to the second bout that occurs after midnight, Anthony & Kunz 1977). This may be especially important for lactating females, who have the highest energy demands

and were recorded consuming the most prey. Beyond access to prey, it is plausible that emergence order could also reflect dominant individuals leaving first to have the best access to food (such as alpha wolves, Thurber & Peterson 1993), or dominate individuals forcing submissives to leave, although dominance has not yet been recorded amongst female bats (Kerth 2008).

Bats are volant and thus able to travel quickly, which makes tracking them a challenge for researchers. They are also very small, which excludes the possibility of using certain technologies, such as GPS locators. The use of passive integrated transponder (PIT) tags, first used on bats by Kerth & Konig (1996), allows researchers to uniquely identify individuals with a permanent tag and monitor them without recapturing. PIT tags are small, ~7 mm long and <5% of the body weight, and in one long-term study have been found to have no significant effect on survival or reproduction (Rigby et al. 2012). By monitoring roosts with antennas that will record the unique code of each tagged bat as well as the time it passed by the antenna, researchers are able to investigate the fine scale movements and interactions of bats around these monitored roosts. Through this technology, it is possible to examine emergence behaviour at the individual level.

Gillam et al. (2011) examined emergence order of PIT tagged big brown bats at 16 roosts over 5 years and found that there was concordance of emergence order from day to day but that overall it decreased over the season. Bats were considered associated if they emerged within 15 seconds of each other, which produced low association rates that degraded after approximately 10 days. Overall, the authors concluded that emergence order can inform researchers about social behaviour. They state that combining emergence order with information of within roost movements and subgroup information could reveal overall social structure. Gillam et al. (2011) also note that patterns in roost emergence may be

important for bat species that live in human-made structures, which are expected to have stronger roost fidelity than tree roosting bats (since there are less roosts to choose from) and thus multiple groups may inhabit that same roost (which is usually larger than a tree roost).

Little brown bats (*Myotis lucifugus*) are long-lived, social microbats with females forming maternity colonies of 10s to 1000s of individuals (Fenton & Barclay 1980). They are generalist predators and have a more varied diet in northern than southern latitudes (Fenton & Barclay 1980). They often forage over water, and lactating females consume larger prey than others. Fertilization takes place in spring, and torpor delays gestation, so females seek warm roosts during this time (Fenton & Barclay 1980). Energy demands are higher toward the end of pregnancy but are highest during lactation. Maternity colonies consist of females and their young, with the rare occasional male. Young can thermoregulate by 10 days old, and are volant by 3 weeks, and continue to nurse for an additional 2 weeks, at which time they are nearly indistinguishable from adults. During the summer they typically roost in man-made structures in the day, but have been found in trees, under rocks and infrequently in caves.

The social behaviour of little brown bats around the roost is not well understood. Little brown bats that roost in trees have larger and more variable group sizes in trees with larger diameters (Olson & Barclay 2013). Further, larger diameter trees were used more near the beginning of parturition, and this is when the bats formed the largest groups. My study aims to answer a broad question: what is the social behaviour around roosts of female bats in maternity colonies? I hypothesize that if females maintain long-term social links with one another and exchange information about resources, there will be predictable patterns in emergence order of individuals. Specifically, bats will emerge in groups of individuals they have social bonds with, and there will be a great degree of concordance of emergence order

that will be maintained over the season. If absolute emergence order is not maintained, females will at least emerge close to other females they have strong bonds with, and thus may be seen to emerge within a short interval of one another.

Materials and Methods

Study area

Bats were captured from two maternity colonies in Eastern Canada, on the island of Newfoundland (Table 1). The forests in these areas are characterized by coniferous trees, dominated by Balsam Fir (*Abies balsamea*) and Black Spruce (*Picea mariana*) with regular occurrence of precipitation and fog (Thompson et al. 2003). One study site was located in Pynn's Brook, where 4 bat boxes were located outside of a building bordering the woods (bat boxes attached in pairs to posts located about 3 meters apart). The other study site was located at Salmonier Nature Park, which has 11 bat boxes: 8 were located on site (in pairs on poles, with two poles 20 m apart near one building, and the others adjacent to a building 0.5 km away about 10 m apart from each other), and three other boxes were located 1 km from these (2 boxes on one pole 1 meter from a garage which has another box attached to the side of it). All bat boxes were of similar size, with 4 internal chambers of varying depth.

Capturing and tagging

In 2011 and 2012, bats were captured as they emerged from the roosts at dusk using 6 m and 12 m mist nets approximately 1 m from the roost (Avinet Inc, Dryden, New York, USA) and a harp trap (Aust-bat Research Equipment, Lower Plenty, Victoria, Australia). During 2013, captures were made using the 6 m and 12 m mist nets at distances of 30 m to 2100 m from the bat boxes. Passively integrated transponders (PIT tags; EID-ID 100 implantable transponders, EIDAP Inc., Sherwood Park, Alberta, Canada) were placed subcutaneously between the shoulder blades of each bat, and physical measurements were

taken, age estimated, reproductive status was determined, and hair and tissue samples were collected. All the animal handling protocols were approved by the Saint Mary's University Animal Care Committee, and permits were granted by the Government of Newfoundland and Labrador.

Monitoring

PIT-tag antennae at the entrance of each bat box monitored its use by tagged bats. Ideally each time a tagged bat passed through an antenna, the date and time, bat box location and unique code for that individual were recorded. These monitoring units were deployed at both sites from May-August in 2012 and May-October in 2013 (monitoring equipment was not deployed during 2011).

Analysis

Analysis was modelled after Gillam et al. (2011). Two types of analyses are outlined below: concordance (comparing the order bats emerge in between days, regardless of the time of emergence) and associations (comparing the proximity in time of bats emerging from day to day). To precisely characterize emergence time, emergence counts were conducted throughout the season and it was found that emergence generally occurs between 1 and 3 hours after sunset. Within this period, the first record of each bat was taken as its emergence time, and any subsequent records from that individual were removed.

Concordance

To evaluate concordance between nights, the 5 nights with largest sample size were selected and bats present on all those nights were chosen for the analysis. Through emergence observations it had been noted that bats often emerged from one bat box roost and would fly to an adjacent box. Whether communication was occurring was unclear but, for that reason, the emergence order from nearby roosts might not be independent. Only

data from each roost (only sufficient data for roost 6, SNP) or pair of roosts (i.e., those 2 roosts attached to a single pole) were considered separately (data was not pooled for all of Salmonier since bats were likely not in contact/communication with those at more distant boxes).

First, I evaluated whether reproductive and non-reproductive bats emerged at different times, which would affect whether they would be grouped for the next analysis. Kendall's coefficient of concordance (W) was calculated in R (R Core Team, 2013) using `vegan: Community Ecology Package` (Oksanen et al. 2013), 10 000 random permutations were performed to determine probability of the outcome. For Kendall's coefficient, if W is 1, then the order of emergence was the same each night, whereas if W is 0, none of the orders was the same. To evaluate if concordance values were related to the number of days between nights, a mantel test was performed to compare the W value between each pair of top nights to the temporal distance (number of days) between each pair. I was unable to evaluate if concordance changed with reproductive period, since the top 5 nights for each roost mostly occurred during the pregnancy period defined as before July 4th (first babies appeared in bat boxes June 30th at SNP, with a significant portion of 30 young present by July 4th). There was also much variation in birthing time, with pregnant females being captured throughout July, which complicated defining distinct reproductive periods.

Association data

For association data, the busiest roosts were chosen at each site, and bats were considered associated if they emerged within 15 seconds of one another (Gillam et al. 2011). This seems reasonable given that Wilkinson (1992a) found that associated females leave within 10 seconds of one another on subsequent foraging bouts within the same night more often than expected by chance. Using `SocProg` (Whitehead 2009), temporal analysis was

conducted with each day set as a different sampling period, and for Salmonier, only bats with at least 10 records (Pynn's Brook = 5 records) and days with at least 20 bats (Pynn's Brook=10) present were included (as per Gillam et al. 2011). The half-weight association index was used to calculate the standardized lagged association rate (SLAR), which is the measure of likeliness for a pair of bats associated at time zero to be associated at following time periods (Whitehead 2008), between bats both within a season and between seasons. Half-weight association index measures the number of times a pair is observed in the same group, underestimates associations, allowing for tagged individuals which are present but not recorded as such (Whitehead 2008). This metric was standardized because the bats were recorded for different amounts of time and many were not recorded every day (see Whitehead 2008 for discussion). To calculate the standard error of the SLAR, a temporal jackknife method, where the analysis is run multiple times, each time omitting one or more sampling days (note: this was not performed for all of the Pynn's Brook roosts as there were not enough data).

Results

From the initial 228 992 PIT-tag records at Salmonier, after filtering for first record during emergence, 12 469 records remained; at Pynn's brook, 52 670 initial PIT-tag records, with 4 609 filtered records remained. Since there was no obvious difference between emergence times of reproductive and non-reproductive females at Salmonier (Figure 1), they were pooled for subsequent analysis.

Concordance of emergence between the top five nights at Salmonier was significant for all roosts and roost combinations except roost 6 in 2012 and roosts 7 and 8 in 2012 (Table 2). The two non-significant concordance roosts only had 5 and 4 bats available for analysis, respectively, and W values of 0.42 and 0.33. Significant concordance values had W

values ranging from 0.49 to 0.86 ($p > 0.05$). For all roosts, despite large differences of greatest time between pairs on the top 5 nights, there was no significant relationship between concordance of emergence and time between nights (mantel test, $p \geq 0.363$). Kendall's W between each pair of nights at each roost was between 0.6 and 0.9, despite the number of days between the pair (Figure 2). The values at 0.4 and below were from roost 6 2012 and roosts 7 and 8 2012, both of which had a low number of bats present (5 and 4) and insignificant W values. Roosts at Pynn's Brook and the remaining roosts at Salmonier (Roost 1&2, 3&4, and 9&10&11) had too few individual records for the concordance analysis.

Based on associations of emergence within 15 seconds of one another, there were no strong associations between individuals, with a mean association of 0.01 and a maximum association of 0.10 for the two busiest roosts at Salmonier both within each season and between seasons (Table 3). There was a general decrease in association rate over time, however temporal analysis of standardized association rate was not significantly different from the null within each year (Figure 3). When data was restricted to only bats present for both seasons, and associations were evaluated from one season to the next, there was a decrease in SLAR through the first season and this remained around the null for the second season, suggesting bats do not maintain their weak associations from one season to the next (Figure 3).

At Pynn's Brook, mean associations were low, ranging from 0.01 to 0.02, with a maximum association of 0.19. Pynn's Brook was quite different from Salmonier for temporal analysis; at roost 1&2, in 2012 the standardized association rate was not significantly different from the null, but in 2013 it was higher than the null (Figure 4). Between years, roost 1&2 showed an increase of standardized association rate in the second season, similar to the pattern observed in the first season (Figure 4), indicating pairs associate more as the season

progresses. At roost 3&4, the association rate in 2012 is significantly higher than the null until approximately 25 days, and analysis could not be performed on 2013 due to lack of data (Figure 4). Comparing both years at roost 3&4, the association rate did not increase in the second year (Figure 4). Finally, when all bats were pooled at the site, those that were present both years had a standardized association rate that did not differ from the null (Figure 4).

Table 1. New bat captures (not previously tagged) from 2011-2013 at Pynn’s Brook and Salmonier Nature Park, Newfoundland. F=female, M=male.

