SOCIAL ECOLOGY OF THE NORTHERN LONG-EARED BAT
(*MYOTIS SEPTENTRIONALIS*)

Colin James Garroway

A Thesis Submitted to
Saint Mary's University, Halifax, Nova Scotia
in Partial Fulfillment of the Requirements for
the Degree of Master of Science in Applied Science.

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Halifax, Nova Scotia

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ISBN: 978-0-494-23852-3
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ISBN: 978-0-494-23852-3

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By Colin James Garroway

ABSTRACT

A population's social system influences its mating patterns, the spatial and temporal distribution of individuals, their dispersal, and consequently the distribution of alleles, thereby affecting its evolutionary trajectory. There are also important implications for species management and conservation if degradation of social relationships due to anthropogenic environmental alteration result in negative fitness consequences. The objectives of this thesis were to 1) examine whether associations among female northern long-eared bats (*Myotis septentrionalis*) at maternity roosts were random or social in nature and; 2) examine variation in tree and forest features selected by individuals as maternity roosts. Maternity roosts were comprised of non-randomly assorting social groups with some individuals remaining associated for the entire roosting season. Roost tree selection by bats varied with reproductive periods. During the lactation period bats selected roosts high in tall trees in areas with a low tree density and low canopy cover relative to pre- and post-lactation periods.

July, 2006

ACKNOWLEDGEMENTS

I would like to first thank Hugh Broders for providing me the opportunity to work on this project and contributing valuable ideas and insights throughout project design and analyses. I would also like to thank my supervisory committee Colleen Barber, Philip Giles, and Jeremy Lundholm for ensuring scientific integrity of the project. The hard work of Joe Poissant in the field was integral to the projects success. I would like to thank Kathleen Gould for support and encouragement throughout this degree as well as her unfailing willingness to help with field work whenever and wherever asked. I would also like to thank Hal Whitehead for reviewing Chapter 2. The Nova Scotia Department of Natural Resources provided in kind accommodation at Dollar Lake Provincial Park. Financial support for this project was provided by the Natural Sciences and Engineering Research Council of Canada (CGS M to CG and Discovery and Tools and Equipment Grants to HB) and internal funds were provided by Saint Mary's University.

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CHAPTER 1:

Social ecology of northern long-eared bats: introduction

Levels of social interaction between animals occur on a continuum ranging from solitary individuals that interact only for mating (e.g., sloths) through to complex multi-levelled interactions for specialized purposes (e.g., humans) (Lee 1994). Variations in sociality are characterised by the stability, persistence, and predictability of interactions. This variability makes sociality difficult to define generally. The definition that I will use throughout this thesis is that a society is a group of cooperating and competing individuals with organized relationships developed through repeated interactions, the context of which are related to individual fitness (Robinson et al. 2005). Social grouping is differentiated from temporary, random, unstructured aggregations by the fact that fitness benefits derived from social groups are conditional upon interacting with specific individuals whereas aggregating species may only form groups at a limiting resource, gaining fitness benefits from merely being in a group and not necessarily interacting with other group members (Wilkinson 1985).

Intrinsic and extrinsic factors influence the costs and benefits of social interactions. Where intrinsic and extrinsic factors vary considerably through time and space, social behaviours characteristic of a flexible fission-fusion model may be the most beneficial. The umbrella term ‘fission-fusion sociality’ is generally used to describe social systems characterised by flexible (in size, composition, and duration) social group formation. Often these interactions take place at various hierarchical grouping levels that vary in size and cohesiveness. To date there is no clear theoretical framework to explain the evolution of this social system (Lehmann and Boesch 2004). For example, chimpanzee (*Pan troglodytes*) social group size and composition varies with predation pressure (Sakura 1994), the presence of reproductive females (Hashimoto et al. 2001), the quality and patchiness of food sources (Matsumoto-Oda et al. 1998), and whole social unit size (Lehmann and Boesch 2004). Benefits of social group formation to cetaceans may include communal care of young in the form of other group members protecting the offspring of a diving mother from predators while she forages (Arnbom and Whitehead 1989) and coordinated foraging may allow group members to capture prey that have eluded others (Whitehead 1989). Adult female spotted hyena (*Crocuta crocuta*) association patterns are strongly based upon kinship (Holekamp et al. 1997). Kin are more likely to be tolerated at a carcass and are more likely to be involved in coalitionary attacks than are unrelated individuals (Mills 1985). Maintained associations among spotted hyenas and associations amongst close kin may facilitate long-term stability in packs and maintain social hierarchies.