		Adult		Juvenile	
		F	M	F	M
Pynn’s Brook	2011	17			
	2012	106			
	2013	166¥	1	32	31
Salmonier Nature Park	2012	322*	2	61	67
	2013	345€	6	20	18

¥ An additional 34 previously tagged adult females were recaptured in late summer

* An additional 14 previously tagged adult females recaptured in late summer

€ 67 previously tagged adult females and 1 previously tagged male were recaptured throughout the season

Note: One trapping session occurred in 2011 at Pynn’s Brook for a single night in late July. In 2012, there was an initial trapping session of 2 days at Pynn’s Brook and 3 days in Salmonier in May, and a second trapping session over two weeks in August only at Salmonier. In 2013, two trapping sessions occurred in Pynn’s Brook – early June and early August for 2-3 nights; at Salmonier, trapping occurred from the beginning of June through to the end of July.

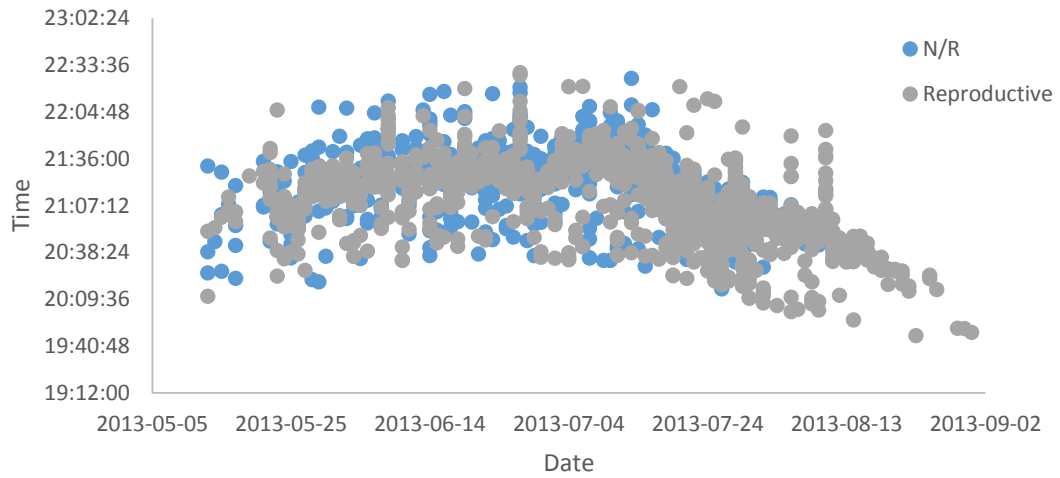


Figure 1. Comparison of emergence time of adult female *M. lucifugus* of known reproductive status at Salmonier Nature Park, 2013. N/R=non-reproductive.

Concordance

Table 2. Concordance analysis of *Myotis lucifugus* bats emerging from busiest roosts (most records) at Salmonier Nature Park on all top 5 nights (nights with greatest number of tagged bats emerging through each season).

Roost	Year	<i>n</i>	Max days	Kendall W	<i>P</i>	Mantel r	<i>P</i>
Roost 6	2012	5	26	0.424	0.061	0.144	0.420
	2013	11	27	0.717	*5.93x10 ⁻⁸	-0.665	1.000
Roost 5&6	2012	7	25	0.646	*2.52x10 ⁻⁴	-0.412	0.753
	2013	14	6	0.859	*4.05x10 ⁻¹⁷	-0.030	0.599
Roost 7&8	2012	4	31	0.328	0.186	-0.207	0.688
	2013	10	11	0.597	*6.76x10 ⁻⁵	0.268	0.363
Roosts 5-8	2012	17	11	0.497	*5.08x10 ⁻⁵	-0.899	0.991
	2013	15	33	0.491	*1.70 x10 ⁻⁴	0.079	0.513

*significant results

Note: Only roost 6 had sufficient data for independent analysis, all others were analyzed as pairs of roost boxes attached to the same pole. The last analysis pools all roosts, 5 through 8, where roost 5&6 are located ~20 m away from 7&8. Kendall W indicates the level of concordance between the emergence orders of the 5 nights, with *P* indicating significance. *n* = number of individuals. Max days = greatest number of days between any pair of top roosting nights at that site.

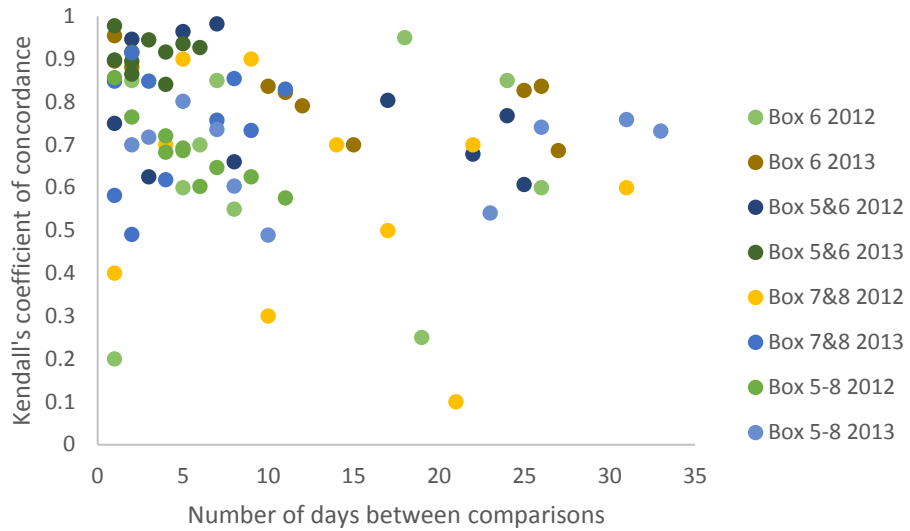


Figure 2. Kendall's coefficient of concordance of emergence order between each pair of days at Salmonier. Kendall's coefficient was calculated between all pairs of days for each site, and this was compared to the number of days between the pair of days analyzed. All the points under a coefficient of concordance of 0.4 are from roost 6 in 2012 and roost 7&8 in 2012 where only 5 and 4 bats respectively were available for analysis, which was the lowest amount used for analysis.

Associations

Table 3. Association analysis of emergence order of *Myotis lucifugus* from multiple roosts at Salmonier. Association index mean and maximum was calculated for each season and both seasons combined using half weight index. Only days with 20 bats emerging and only bats with at least 10 records were included. n = number of individuals.

Roost	Year	N	Association (SD)	
			Mean	Maximum
Roost 5&6	2012	58	0.01 (0.01)	0.09 (0.02)
Roost 5&6	2013	82	0.01 (0.00)	0.09 (0.04)
Roost 5&6	2012-2013	104	0.01 (0.00)	0.09 (0.03)
Roost 7&8	2012	46	0.01 (0.01)	0.10 (0.04)
Roost 7&8	2013	88	0.01 (0.00)	0.09 (0.04)
Roost 7&8	2012-2013	84	0.01 (0.01)	0.09 (0.05)

Table 4. Association analysis of emergence order of *Myotis lucifugus* from multiple roosts at Pynn’s Brook. Association index mean and maximum was calculated for each season and both seasons combined using half weight index. Only days with 10 bats emerging and only bats with at least 5 records were included. n = number of individuals.

Roost	Year	n	Association (SD)	
			Mean	Maximum
Roost 1&2	2012	78	0.01 (0.00)	0.11 (0.04)
Roost 1&2	2013	58	0.01 (0.01)	0.19 (0.08)
Roost 1&2	2012-2013	32	0.02 (0.01)	0.08 (0.02)
Roost 3&4	2012	58	0.01 (0.01)	0.12 (0.04)
Roost 3&4	2013	46	0.01 (0.01)	0.19 (0.11)*
Roost 3&4	2012-2013	24	0.02 (0.01)	0.09 (0.03)
All	2012-2013	56	0.02 (0.01)	0.10 (0.02)

* based on 20 days of data

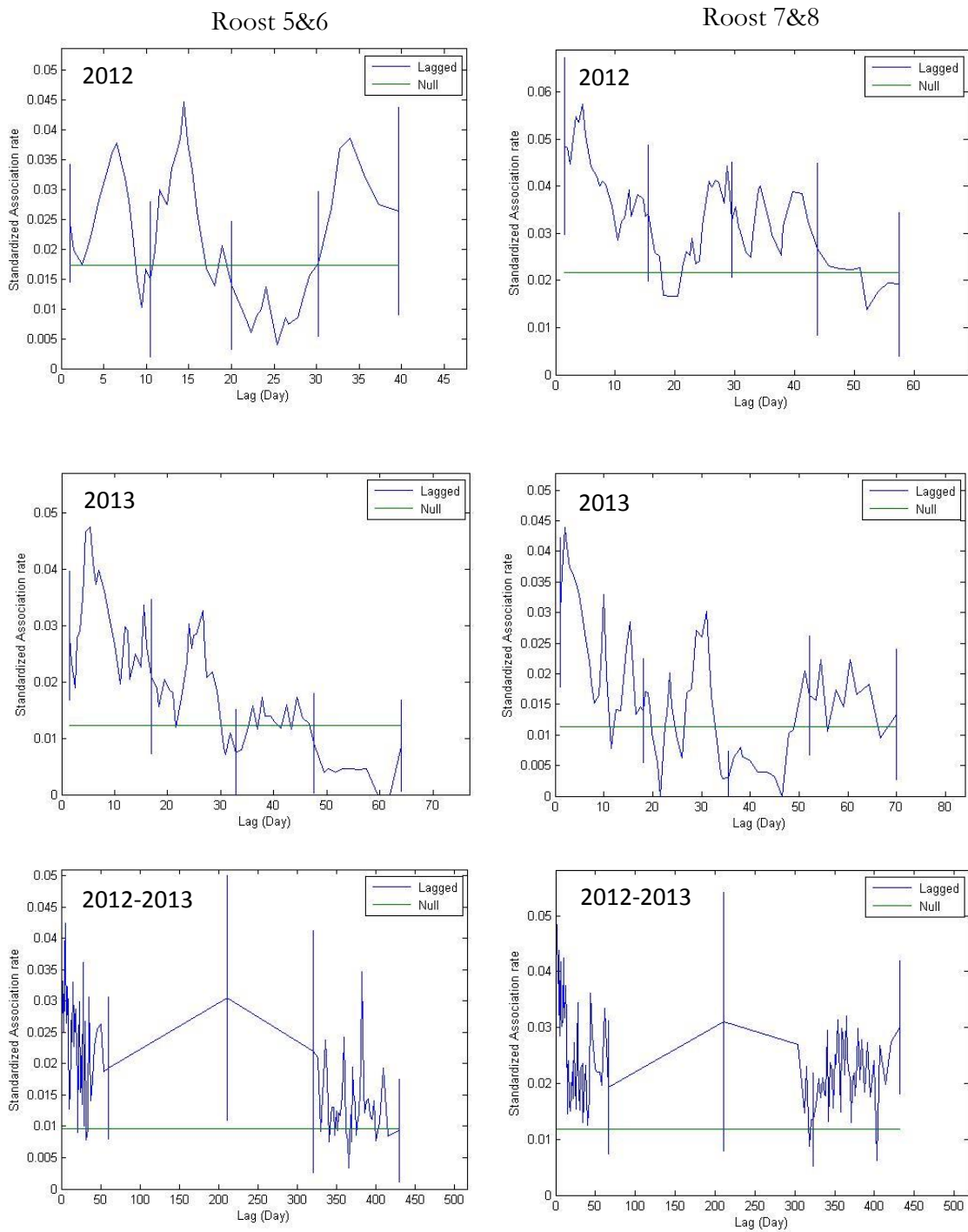


Figure 3. Temporal analysis associations (half-weight index) for two roost sites of one colony at Salmonier Nature Park of *Myotis lucifugus*. Roost 5&6 and Roost 7&8 during 2012, 2013 and over both seasons. Analyses of standardized lagged association rate of individuals over time. Vertical lines represent standard error for lagged associations.

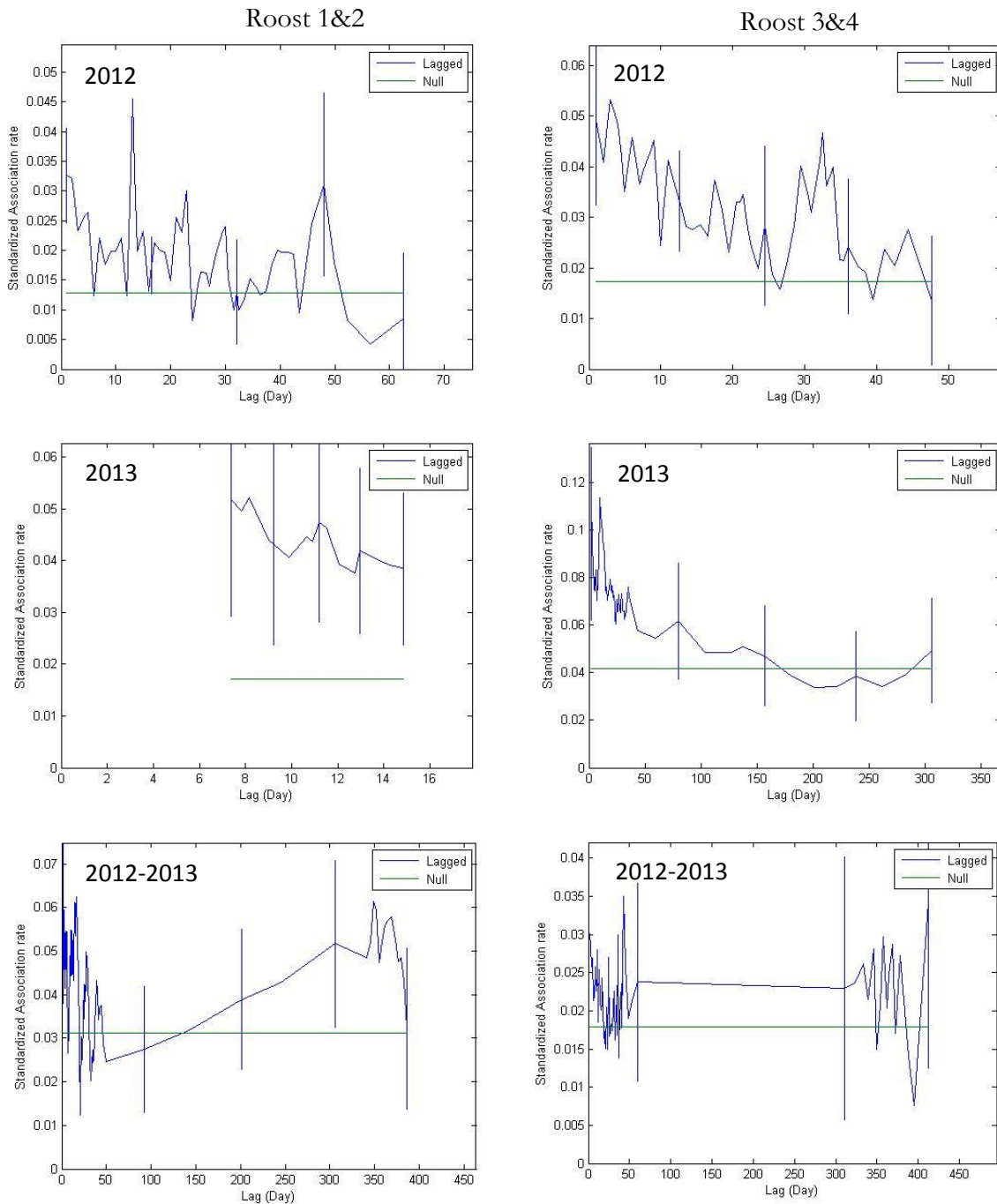


Figure 4. Temporal analysis for two roost sites of one colony at Pynn’s Brook of *Myotis lucifugus*. Roost 1&2, Roost 3&4, and all roosts combined during 2012, 2013 and over both seasons. Analyses of standardized lagged association rate of individuals over time. Vertical lines represent standard error for lagged associations. Note: Roost 3&4 2b is missing, only 20 days of data was not sufficient for temporal analysis.

Discussion

My study found support for the hypothesis that female little brown bats maintain somewhat long-term social links that are reflected through the maintenance of dusk emergence order patterns for up to 33 days. There was significant concordance ($p > 0.05$) between the top 5 nights at the busiest roosts of Salmonier, with Kendall's W ranging from 0.49 to 0.86, which is higher than W observed in big brown bats, ranging from 0.32 to 0.77 (Gillam et al. 2011). There was no relationship between concordance and distance between pairs of days on which it was analyzed, suggesting that concordance of emergence is maintained throughout the season in *M. lucifugus*, unlike the big brown bat which only maintains concordance for short periods (Gillam et al. 2011).

Association rates for both Salmonier and Pynn's Brook were low, with mean associations of 0.01 to 0.02, and a maximum association of 0.19. Generally, standardized lagged association rates did not differ from the null association rate, meaning there was no evidence of persistent groups being formed during emergence; the same trend was also observed in big brown bats (Gillam et al. 2011). The observed concordance of emergence order but lack of significant associations may mean that emergence order does not indicate sociality, or that my definition of association, emerging within 15 seconds of one another, is not appropriate for the colonies under study. There was a trend at both Salmonier roosts for an increase in standardized association rate in the second season, after a decline through the first season. This suggests that when the bats return from hibernation, they tend to have stronger associations with the same individuals during this time than they had in the previous year. It is possible then that long-term social bonds are maintained from year to year, but not throughout the season. This result is not statistically significant for roost 5&6, although the pattern is visible in the graph, but for roost 7&8, it is above the null (but only for that short

window of time). The next step for this study would be to investigate how reproductive status affects the associations (we did not have the reproductive information for the bats after censoring data) and monitoring how that status changes from year to year (there were always non-reproductive adult females captured throughout the season).

Given that the bats maintained relative emergence order, evidenced by their general emergence concordance between nights, it is somewhat surprising that standardized association rates were not, on average, higher than the null association rates. The emergence order analysis involved a small subset of tagged individuals, which is due to the nature of the Kendall's coefficient of concordance, which requires only individuals present on all days evaluated are included. In contrast, the association analysis included many more individuals, and instead of evaluating relative emergence order for comparison, it examines absolute emergence order. Therefore, it seems that the bats emerge relative to one another, but when associations are based on emerging within a short time period of 15 seconds of each other, this is not the case. Data from roost 6 and roost 7&8, suggests that the number of bats included may be correlated to the ability to detect trends; these two roosts had the smallest number of bats included in their analysis, and were the only roosts to have no significant concordance between nights. I conducted a power analysis for a correlation test (there is no power analysis for Kendall's coefficient) and the sample size was not large enough to detect a small effect size. By including more individuals into the Kendall's relative emergence order analysis, researchers may be better able to understand the connection between relative and absolute emergence order and the importance they have for the bats.

Other factors concerning equipment may have influenced my ability to investigate emergence order. In my study system, not all individuals are tagged, and those that are tagged are not always recorded due to equipment failure or lack of sensitivity. Furthermore, there

may have been bias resulting from limiting emergence time to the time from 1 hour after sunset to 3 hours after sunset, which left a 2 hour ‘window’ for emergence. The longest emergence count observed in the field was 1h 20min, which means that in a two hour emergence window, there is the opportunity for bats to come from unmonitored roosts or roosts where their tag was not recorded due to some malfunction, and they can enter another roost, and this is actually a roost switch or return from foraging, but may be recorded as an emergence for that individual. Further, only taking the first recording of each bat for each night may have biased the data since it has been observed that bats may wait at the edge of the bat box, often on the antenna, and will sometimes crawl back into the box – thus their emergence record may not reflect their true emergence time (this behaviour was observed several times during emergence counts, but may be due to the presence of researchers and not a true reflection of the behaviour of the bats). The approach of using the first record during the emergence period eliminates the chance of using an emergence time that is the bat returning to the roost, and this is a trade-off.

In comparison, big brown bats have shown concordance between nights that were close together, but this degraded with increased time intervals (Gillam et al. 2011). Association rates were low and the lagged association rates did not differ from the null associations. Gillam et al. (2011) hypothesized that these results could be the reflection of the fission-fusion dynamics of big brown bats, where individuals form short-term groups which break apart and reform into new groups. The social structure of colonies of *M. lucifugus* is unknown, but from my findings it is likely that this species does not randomly associate. It is likely that many more years of data may be required for such large colonies, given that for small colonies of 20-45 Bechstein’s bats, long term data sets of 15 years were necessary (Kerth & Van Schaik 2012).

In a similar species, the standardized lagged association rate has shown that *Myotis septentrionalis* form groups which remain for approximately 10 days before dissociating, and some individuals form long-term relationships that are maintained throughout the season (Garroway & Broders 2007). Their study differs in their definition of bats being associated. For this chapter, and Gillam et al. (2011), bats were only considered associated if they emerged within 15 s of one another, whereas in the Garroway & Broders (2007) study, bats were considered associated if they shared the same day roost. For all the bats in the Gillam et al. (2011) study, they all shared the same day roost, and thus would be considered always associated according to the definition of association used in Garroway & Broders (2007). The study system of Gillam et al (2011) was fundamentally different because only 1 roost was monitored at each site, and thus roost switching could not be recorded, necessitating a more strict definition of association. I limited my data in this chapter to look at each roost or pair of roosts separately, for the data to be comparable to Gillam et al. (2011), however the following chapter will evaluate associations similarly to Garroway & Broders (2007).

Another hypothesis proposed by Gillam et al. (2011) is that individuals may be under different energetic constraints depending on their body condition or reproductive status, and bats with higher energy demands (reproductive, poor body condition) emerge earlier. When considering all females at Salmonier for which I have reproductive status information, emergence time overlaps between reproductive and non-reproductive individuals. Unfortunately, I did not have enough data for analysis of concordance of emergence order between reproductive periods. Gillam et al. (2011) suggest that body condition is more likely to influence emergence order, hypothesizing that bats with poorer body condition must emerge earlier to have more foraging time. In future studies, body condition and emergence time should be compared in female *M. lucifugus* and other bat species.

With my results it remains unclear whether information transfer occurs in colonies of *M. lucifugus*, since this was not directly assessed. If individuals emerged in groups, it is possible that they had shared information about resources, such as prey, but no consistent pattern was observed in emergence behaviour. This begs the question of why this species gathers in colonies – is it only for the shelter of the bat boxes? At Salmonier there are 11 bat boxes of similar dimension, although some are higher than others, different colours, differing clutter/tree branches around the entrance, differing proximity to the woods and water, and there is greater variance in the number of bats that consistently occupy them. Olson & Barclay (2013) found larger and more variable group sizes occupied tree roosts of larger diameters, however the bat boxes in my study site were of similar diameter. Perhaps information transfer does occur but is not reflected in the fine scale of absolute emergence, but there could be following that occurs with the maintenance of relative emergence order.