It has recently been demonstrated that complex social systems have evolved in some bat species (Kerth and Konig 1999; O'Donnell 2000; Vonhof et al. 2004; Willis and Brigham 2004). Bats have many of the likely requirements for the evolution of sociality including the ability to communicate and a tendency to live in groups. They are also long lived, which make them potentially well suited for studying the evolution of sociality. The objective of this thesis is to elucidate the social system and roosting ecology of a typical temperate bat species, the northern long-eared bat (*Myotis septentrionalis*). The northern long-eared bat is common throughout northeastern North America ranging as far west as Alberta and as far south as Wyoming (van Zyll de Jong 1985; Caceres and Barclay 2000). Adult females on average weigh more than adult males, but both sexes range between 5-8 g (Broders et al. 2003). The northern long-eared bat over-winters in caves and abandoned mines throughout its range, often with other species (Caire et al. 1979; Schowalter 1980; Thomas 1995). Copulation occurs in the autumn at hibernacula (Caire et al. 1979) and sperm is then stored over-winter after which a single egg is released and implantation occurs in early spring upon arousal from hibernation (Racey 1982; Uchida and Mori 1987). In Nova Scotia parturition occurs at forest maternity roosts in late June or early July (Broders et al. 2003).

The northern long-eared bat is a forest interior species (Caire et al. 1979; Jung et al. 1999; Broders et al. 2003) capable of both aerial hawking and gleaning insects off surfaces (Faure et al. 1993; Ratcliffe and Dawson 2003). Lepidoptera and Coleoptera seem to be the primary prey selected by these bats (Broders 2003). Northern long-eared bats commonly roost singularly or in groups in cavities and under peeling bark and in mature stands (Broders and Forbes 2004).

Specific hypotheses and predictions tested in this thesis are:

Chapter 2 hypothesis: Ecological constraints have led to the evolution of sociality in northern long-eared bats. Predictions: 1) both the composition and duration of association patterns between individuals at roost trees will be different from random; 2) social group cohesion will be related to the energetic constraints of temperature and reproductive status.

Chapter 3 hypothesis: energetic constraints associated with both reproduction and the tendency to be social influence roost tree and site selection. Predictions: 1) bats select specific roost types during the lactation period relative to pre- and post-lactation.

Chapters 2 and 3 are written as standalone manuscripts formatted for publication.

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CHAPTER 2:

Non-random social-group formation at northern long-eared bat (*Myotis septentrionalis*) maternity roosts

Abstract: Bats (Order: Chiroptera) are among the most ecologically diverse and specious mammalian orders. Most species live in groups for at least a portion of their life cycle and behavioural evidence suggests that individuals of many species live within complex social systems. However, rigorous, quantitative characterisations of social systems within these groups have been rare due to difficulties inherent in studying these highly mobile, small, nocturnal animals. Here we use an automated monitoring system (PIT-tags), telemetry, and recently developed analytical techniques to investigate the social organisation (size, sexual composition, and spatio-temporal cohesion) and social structure (pattern of social interactions and relationships among individuals) of free-living northern long-eared bats. Cluster analysis of half-weight association index values for all pairs and permutation tests indicate that maternity roosts are comprised of multiple, non-randomly assorting social-groups. Lagged association rates showed that roosting groups dissociate over periods of approximately ten days after which subsets of individuals remain associated throughout the summer roosting season. A model representing a two-levelled social structure of long-term (whole summer) and short-term (up to ten days) acquaintances best fit the lagged association rate. Social-groups were most cohesive during the lactation period but we found no evidence for effects of minimum nightly temperature on social group cohesion. The high species diversity, propensity for social living, and dynamic behavioural responses of many bat species to a wide range of environmental and ecological conditions may make this Order a valuable species group for studying the evolution of sociality.