In conclusion, *M. lucifugus* exhibit significant concordance in relative emergence order yet they do not form groups based on associations of emerging within 15 seconds of one another. It seems likely that this observation may be due to individual qualities, such as social status or body condition, but not reproductive status. Between seasons there is an increase in lagged association rates at the beginning of the second season, and this may be an indication of long-term bonds, but it is unclear. Future research should focus on whether groups are formed after emergence, which could be answered through telemetry studies. Additionally, analysis of behaviour within the bat boxes would inform us about their social structure, if any, albeit it is challenging given the numerous amount of individuals within each roost.

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Chapter 3: Patterns of roost use

Abstract

The way bats use roosts has often been used to discern their sociality. I examined day and night roost use of little brown bats (*Myotis lucifugus*) in Newfoundland. I found that bats at a smaller site with fewer roosts tended to use a larger portion of those roosts whereas at the larger site, they used only a few. Bats switched their day roosts up to 37 times throughout the season, but when analyzing night roosting activity, it was found that bats would switch roosts often, up to 60 times within a night, with reproductive bats switching more frequently. Associations based on day roosts revealed weak social bonds between individuals. Overall, little brown bats seem to switch roosts more often than expected but possibly not based on relationships with other bats.

Introduction

Behaviour is the most immediate and direct way an animal can acclimatize to a change in the environment and this may be of utmost importance to the persistence of a species (Kappeler et al. 2013). The diversity observed in mammals, from brain size, longevity, and especially social complexity, amongst other traits, make this group ideal for studying the causes of flexibility in social behaviour (Crook 1970, Ebensperger et al. 2012). In a review of flexibility in mammal sociality, Kappeler et al. (2013) suggested that a Tinbergian approach is necessary to better understand sociality, considering both ultimate and proximate causes. The authors outline developmental, genetic, ecological and evolutionary constraints as the main factors affecting sociality, insisting they must be examined in conjunction with one another. This chapter will focus on proximate causes, specifically environmental constraints of suitable roost availability as well as the intrinsic trait of reproductive status.

Unlike most mammals, most bat species cannot create their own roosts, and this is thought to pose strong ecological constraints on them, especially for temperate zone bats, which are exposed to extended periods of cold without a food source (Kerth 2008). Bats comprise 25% of all mammal species, and exhibit a wide range of social behaviours (e.g., pup-guarding, Bohn et al. 2009; food sharing, Wilkinson 1984; group hunting, Dechmann et al. 2010), however there are gaps in the understanding of the factors influencing their sociality (Kerth 2008). In bat research, there has been much interest in roost use by bats, especially in terms of factors and key roost characteristics driving roost selection (Brigham et al. 1997, Henderson & Broders 2008, Clement & Castleberry 2013). It is unclear whether the limited supply of roosts is the main cause for bats to gather in groups, but given the many environments (tropics and temperate areas, availability of different types of roosts in the area, and so on) in which bat sociality occurs (from leaf roosts to rare large caves), it is unlikely this constraint can explain sociality in bats (see Kerth 2008 for a full discussion). To uncover the factors causing sociality in mammals, ecological constraints must be considered in conjunction with other factors, such as life history, genetics and mating system (Kappeler et al. 2013).

Along with ecological constraints, animals also experience social constraints, where social interactions with others are part of the environment affecting their behaviour and fitness (Kappeler et al. 2013). In a recent review of methodology employed in the study of bat social behaviour, Johnson et al. (2013) contends that many studies on bat sociality focus on day roost co-habitation as the measure of sociality, and this may provide a mere superficial understanding of their sociality. The authors give the example of the common vampire bats studied by Wilkinson (1984) where many individuals may inhabit the same roost but only food share with certain individuals, and thus there are varying levels of social

interactions within a co-inhabited roost. They also give an example from the social analysis of striped free-tailed bats by Rhodes (2007). Bats captured at one communal roost were radio-tracked to other small day-roosts. Based on day-roost use, bats associated with their day-roost mates less frequently than expected, however they would all congregate at the large communal roost during the night; the author suggests that night time behaviour be included in association analysis to gain complete insight (Rhodes 2007).

Day roosting behaviour

Little brown bats, *Myotis lucifugus*, form maternity colonies consisting of 10s to 1000s during the summer, and may use roosts during the day and night (these are usually physically separate), however day roosts are often in human-made structures (Fenton & Barclay 1980, Anthony et al. 1981). Maternity colonies that use trees during the reproductive period have been observed to use larger trees at the beginning of parturition which is also when group sizes are largest (Olson & Barclay 2013). Individual little brown bats also switch between roosts throughout the season, but the patterns of this roost use are not known. Big brown bats *Eptesicus fuscus* are non-randomly associated in a fission-fusion network, frequently switching day roost trees, with the amount of switching correlated with the number of bats using the roost (Willis & Brigham 2004). A well-studied species, *Myotis bechsteinii*, lives in maternity colonies and switches between communal day roosts on an almost daily basis, and individuals are able to maintain long-term social bonds within structured communities connected together by older individuals (Kerth 2005, Kerth et al. 2011). When the group of bats under study experienced a sharp decline after a harsh winter, long-term bonds were maintained but the substructure of two communities within the colony disappeared (Baigger et al. 2013).

Day roost use may vary as energetic needs change. In Daubenton's bats, where both females and males form separate social groups (with different structure), both sexes use different roosts through the season (Lučan & Hanák 2011). During gestation, females use warmer roosts whereas males almost exclusively use colder roosts, and this is likely due to the costs of torpor during pregnancy. As juveniles become volant, adult females use colder roosts, which may help the bats take advantage of torpor; At the same time, males are found in the warmer maternity roosts, as mating begins (Lučan & Hanák 2011). Therefore, looking at roost use over a season may mask the more subtle roost selection that occurs as energetic and environmental factors change, and temporal use must be taken into account.

Night roosting behaviour

For *M. lucifugus* night roosts are generally separate from day roosts and are used between foraging bouts (Anthony et al. 1981). Night roost use varies through the season, depending on prey, temperature and reproductive status, with night roosts used most during late summer, once juveniles are volant. Night roosting duration is longest on cold nights, and they are rarely used by reproductive females during lactation, as they must return to the maternity roost for the young at this time (Anthony et al. 1981).

I hypothesized that given the general grouping behaviour of *M. lucifugus*, combined with female roost fidelity (0.23 to 0.53 probability of young to return in next year, Frick et al. 2010) and longevity of up to 34 years (Davis and Hitchcock, 1995), they will form social bonds which will be apparent in their day roost use, but that these bonds may vary with reproductive status, and if so, I expect that lactating females may form stronger social bonds than non-reproductive females. Social bonds may be long-term associations that persist throughout and between seasons, or there may be some variation of strong and weak bonds that may degrade over time. Further, I may expect that individuals that have a high incidence

of nightly roost visits may have a higher connectedness to others, forming stronger social bonds, since they are exposed to more individuals and thus have more opportunity to interact and form bonds. Alternatively, those that remain in the same roost may maintain stronger bonds with a subset of individuals rather than weak bonds with many individuals.

Methods

Study area

Bats were captured from two maternity colonies in Eastern Canada, on the island of Newfoundland (Table 1). The forests in these areas are characterized by coniferous trees, dominated by Balsam Fir and Black Spruce with regular occurrence of precipitation and fog (Thompson et al. 2003). One study site was located in Pynn's Brook, where 4 bat boxes were located outside of a building bordering the woods (bat boxes attached in pairs to trees located about 3 meters apart). The other study site was located at Salmonier Nature Park, which has 11 bat boxes: 8 were located on site (in pairs on poles, with two poles 20 meters apart near one building, and the others at a building 0.5 km away about 10 meters apart from each other), and three other boxes were located 1km from these (2 boxes on one pole 1 meter from a garage which has another box attached to the side of it). All bat boxes were of similar size, with 4 internal chambers of varying depth.



Figure 1. Site map of Salmonier Nature Park. FH area is 1 km from the main park and has three roosts within 1 m. Within the park there are 8 roosts, 1-4 are by headquarters (HQ) and 5-8 are by the visitors centre (VC). All roosts were monitored in 2012 and 2013 except for roosts 9-11 were not monitored in 2012.

Capturing and tagging

In 2011 and 2012, bats were captured as they were emerging from the roosts at dusk using 6 m and 12 m mist nets ~1 m from the roost (Avinet Inc, Dryden, New York, USA) and a harp trap (Aust-bat Research Equipment, Lower Plenty, Victoria, Australia). During 2013, captures were made using the 6 m and 12 m mist nets at distances of 30 m to 2100 m from the bat boxes. Passively integrated transponders (PIT tags; EID-ID 100 implantable transponders, EIDAP Inc., Sherwood Park, Alberta, Canada) were placed subcutaneously between the shoulder blades of each bat, and physical measurements, age, reproductive statuses, hair samples, and tissue samples were collected. All the animal handling protocols were approved by the Saint Mary's University Animal Care Committee and permitting was granted by the Government of Newfoundland and Labrador.

Monitoring

PIT-tag monitoring equipment was used to monitor the use of bat boxes by the tagged bats, with an antenna placed over the entrance of each box. Each time a tagged bat passed through an antenna, the date and time, bat box location and unique code for that individual was recorded. These monitoring units were deployed at both sites from May-August in 2012 and May-October in 2013.

Analysis: Roost use

Whole season: To understand how bats used the roosts available to them, the number of roosts used in a season (Figure 2), and specifically the area of roosts used at Salmonier Nature Park (map Figure 1, roost use Figure 3) were examined. *Day use:* the number of day-to-day roost switches for each year at each site was estimated (Figure 4). *Night use:* to evaluate night roost visiting frequency, the number of roosts visited within each 24-hour period was

estimated (Figure 5). This night visiting behaviour was compared to multiple network statistics (defined below) for each individual with a known reproductive status.

Analysis: Social structure

To evaluate social structure, I used the two seasons of data from each site, including only bats recorded on >9 days, and only days for which there was day-roost location data for >9 bats. Analysis was performed on each year separately, and on bats only present for both seasons. To analyze associations, day-roost use for each bat was entered into SocProg (Whitehead 2008) and the half weight index (ranging from 0=no associations to 1=always associated) was used to calculate individual and average associations. Network analysis was performed, calculating individual and overall strength, eigenvector centrality, reach, clustering coefficient and affinity as defined by Whitehead (2009). Strength for an individual is the total of all their associations with every other bat in the analysis. Eigenvector centrality measures how connected an individual is to others, and how well the other bats it associates with are connected, essentially measuring if bats that form strong associations will associate more with other bats that form strong associations. Reach is important for seeing how behaviour can propagate through a society, and evaluates how individuals are indirectly connected to others in the network. Clustering coefficient evaluates how well connected the bats associated with an individual are. Affinity combines strength and association indexes, comparing the strength of associations of a bat associated with the individual and weighting this by the association index value between the bat and the associated bat. Temporal analysis was calculated for each season and the combined seasons for each site.