Introduction

A society is a cohesive group of cooperating and competing individuals with organized patterns of relationships developed through repeated interactions, the context of which are related to survival and reproductive success (Robinson et al. 2005). Individuals of social species possessing traits that predispose them to vary competitive and cooperative strategies in response to ecological and environmental variation so that fitness benefits are maximised are expected to be naturally selected (Chesser 1998). Of those species that live in groups, social species are differentiated from aggregating species via the mechanisms through which individual fitness is enhanced. Social species derive fitness benefits based upon group composition and interactions with specific individuals (active benefits (Wilkinson 1985)). However, aggregating species form groups at limiting or patchily distributed resources, possibly gaining byproduct fitness benefits simply by being part of a group, regardless of its membership (passive benefits; (Wilkinson 1985)). Kappeler and van Schaik (2002) suggest that societies are characterised by three basic elements: social organisation, social structure, and mating system. Social organisation is a broad descriptor of group size, sexual composition, and spatio-temporal cohesiveness. Social structure characterises the pattern of dyadic social interactions within a society. Finally, the mating system describes social interactions of mating couples and the genetic consequences of these interactions.

Social systems across a wide variety of mammalian taxa have been described under the umbrella term of 'fission-fusion sociality' where social units (individuals and/or groups) that vary in size, composition, and temporal permanence form through group fission and fusion (e.g., ungulates, (Conradt & Roper 2000); primates, (Kappeler & van Schaik 2002); chiropterans, (Kerth & Konig 1999); cetaceans, (Christal et al. 1998);

canids, (Owens & Owens 1978); felids, (Packer 1986); marsupials, (Kaufmann 1974)). Although we are unaware of any formal characterizations of fission-fusion societies at least three subdivisions have been described. First, group fission and fusion can occur amongst individuals living within closed communities where individuals from even neighbouring communities rarely or never interact (e.g., chimpanzees, *Pan troglodytes*, (Nishida 1968); Bechstein's bats, *Myotis bechsteinii*, (Kerth & Konig 1999). Second, group fission and fusion similar to that described above can occur in open unbound populations (e.g., bottlenose dolphins, *Tursiops truncates* in Shark Bay, Australia; (Connor et al. 2000). Finally, group fission and fusion can occur among multiple hierarchical units of organization (e.g., African elephants, *Loxodonta africana*, may have up to five social-tiers; (Wittemyer et al. 2005).

Evidence suggests that sociality is particularly widespread and diverse among bats (Order: Chiroptera) likely reflecting selection for behavioural traits adapted for the diversity of ecological conditions under which bat species have evolved (McCracken & Wilkinson 2000; Burland & Worthington Wilmer 2001). Understanding a population's social system can provide insights into population structuring through its influences on mating patterns, the spatial and temporal distribution of individuals, dispersal, and patterns of resource use. There are also important implications for species management and conservation if degradation of social relationships due to anthropogenic environmental alteration result in negative fitness consequences. However, quantitative studies of the various elements of bat societies have been rare. Aspects of social systems have been quantitatively investigated in only three other free-ranging temperate bat species; big brown bats (*Eptesicus fuscus*; (Willis & Brigham 2005), New Zealand long-tailed bats (*Chalinolobus tuberculatus*; (O'Donnell 2000), and Bechstein's bats (*Myotis* *bechsteinii*; (Kerth & Konig 1999). The social systems of each of these species seemed to conform to the closed community fission-fusion social system. If each of these communities are considered to be a colony (*sensu* Burland et al., (2001); based upon level of interaction between individuals potentially at one or more roosts) then in each case whole colonies were most often spread over multiple roost trees on a given day. In each case bats switched roosts often, the composition of individuals within roosts was variable, and interactions between individuals from neighbouring colonies were rare or did not occur.

The goal of this study was to investigate the social structure, organisation, and potential ecological influences on social-group cohesion of a temperate zone bat, the northern long-eared bat (*Myotis septentrionalis*), with a life history pattern similar to that of many other temperate species during the summer months. Specifically, the objectives were to: *i*) determine whether female northern long-eared bat roosting groups are random aggregations or social-groups (i.e., consisting of individuals with their preferred associates); *ii*) characterise the social structure and quantify the temporal permanence of pairwise associations; and *iii*) if they are social, determine what influence ambient temperature and reproductive status have on the variation in social-group cohesion on a daily basis.