Results

From SNP and PB, 281 663 PIT tag records were obtained from monitoring during 2012-2013. Day roost use differed between the two sites. At PB there were only 4 known

roosts, and 90% and 70 % of tagged bats used all the roosts in 2012 and 2013 respectively (Figure 2). At SNP, in 2012 it was found that the majority of bats used 4 roosts through the season. In 2013, with 11 roosts monitored, most bats used 4-8 roosts. When examining SNP roost use by site, it was found that 36% of bats would use both sites that were 1 km apart and the rest were only recorded at one general site (Figure 3), indicating that this is likely the same colony, with colony defined as a group where individuals have the opportunity to interact with each other as per Johnson et al. (2012) (Figure 1, 3).

Roost switching from one day to the next varied by individual. A majority of bats at SNP switched roosts 1-11 times, one up to 37 times (Figure 4). At PB, most bats switched roosts between 1 and 15 times, up to 33, in the season. Night roost visits during 24 hours peaked during July, and was most frequently observed from reproductive females, more so at SNP than PB (Figure 5).

Most associations were weak (0 to 0.1, left panel, Figure 6-7), however PB had a higher frequency of stronger associations. At SNP, mean associations ranged from 0.05 to 0.11 within a season, with a maximum associations ranging from 0.43 to 0.51. When bats present at SNP for both 2012 and 2013 were analyzed, mean association was 0.07 with a maximum of 0.34. At PB, mean associations ranged from 0.08 to 0.14 within a season, with a maximum associations ranging from 0.35 to 0.44. When bats present at PB for both 2012 and 2013 were analyzed, mean association was 0.13 with a maximum of 0.40. Overall network analysis for each site did not reveal any significant strength, eigenvector centrality, reach, clustering coefficient or affinity. In the temporal analysis, associations started higher than the null association until 70-80 days for SNP 2012, SNP 2013, and PB 2012, but only until 25-30 days for PB 2013 (right panel, Figure 6-7). When data sets from both seasons were combined (bottom right panel, Figure 6-7), both sites initially showed a significantly

high association rate which decreased throughout the first section of the time lag, but in Salmonier there was an increase in association rate in the second portion, and these reflect associations taking place during the second season exclusively given the time elapsed between the first day associated and 250 days or more later (note: during the first portion of the time lag, there may be both associations from either the first or second season). When a similar analysis was conducted for Pynn's Brook, the second portion of the time lag had association rates that did not differ significantly from the null.

Comparisons of network measures between reproductive classes to maximum night roost visits did not show any statistically significant relationships (Figure 8). Although reproductive bats switched roosts more often, they were not more socially connected in any aspect of network analysis than the non-reproductive bats.

Table 1. Mean and maximum association values using half weight index for both sites of *M. lucifugus* over two years analyzed separately and together. For analysis of combined years, only bats present both years were included.

Roost	Year	<i>n</i>	Association (SD)	
			Mean	Maximum
SNP	2012	112	0.11 (0.04)	0.51 (0.14)
	2013	267	0.05 (0.02)	0.43 (0.16)
	2012-2013 (bats both years)	149	0.07 (0.03)	0.34 (0.14)
PB	2012	81	0.14 (0.03)	0.44 (0.11)
	2013	63	0.08 (0.02)	0.35 (0.08)
	2012-2013 (bats both years)	71	0.13 (0.03)	0.40 (0.10)

Table 2. Network analysis values from associations calculated using half weight index for both sites over two years analyzed separately and together. For analysis of combined years, only bats present both years were included.

Roost	Year	Strength	Eigenvector centrality	Reach	Clustering coefficient	Affinity
SNP	2012	11.98 (4.32)	0.09 (0.04)	161.92 (67.13)	0.22 (0.05)	13.05 (2.00)
	2013	12.61 (6.18)	0.05 (0.03)	197.09 (120.14)	0.15 (0.06)	14.40(3.30)
	2012-2013 (bats both years)	10.68 (5.12)	0.07 (0.04)	140.19 (77.74)	0.16 (0.04)	12.52 (1.71)
PB	2012	11.24 (2.78)	0.11 (0.03)	134.05 (35.90)	0.26 (0.03)	11.86 (0.48)
	2013	5.25 (1.47)	0.12 (0.04)	29.72 (9.57)	0.22 (0.03)	5.58 (0.43)
	2012-2013 (bats both years)	8.98 (2.24)	0.11 (0.03)	85.65 (23.09)	0.25 (0.03)	9.49 (0.38)

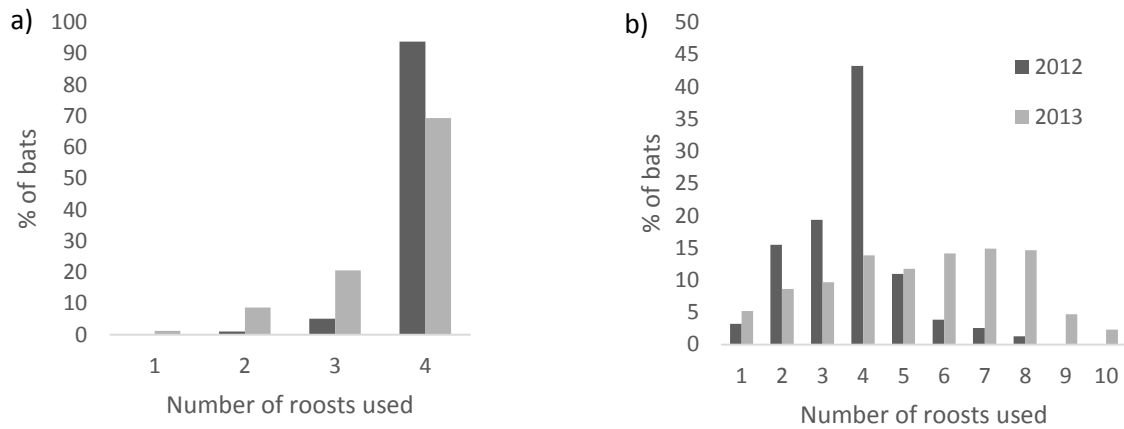


Figure 2. Day roost use by *Myotis lucifugus* at Pynn's Brook (a) and Salmonier Nature Park (b) in Newfoundland. Only bats present on 10 days or more were included. Day roosts characterized by the first record of each bat during the emergence period. Only 8 roosts were monitored at Salmonier during 2012, and this was expanded to 11 roosts in 2013.

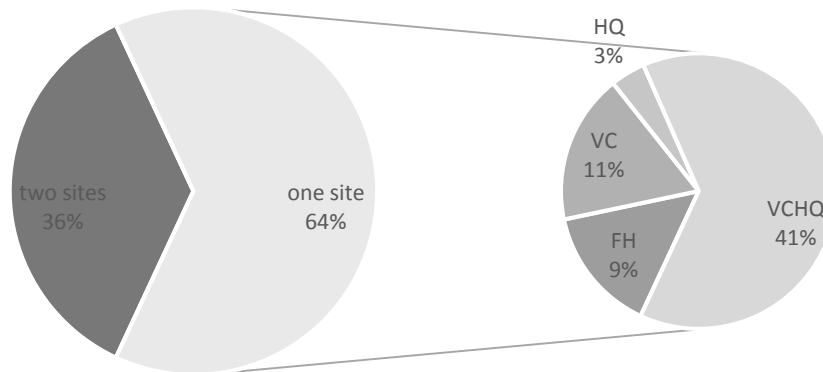


Figure 3. Roost use at Salmonier Nature Park (refer to site map for locations, Figure 4). Two sites = bats used both the main park area and the FH area 1 km away. One site – includes just the FH area used (FH), visitors center boxes only (VC), headquarters boxes only (HQ), and visitor center and headquarters (VCHQ).

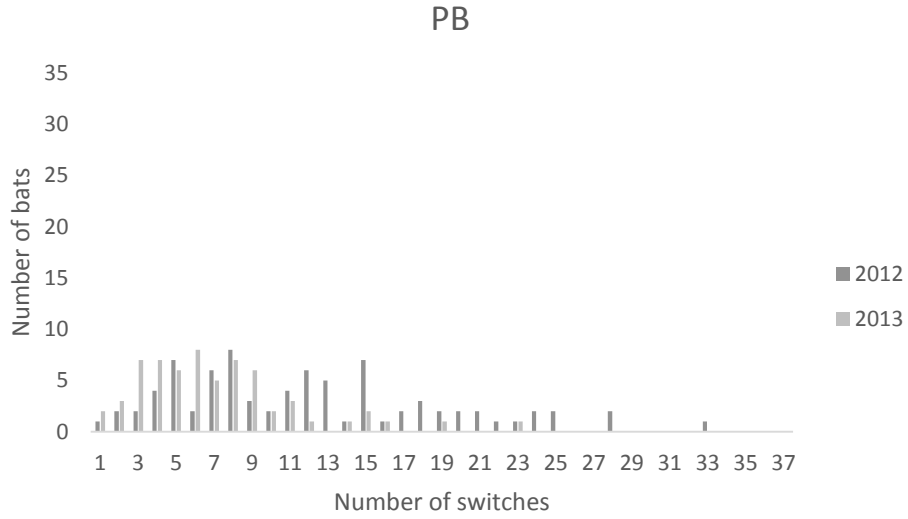
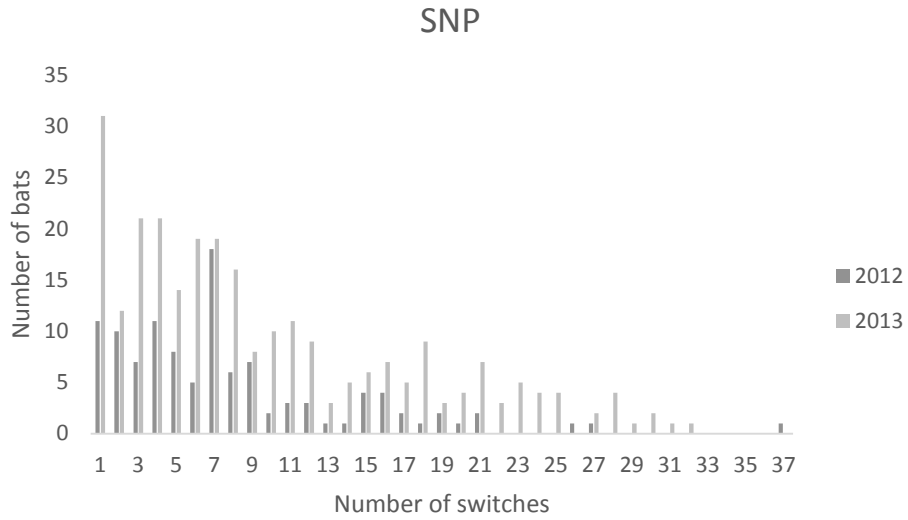


Figure 4. Number of recorded incidences of bats switching day roosts over a season. Only bats with 10 day roosting records for each year were included. SNP= Salmonier Nature Park, PB=Pynn's Brook.