During the summer northern long-eared bats rely on forests for roosting and foraging (Sasse & Pekins 1996; Foster & Kurta 1999; Jung et al. 1999; Lacki & Schwierjohann 2001; Broders & Forbes 2004). Both males and females roost under loose bark or in cavities. Males tend to roost singly whereas females gather at maternity roosts where they give birth and raise offspring (Sasse & Pekins 1996; Foster & Kurta 1999; Lacki & Schwierjohann 2001; Broders & Forbes 2004). Because males roost singly throughout the summer our analysis is constrained to adult females at maternity roosts. The northern long-eared bat (5 - 8 g) is common throughout northeastern North America and ranges as far west as Alberta and as far south as Wyoming (van Zyll de Jong 1985; Caceres & Barclay 2000). Copulation occurs in autumn at hibernacula (Caire et al. 1979) and sperm is stored over-winter after which a single egg is released and implantation occurs in early spring upon arousal from hibernation (Racey 1982; Uchida & Mori 1987). In Nova Scotia parturition occurs at maternity colonies in late June early July (Broders et al. 2003) and bats are hibernating by early- to mid- October. Thus, there are severe constraints on the time available (≈ 4 months) for the replenishment of fat reserves after hibernation, gestation, the rearing of offspring, and the accumulation of fat reserves before hibernation.

Methods

Study-site

Fieldwork was conducted 3 June- 31 August 2005 at Dollar Lake Provincial Park, Nova Scotia, Canada (44°55' N, 63°19'W). The forest within the park is characterised by stands of mature eastern hemlock (*Tsuga canadensis*) interspersed with yellow birch (*Betula alleghaniensis*), red maple (*Acer rubrum*), red spruce (*Picea rubens*), white pine (*Pinus glauca*), and balsam fir (*Abies balsamea*). Within this system there was a patchwork of blowdowns in the very early stages of succession, caused by a hurricane in 2003. Much of the area outside of the park and some areas within the park have been cut within the last 30 years and are in various stages of regeneration.

Capture, Marking, and Radio-tracking

Bats were trapped along forested trails using harp traps (Austbat Research Equipment, Lower Plenty, Victoria, Australia) and at roost trees using cavity-traps (modified harp trap design) placed over cavity exits (Kunz & Kurta 1988). Reproductive status of females was classified as pregnant (based upon gentle stomach palpation), lactating (bare patches around nipples or presence of milk), or no evidence of reproduction.

Passively integrated transponders (PIT-tags; (Gibbons & Andrews 2004)) were subcutaneously injected into all individuals for permanent identification. PIT-tags have been used successfully to mark small mammals, including bats, in both field and laboratory situations (Barnard 1989; Rao & Edmondson 1990; Kerth & Konig 1996; Horn 1998; Gibbons & Andrews 2004). In each reported case where PIT-tags have been used to monitor bats there were no known instances of mortality, injuries, or infections detected.

Radio-transmitters (0.39 g, Model LB-2NT, Holohil Systems Limited, Carp, Ontario, Canada) were glued (Skinbond, Smith and Nephew United Inc., Largo Florida, USA) to a subset of captured females to locate roost trees. Roost trees were located by homing in on the transmitter with a radio receiver (HR 2000 Osprey VHF Receiver, H.A.B.I.T. Research Limited, Victoria, B.C., Canada) and a 3-element Yagi antenna (AF Antronics, Urbana, Illinois, USA). Bats were track for the duration of the transmitter battery life or until the transmitter fell off.

At roost trees that were deemed safe to climb, automated PIT-tag recorders (EIDAP Inc., Alberta, Canada) were placed at cavity exits to record bats entering and exiting the cavities. Because roost trees often contained multiple cavities it was sometimes necessary to simultaneously deploy multiple PIT-tag recorders on one tree if the cavity exit site had not been previously located by emergence counts and because bats often exited out of multiple cavities. Even with multiple PIT-tag recorders deployed on a single tree there were still occasions when some bats exited out of cavities we were not monitoring.

Association Patterns

When the social structure of a group is not random (Whitehead 1997; Bejder et al. 1998) it can be characterised by the pattern of dyadic interactions (Hinde 1976). Because direct observation of interactions between individuals was not possible we assumed, due to the likely close proximity of individuals within roost trees, that individuals roosting together in the same roost tree interacted (Whitehead & Dufault 1999). Associations are recorded based only upon marked individuals and thus so are our inferences.