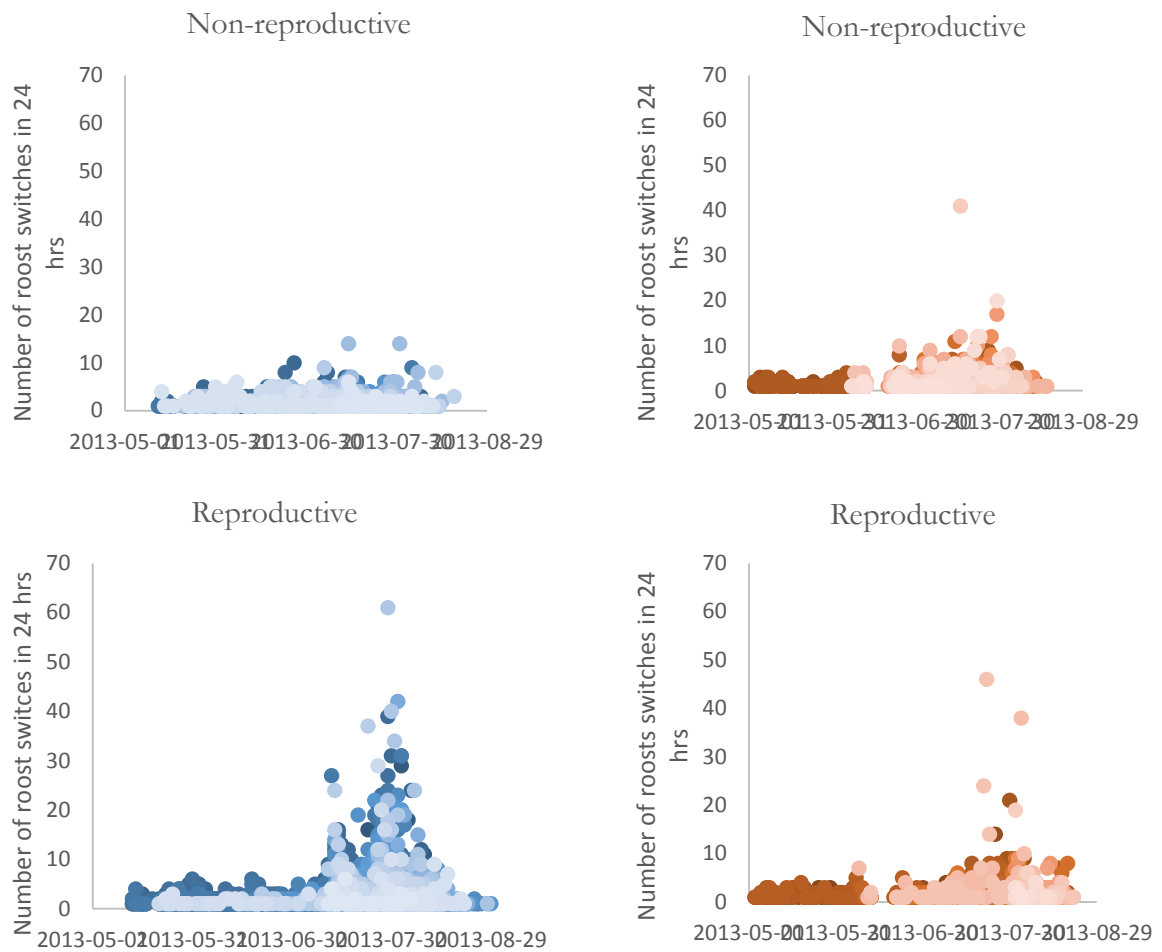


Figure 5. Number of roost switches per 24 hour period during 2013 at Salmonier Nature Park (Right panel) and Pynn's Brook (left panel). Only bats with known reproductive status included. There was a trend for bats to transition roosts more during late summer, and more so if reproductive. Shades of colour represent individuals.

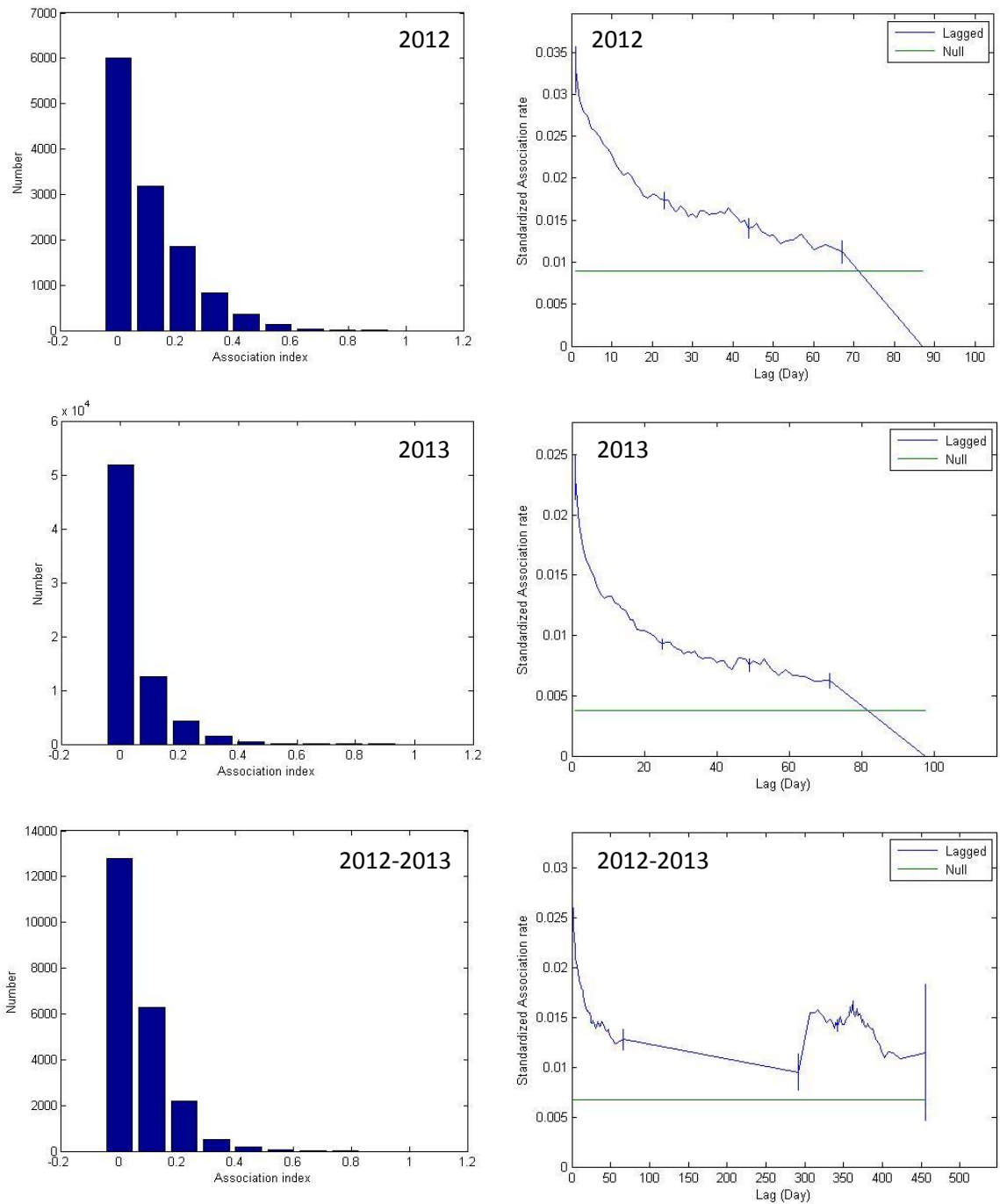


Figure 6. Left panels show association index frequency and number of associations for SNP 2012, 2013, then 2012-13 combined. Right panels show standardized lagged association rates for the above mentioned.

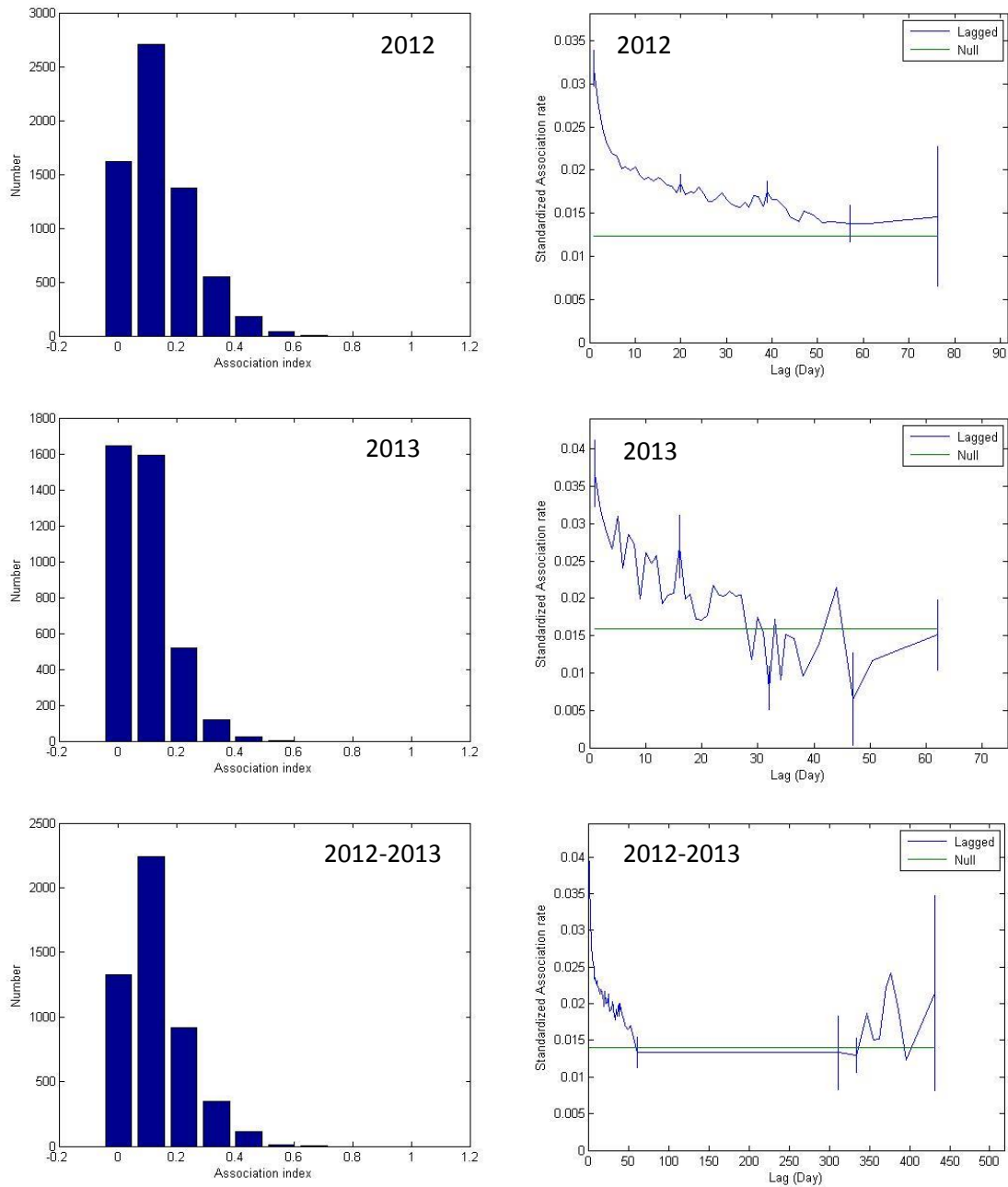


Figure 7. Left panels show association index frequency for PB 2012, 2013, then 2012-13 combined. Right panels show standardized lagged association rates for the above mentioned.