Association data from both PIT-tag recorders and telemetry (on days when three or more individual were monitored) was used in our analysis. Estimates of the strengths of associations are presented using the half-weight association index (Cairns & Schwager 1987). The half-weight association index is calculated as follows $HWI=x/(1/2)(n_A+n_B)$ where x is the number of times individuals A and B were located roosting together and n_A and n_B are the total number of times individual A and B be were located. We acknowledge that the half-weight index will likely underestimate strengths of association where bats were recorded via telemetry and therefore in these cases our results will be conservative estimates of the strength of associations. It is possible that some pairs with low half- weight association index values are more closely associated than what our estimates suggest however high association index values within this analysis represent strong associations.

To determine whether the observed roosting association matrix was different from what would be expected if individuals associated at random the observed association matrix was permuted following Manly (1995) and Bejder et al. (1998) with modifications introduced in Whitehead (1999) and Whitehead et al. (2005). This method randomly selects two individuals from rows and two different individuals from columns from within the observed association matrix and sequentially inverts association values between rows (i.e., 1 becomes 0 and vice versa). This procedure alters the association matrix in such a way that the number of individuals within each group and the number of groups are not affected. As the generated association matrices are sequential and begin with the original data set they are not independent of each other and so the number of permutations needed to generate accurate p-values is higher than that needed using standard Monte Carlo methods (Bejder et al. 1998). The number of permutations required is determined by increasing the number of permutations until p-values stabilize (Bejder et al. 1998). If the standard deviation of the observed association index is significantly greater than that of the permuted data the null hypothesis stating that there are no preferred and/or avoided companions is rejected (Whitehead 1999). Pairwise association patterns are presented in an average linkage cluster analysis. We considered clusters of animals to form distinct social-groups if they clustered above mean (+SD) of the half-weight index value of the randomly permuted data sets.

Temporal Patterning of Associations

The standardised lagged association rate (SLAR) was used to model the temporal nature of associations and is appropriate when not all associates are recorded on every monitoring occasion (Whitehead 1995). The SLAR is the average probability that a pair of individuals recorded together at time zero will be together again at subsequent time periods. Standard errors of the SLAR can be estimated by jackknifing (Efron & Gong 1983) in which data from different sampling periods are omitted in turn. The SLAR can be compared to the null association rate (i.e., that expected if individuals were associating at random (Whitehead 1995)).

Fitting models that approximate features of various social structures to the SLAR provides a quantitative means for estimating the temporal cohesion of social-groups, and the expected number of associates of an individual. Exponential decay models representing simulated social structures were fitted to the lagged association rate and ranked using Akaike's Information Criterion corrected for small sample size and over dispersion (QAICc; (Whitehead 1995; Burnham & Anderson 2002)). Models corresponded to a society of: 1) constant companions (a society of permanent closed social units); 2) casual acquaintances (a society where relationships between individuals within social-units decay over a period of time and are not permanent); 3) constant companions and casual acquaintances (a society where individuals within social units have a both permanent relationships and relationships decay over a period of time); 4) two levels of casual acquaintances (a society with two classes of relationships that decay over time with one more casual then the other but neither permenant). All of the above analyses were conducted using SOCPROG 2.2 ((http://myweb.dal.ca/~hwhitehe/social.htm; (Whitehead 2005)). For each model we calculated the difference between QAICc and that of the best approximating model (Δi), Akaike weights (wi), the probability that the ith model is the best approximating model amongst candidate models, and present the sum of the Akaike weights of the ith model and all higher ranking models (Σwi) (Burnham & Anderson 2002). Akaike weights provide insight into model selection uncertainty and the strength of evidence in the data for competing models (Burnham & Anderson 2002).

Ecological impacts on group fission and fusion

Two univariate logistic regression analyses were run to provide exploratory insight into the ecological factors influencing social-group fission and fusion (Hosmer & Lemeshow 2000). Independent variables were reproductive period (lactation period vs. pre-/post-lactation) and temperature (minimum temperature from night previous to the roosting day) respectively. The dependant variable was social-group pairs (with social-groups delineated from half-weight association values above random), coded as 1 if both individuals of the pair were located together and 0 if both were located, but they are in different trees on a given roosting day. To test whether effects of independent variables differed from random the dependant variable was randomly permuted ten times for 999 iterations. Average p-values (the proportion of permuted values greater than the observed value; one-tailed test), the breadth and position of 95% confidence intervals around parameter estimates, and odds ratios are interpreted when inferring evidence for biological effects.

Results

We captured 43 females, 17 of which were additionally recaptured one or more times. Seventeen adult female bats had radio-transmitters affixed that weighed on average 5.5% of the bats body mass. Between 10 June and 14 Aug thirty-six bats were located at 46 different roost trees for a total of 254 day locations of individuals. Bats were recorded roosting in the same roost tree for 1.6 ± 0.5 days and most roost trees were used on only one or two occasions. Of the 36 bats recorded at roost trees, 26 were recorded on 2 or more occasions for an average of 9.01 (±5.14 SD) identifications at roosts (range 2-21). Emergence counts of bats exiting roosts ranged from 1-67 (average 23). Known roosts were spread over 2.68 km^2.

There was no evidence of adverse effects of marking individuals with PIT-tags for any of the 17 recaptured bats. However, one female seemed to have lost her PIT-tag. It was evident that she was initially captured early in the study as patagium sample holes (taken for subsequent genetic analysis) had healed and fur had been trimmed but we could neither see, feel, nor record a PIT-tag. This individual was above the average weight for captures during this time period with no obvious injuries.

Preferential Associations

The standard deviation of the mean observed half-weight association index was significantly higher than that generated from the permuted data sets ($p>0.999$) and so the null hypothesis that individuals associate at random was rejected (p values represent the proportion randomly generated data sets with standard deviations less than the real data; (Whitehead 2005)). Consequently, the mean of the half-weight association index values of all individuals was low (0.05±0.05 SD). The average of all non-zero half-weight association index values was 0.22 (±0.15 SD) indicating that individuals that associate can be expected to be located together on approximately 22% of days. The average maximum half-weight association index value for each individual was 0.42 (±0.19 SD) suggesting that some pairs were more strongly associated and expected to roost together on approximately 42% of days.

Cluster analysis of half-weight index values delineated 9 social-groups (half-weight index values >0.1; cophenetic correlation coefficient: 0.82; Fig. 1). Within each social-group half-weight index values are quite variable. This could be an artefact of sample size or possibly varying degrees of cohesiveness among members of the same social-group. Social-groups members were often separated into two or more trees on a given day, and almost invariably roosted with members of other social-groups. On some occasions groups of 2-4 individuals roosted together on consecutive days in roosts separated by > 1 km. These results suggest that this species forms non-random fission-fusion social-groups (groups of individuals that associate more than expected at random).

Temporal Pattern and Community Structure

The SLAR falls for approximately 10 days and then stabilises above the null association rate. This indicates that the majority of intermixing occurs during the initial 10 days after group formation after which a subset of individuals remain associated throughout the summer (Fig. 2). Model selection indicated that the model representing a 2-levelled social system of casual (short-term) acquaintances and constant (long-term) companions best fit the data (Table 1, Fig. 2) with 68% probability of being the best candidate model given the data ($w_i = 0.68$). A second model, describing a 2-levelled social system of casual acquaintances had a 32% probability of being the best candidate model (Table1; $w_i = 0.32$). The fitted lines for these models were nearly identical and the inferences drawn from their interpretations were similar. Neither fitted line fell below the line for the null association rate for time lags investigated during this study and so we interpret the constant companions and casual acquaintances model as it had the highest probability of explaining the variation in the data and had fewer estimatable parameters (K=2) than the 2-levelled casual acquaintance model (K=3).

The level at which the lagged association rate stabilises relative to the *y-intercept* can be interpreted as the proportion of individuals within a roost tree that remains with a randomly chosen individual from that roost in the long term (i.e., the estimated proportion of constant companions). The model value when the time lag equals zero (*y-intercept*) is 0.343 and the model stabilises at 0.047. Therefore approximately 14% of marked individuals within a maternity roost may be expected to remain companions throughout the summer.