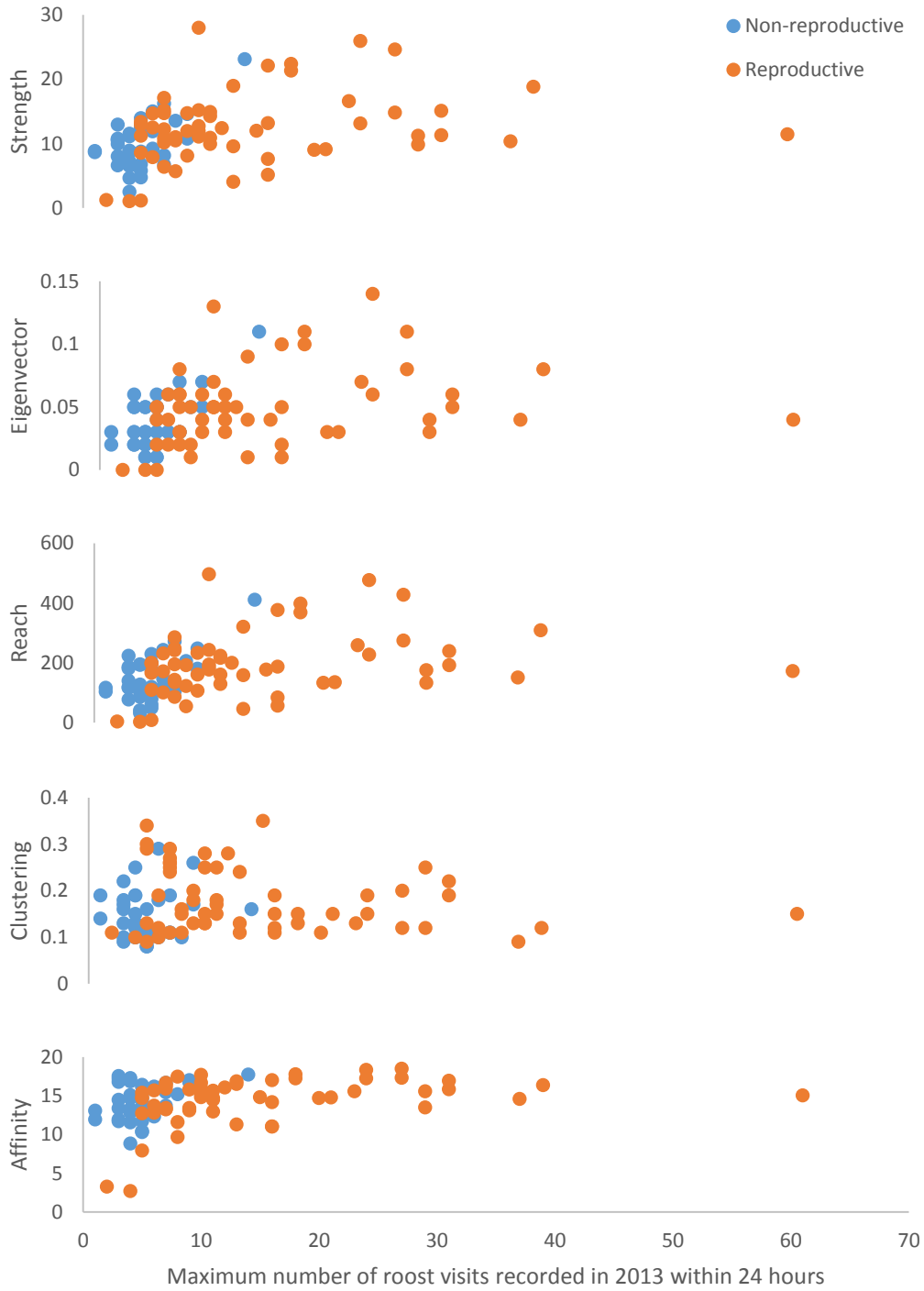


Figure 8. Comparison between reproductive classes of individual maximum number of different roosts visited in 24 hour period during 2013 compared to individual network measures at Salmonier Nature Park. Non-reproductive analysis included 36 individuals, and 57 reproductive.

Discussion

Our hypothesis that the grouping behaviour of *M. lucifugus* would lead to persistent strong social bonds was not supported. I observed mostly weak bonds but these did persist over 30-80 days, and no strong associations (> 0.6) occurred. Females at Pynn's Brook exhibited a higher frequency of medium strength bonds, but this may be a reflection of associations being based on day roosts, and bats at Pynn's Brook were only monitored at 4 roosts; it may also be due to the smaller number of bats within the colony and/or the smaller number of roosts monitored. Interestingly, when evaluating bats present during both years, it was observed that associations degrade as a season progresses, but at Salmonier but not Pynn's Brook, it increases if bats associate in the next season. This finding suggests that the bats are likely to associate with certain individuals again in the next season, and therefore maintaining associations over time; however these associations are weak.

When a limited number of roosts are available for use, bats used all of them, as seen with day roost use at Pynn's Brook. At Salmonier, bats used a number of roosts throughout the season, yet they did not switch more between these roosts than the bats at Pynn's Brook. A large portion of females only used 1 roost throughout the season, especially at Salmonier during 2013.

Roost visits during the night were highest in mid-late summer, with reproductive females visiting multiple roosts more often than non-reproductive females. There was no support for the hypothesis that individuals who were more connected in the social network would switch roosts more often during the night, exploring and interacting with a multitude of other bats and roosts. The maximum number of roost switches observed in the bats was quite high, with a maximum of 60 in individuals of known reproductive status. Anthony et al. (1981) found that *M. lucifugus* had two foraging bouts per night, with a break in between

where they would stay in one night roost. Thus, the most roosts I would expect to observe a bat in within 24 hours is 3: the roost it emerged from, a night roost, and the new roost where it will spend the day. Unfortunately, the nature of the PTT tag data does not inform us whether the bat was entering or exiting the roost, and thus it is unclear if the bat stayed in the roosts it entered or if it entered and exited quickly (both behaviours were observed in the field, but the frequency is unclear). This night visiting behaviour may be exploratory, and perhaps bats are entering the roosts to search for other individuals or to access the microclimates of the roosts.

It is also possible that night visiting behaviour could be linked to personality - perhaps those that switch frequently are dominant individuals maintaining order, or submissive individuals, which are pushed out of the roost. In a study on personality in *M. lucifugus*, adults maintained consistent personality over a short time period, maintaining the same scores on all tests, but juveniles increased in personal activity from summer to fall, where they showed little willingness to participate in the summer, but were active and exploratory by the fall (Menziez et al. 2013). The study could not gauge the degree of variability between individuals or aggressive or dominant behaviour. The day roost switching and night roost visiting vary greatly between individuals, and this may be tied to personality. Further capturing efforts should include personality tests as part of the bats evaluation.

Anthony et al. (1981) found that lactating females would return to the maternity roost during the night to nurse their young and did not use the separate night roost during that time. In my study, it seems that this is the time when reproductive bats are visiting roosts most frequently, where I would have expected them to use one roost - presumably where their babies are. The reproductive females may have to switch their babies between different roosts to find the appropriate microclimate for them, since the young cannot

thermoregulate until 10 days of age (Fenton & Barclay 1980). During my trapping sessions in 2013, twice I captured a mother with a non-volant young attached to her at Salmonier, and once at Pynn's Brook. It is also possible that with the large number of bats using the roosts, the mothers may have to search through the roosts to find their baby. There was less night roost visiting at Pynn's Brook, and this may be due to all the boxes being within a 10 m radius of one another, and likely having a similar microclimate.

Given the day-to-day roost switching and nightly roost visits of females, combined with the persistence of weak social bonds, it seems that colonies of *M. lucifugus* follow a broad definition of fission-fusion social structure. I did not find substantial clustering, and no subgroups were observed. Johnson et al. (2013) suggest that subgroups may not reveal much about social structure in bats, and that other aspects of social behaviour need to be evaluated. A similar species, *Myotis septentrionalis*, consists of colonies with non-randomly associating subgroups (Garroway & Broders 2007). In this study, roost groups were maintained for about 10 days before dissociating, although subsets of individuals remained together over the season. The social structure was best modelled by a mixed model of casual acquaintance and constant companions (some short term relations, some long term). Cohesiveness of groups was greatest during lactation, and there was no effect of minimum night temperatures. In a subsequent study on *M. septentrionalis*, Patriquin et al. (2010) found the opposite of Garroway & Broders (2007), with females forming stronger associations during pregnancy than lactation. In my study, none of the fitted models were found to be appropriate for the observed associations.

To have an accurate understanding of social structure in this species, a long-term data set is needed (Kerth et al. 2011). Analysis on how juveniles integrate into the social system would also be interesting, however in my study only had 13 of 60 tagged juvenile females

return to the site and no males (the latter being expected). Patriquin et al. (2010) found that *M. septentrionalis* adult females associated more with younger individuals, maintaining connections within the colony, which may be due to an increased interest in juveniles to explore.

With a better understanding of factors influencing roost switching, I may be able to have a better grasp of the factors shaping social structure beyond the ecological constraints of roost availability. Ecological constraints and social constraints seem to affect the behaviour of the bats, but genetic and evolutionary information (Kappeler et al. 2013) would likely help explain some of the variation observed. The bats in this study use bat boxes that are of similar size, and especially at Pynn's Brook, similar location, thus the high day-to-day switching and night roost visiting frequency was much higher than expected compared to tree-roosting bats (Olson & Barclay 2013).

In conclusion, there was no support of strong long-term associations in *M. lucifugus*, but this will need to be confirmed with more records of where each bat is roosting as well as tagging the majority of bats present in the area and monitoring them over multiple years. Weak associations within seasons were observed, degrading throughout, yet peaking at the beginning of the next season. Bats generally used multiple day roosts, especially when limited to a low number of available roosts. In mid-summer, the highest amount of switches during the night occurred, and this was inflated for reproductive individuals. Night roost visiting however was not correlated with how connected individuals were to the social network, and the factors influencing this behaviour need to be explored further.

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Chapter 4: Conclusions

The investigations into emergence order from roosts at dusk, roost switching from day to day and within a night, and social structure based on proximity of emergence of bats each evening as well as shared day roosts, yielded both expected and surprising results. In terms of emergence order, there was an expected significant concordance between the busiest nights at the busiest roosts at Salmonier Nature Park, and this concordance did not degrade over the time period observed. This finding suggests that *Myotis lucifugus* emerge relative to other individuals, and this structure of emergence supports the contention that the bats are non-randomly associating with one another. In big brown bats, there was maintenance of emergence order on subsequent days in the short term, but this degraded with time, but also supported the claim that these bats were non-randomly associating (Gillam et al. 2011). Discerning the significance of why one species maintains emergence order longer than the other is not clear, but may be a result of the two species having sociality result from different contexts. Perhaps the one species is emerging in the same order due to dominance, and this persists over time (which could explain the results observed in little brown bats in my study. Perhaps the other species is emerging due to body condition, where bats with poor body condition leave earlier to have longer access to food, and after several days their body conditions improves and they do not have to leave to forage early any longer. Video recordings of the nature of bats interactions within the box (e.g. aggressive), radio tracking after emergence, and accurate daily weight measurements of the bats would be of great assistance in untangling the differences observed between the two species.

When social structure was evaluated, defining bats as associated if they emerged within 15 seconds of one another, the mean association rates were surprisingly low, ranging

from 0.01 to 0.02 at roosts in Salmonier and Pynn's Brook both within and between seasons. Therefore, these bats do not maintain associations based on the absolute emergence time, with only weak bonds that do not differ from the null. This suggests that there is little social structure at such a fine scale of temporal associations during emergence, however this association analysis included many individuals, unlike the relative emergence order analysis which only included a few. This second analysis is important because can distinguish the proximity in which the bats emerge. The initial analysis considers bats emerging in the same order whether they were one minute apart or one hour apart, and one would suspect that bats emerging one hour apart are likely not socially interacting with one another the way bats emerging within one minute of one another may be. For me, the concordance analysis is superficial and asks whether the bats emerging can even be considered social, whereas with the second analysis I can ask, well given this appearance of a pattern, would one truly want to call this social, and in my study it does not seem to be so. The bats do not emerge relative to one another, which may indicate an absence of complex sociality, unless the bats come together after emergence to socialize with preferred individuals.

Thus emergence order may not reveal social groups, especially if these groups are formed away from the roosts, after the bats have emerged, as in Molossid bats (Dechmann et al 2012). Perhaps little brown bats do not form social groups for foraging, similar to the solitary foraging of Bechstein's bats (Kerth et al. 2001), but this has not been explored. Further research involving radio telemetry work has the potential to answer questions on the nature of social interactions, after the bats leave the roost. Also, modification of Kendall's coefficient of concordance to allow for missing records of individuals would allow for more individuals to be included as well as more emergence days, with the potential to further

evaluate how concordance is affected by time, as well as the inclusion of sites with fewer individuals present.

Over the season, most bats used multiple day roosts, especially at the smaller Pynn's Brook site with only 4 known roosts, having all been used by most bats. In the second season at Salmonier, more roosts were monitored and this revealed that most bats used 4 to 8 roosts of the 11 monitored. This is an interesting finding because it may indicate that if bats have more roosts, they may segregate further, and perhaps it is only when many roosts are provided that it is possible to see social groups when looking at which day roosts bats utilize. Gillam et al. (2011) assume sociality in big brown bats based on their emergence from one roost within one site, yet no other roosts in the area are monitored (and there may not have been any other roosts there). Perhaps having only one roost simplifies the researcher's perception of the species' sociality since all are forced into one day roost. It would be interesting to observe if, when the bats are given additional roosts, if they would prefer to segregate from the main colony into smaller groups, and if stronger associations would then be detected. In my study, I think that there could have been more opportunity to observe social patterns of behaviour if more roosts were available (especially at Pynn's Brook).

Despite that some of the roosts at Salmonier were 1 km apart, 36% of the tagged bats used roosts at both locations, which suggests this is the same colony, where a colony consists of members which have the opportunity to interact with one another (as per Johnson et al. 2012). Thus at the level I looked at, which is assumed to be the colony, it seems there are multiple groups of bats that use certain roosts very specifically, however there are individuals that have used multiple roosts within the separate areas of the Salmonier site, suggesting connectivity within the colony. From the roost use data at Salmonier, it seems possible that the park area and the FH area could be two groups or communities,

where individuals interact more frequently with those in their group, but that these groups are held together by certain individuals that use both areas for roosting. Bechstein's bat colonies, which numbered over 20, were observed to have two communities where bats had stronger bonds with one another rather than with those in the other community, but that there were older females who were strongly connected to both communities (Kerth et al. 2011). Unlike Bechstein's bats, the bats in my study had only weak bonds, and did not appear to form any strong bonds or variation of strong and weak bonds.

From day to day, there was a lot of variation in roost switching, from many bats using one roost throughout the season to one bat switching day roosts 37 times. During the night, it appeared that night roost switching frequency was highest during July, during parturition, and there was a greater tendency for reproductive females to switch than non-reproductive. If I consider Emlen's predictions concerning family social structure (Emlen 1995), he predicted that decreasing ecological constraints would increase reproductive sharing (prediction #12 of Emlen 1995). This could indicate that the bats in my colony, which consist of both breeding and non-breeding females, may be under strong ecological constraints. Interestingly, Emlen (1995) also predicted that there would be more reproductive suppression between individuals that were closely related, and thus it is possible that ecological constraints are not responsible in this case, but perhaps my colony consists of closely related individuals. Genetic information for each individual to determine relatedness combined with an investigation into the mechanisms regulating who breeds each year and whether females can suppress other females from reproducing would provide insight.

In my social analyses that evaluated associations between bats, where bats were considered associated if they shared the same day roost, it was found that there were weak bonds and these did persist over short periods of time. Additionally, from one season to the

next, bats seem to initially prefer to associate with individuals from the previous year. When network analyses were conducted, it was expected that eigenvector centrality, the connectedness of individuals within the social network, would be correlated with increased night switching behaviour. If bats switch roosts more at night, they may be exposed to more individuals and thus perhaps have an increased opportunity for social interactions, and this behaviour should be reflected in social bonds based on day roost selections. I found no connection between night switching behaviour and the connectedness of an individual within their social network based on day roost selection. Perhaps bats that switch roosts frequently through the night have more social interactions, especially since this is the time of day when they are most active, and it is this behaviour that truly reflects their social structure rather than day roost selection. Activity during the day in the roosts was not observed, but it is likely that the bats are asleep for a majority of the time, and are not socializing, and therefore day roost selection may not be an accurate indicator of social relationships. Johnson et al. (2013) state that day roosting social data may only provide a superficial view of bat sociality, and more detailed information about interactions between individuals, amongst other characteristics of their social behaviour, is needed for an accurate assessment. More research evaluating the patterns of night switching behaviour, especially with the resolution of whether bats are entering or exiting the roost, may reveal a more accurate representation of bat sociality.

Overall, my study found little evidence for strong social structure in *Myotis lucifugus*, given the weak associations observed and lack of subgroups. That is not to say that there is no structure, as Kerth and Van Schaik (2012) highlight that long-term data set are often required to detect structure. Given the size of the colony and the small proportion of bats tagged, it is likely that there are not yet sufficient data to detect social structure if present. At

the same time, it is important to note that there has been a large focus by bat researchers on finding structure in terms of subgroups, however this is only one way to analyze a network (Johnson et al. 2013). Some of the suggested alternatives are difficult to apply to my study system, such as network mapping. For example, at Salmonier, with over 1000 tagged individuals, a network map does not provide a clear idea of how the bats are interacting, even when excluding weak associations. Focusing on how roosts are used and potentially affect sociality would be of great interest for those studying *Myotis lucifugus*. In Rafinesque's big-eared bats, one roost amongst 64 day roosts served as a central hub, which hosted a great majority of the bats (Johnson et al. 2012). Additionally, when more suitable roosts were present, bats formed less dense networks, thus highlighting the connection between roost availability and social structure. Roost availability is an extrinsic factor that has been evaluated for many bat species (i.e., Clement & Castleberry 2013, Henderson & Broders 2008, Brigham et al. 1997) however it does not explain all bat sociality (Kerth 2008), but may play an important role for some species, such as Rafinesque's big-eared bat.

Other extrinsic factors, such as habitat use by bats surrounding the roosts would illuminate the factors that are key to them within the environment. Radio-tracking, combined with environmental monitoring, could shed some light. If the environment around roosts was closely monitored, such as location of water which fluctuates throughout the season, as well as location of insect emergences, this could lend insight into roost use by *Myotis lucifugus*, potentially untangling these extrinsic factors from more intrinsic ones - such as social obligations and relations. Emlen (1995) suggests that stable environments with limited resources may cause families to continue to live together, which is possibly why female juveniles return and males do not, if the communal roost is specifically something the female require for successful rearing. If it was just the communal roost that the female juveniles

required then they could disperse to any other colony, and not remain at their natal one. Five of the female juveniles returned the following year at Salmonier Nature Park and none of the males, although it is possible the males did return and did not use the bat boxes but roosted in the forest nearby. Further investigation into whether juvenile females reproduce during the first year they return to their natal site as well as the interactions between reproductive and non-reproductive females both young and old are needed to determine if there are other factors at play (such as helping behaviour in raising young).

Nightly roost switching occurred most frequently later in the season, near the time of lactation, with reproductive females switching more often than non-reproductive bats. Are the reproductive bats switching to find the most suitable roost for their young? In the summer of 2013, twice at Salmonier and once at Pynn's Brook mother bats were caught flying with their non-volant young, suggesting that it is possible they are moving them between roosts. Also, in the limited data I have for the juveniles before they leave for the season, they display some roost switching behaviour, visiting up to a few roosts within a night. It is possible that the mothers are having difficulty finding their young, especially if it is the case that they frequently move the babies and the babies can also move between boxes on the same pole structure (we did observe a few instances of young moving as such on their own).

Understanding the social behaviour of *M. lucifugus* is important for adding to the understanding of female social behaviour in general, providing grounds for individuals to respond to changes in the environment. In Bechstein's bats, when a devastating harsh winter caused a large reduction in the number of bats, the social structure changed such that individual strong associations persisted but community structure disappeared (Baigger et al. 2013). This finding supported a hypothesis suggested by Kerth et al. (2011) that community

structure is formed when many bats are present because bats are only able to maintain a limited number of strong bonds. In the case of Bechstein's bats, the critical number of bats in a community is about 20 (Kerth et al. 2011, Baigger et al. 2013). This is interesting because in my study systems, especially at Salmonier, where at least 800 bats use the 11 known roosts, no structure was found, leading us to suggest that the bats either do not maintain social bonds or perhaps they are able to maintain many bonds. Bottlenose dolphins in a specific location have been found to live in an open fission-fusion network where females form only temporary bonds with one another and their young whereas males form long lasting bonds with each other; yet there is no segregation in this population, and all individuals interact with one another (Randic et al. 2012). Could the *M. lucifugus* colonies studied here consist of females in an open fission fusion network or do they just randomly associate? It does not seem like these two scenarios would appear different in network analysis values, but only in long-term detailed information about how the individuals interact. By uncovering the details of how individuals are interacting, it is possible to discover the context that is necessary to induce specific social structures. Thus the bats in my study, being temperate, promiscuous and mobile female mammals, indicate that this context may lead to either an open social network with individuals associated with many others in a complex way, or perhaps randomly associating with any individual who happens to share that area. If researchers are able to follow up my study with an analysis of the nature of the social interactions, through direct observation of how the bats interact with one another (e.g. through video), then I think it is possible to distinguish between open network at random association. If it is found that little brown bats do live in an open social network with individuals associating with many others but forming close bonds with a few, it would call into question the uniqueness

of the open network social structure presented by Randic et al. (2012), as well as perhaps the cognitive abilities required to exist in such a network.

My study investigated only two of the four constraints on female mammal sociality, ecological and social constraints to the exclusion of genetic and evolutionary constraints. In a review of mammalian sociality literature, Silk (2007) states that the presence of kin increases individual female fitness. The relatedness in the colonies of my study is unknown, yet this information may play a key role in why the bats are social. Given the high fidelity of juvenile female little brown bats to return to their natal roosting area, there may be high relatedness, and this may be beneficial for individuals present (Frick et al. 2010). With an integrative approach, examining constraints and their potential interactions and their effects on sociality, a more comprehensive understanding of sociality may be attained. If we found that all individuals were closely related at my study sites, it would indicate that family units are integral to sociality in this species in this area, and perhaps there are benefits of kin selection present. If individuals are not closely related, then it is possible that the bats are congregating around resources, or perhaps they form relationships with others beyond their next of kin, potentially revealing complex social relations – all of this may only be revealed through direct observation of behaviours displayed between individuals.

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