Ecological impacts on group fission and fusion

The analyses of social-group cohesion indicated that the odds of a pair within a social-group being located together on a day during the lactation (n=32) period were 2.35 times greater than pre- and post-lactation (n=67; $\beta_o = -0.56$ (SE 0.39), $\beta_1 = 0.86$ (SE 0.42), odds ratio: 2.35, 95% CI: 1.04 – 5.38, p=0.037). The minimum temperature from the night before a pair was located together during the day seemed to have little effect on social-group cohesion as indicated by the odds ratio and its confidence interval, small effect sizes over the range of temperatures that occurred during the study, and non-significant p-value ($\beta_o = -0.93$ (SE 0.76), $\beta_1 = 0.074$ (SE 0.050); odds ratio: 1.07, 95% CI: 0.98 – 1.19, p=0.11).

Discussion

We show that northern long-eared bats at maternity roosts actively associate in non-random fission-fusion societies. This is demonstrated by: 1) the permutation test of half-weight association index values showing that individuals associated more often with specific individuals than would be expected if associations were random; 2) near daily roost switching with very little reuse of roosts which indicates that suitable roosts are not a limiting factor and that our results are not a product of individuals aggregating at a limiting resource; 3) evidence that grouping is related to reproductive status (potentially active association) and not thermoregulation (passive association); and 4) model selection indicating two levels of association patterns (short- and long- term) above the expected null association rate. Social-group roosting areas overlapped extensively and although not explicitly demonstrated it seems likely that most individuals within the study area roosted together at some point during the summer season.

The composition of maternity roosts on whole was largely ephemeral in nature and social-groups most often roosted in smaller sub-units of social groups spread across multiple roost trees. The model that best fit the SLAR described a 2-levelled social system comprised of constant companions and casual acquaintances. The rate of decay of the SLAR suggests that the majority of intermixing at maternity roosts takes place and decays over periods of approximately 10 days after group formation (casual acquaintances). Subsets of individuals (14%) within maternity roosts however, remain closely affiliated throughout the season (constant companions; corresponding to between 2-9 individuals in this study).

We expected that female choice of roost mates would reflect probable reproductive benefits gained by group-living. We can provide no evidence of mutualistic or cooperative behaviours but we show that social-group pairs were 2.35 times more likely to be found together during lactation than prior to and after lactation suggesting that these behaviours may exist. Reproductive females may choose to roost in larger groups and/or select warmer cavities to reduce exposure to low temperatures that might delay gestation (Racey & Swift 1981) and decrease milk production delaying offspring development (Wilde et al. 1995; Wilde et al. 1999). Conversely, pregnant females may select cooler cavities during pregnancy in order to conserve energy, offset the increased costs of flight while carrying a foetus, and facilitate torpor use (Kerth et al. 2001b; Willis et al. 2006). However, we did not find evidence that the minimum night time temperature affected the probability of social-group members roosting together the following day. The positive relationship between reproductive period and social-group cohesion suggests that associations are possibly active and that there are potential reproductive benefits beyond those expected to occur as a result of passive clustering for thermoregulatory benefits which would not likely require specific roost mates. It is possible that thermoregulatory costs related to reproductive status and temperature are mediated primarily through roost selection and not related to social group size as has been demonstrated for Bechstein's bats (Kerth et al. 2001b).

Strong matrilineal substructure within colonies can occur among species in which females are philopatric (Kerth et al. 2000; Castella et al. 2001; Rossiter et al. 2002). For example, greater horseshoe bat (*Rhinolophus ferrumequinum*) colonies have been shown to contain multiple matrilines (Rossiter et al. 2002). Within the whole colony relatedness was low, however within matriline relatedness, logically, is quite high and individuals from the same matriline tended to roost together more often than with unrelated individuals (Rossiter et al. 2002). These circumstances provide a possible pathway through which inclusive fitness benefits may facilitate the evolution of sociality if cooperation is directed toward kin. If this scenario is typical of temperate bat species then it is possible that the social-groups delineated here are matrilineally related.

Flexible fission-fusion association patterns quite similar to that described here for northern long-eared bats have been described across a diversity of bat species with varying life histories. In each case group composition was variable, associations were different than random, and individuals from social-groups were most often spread over multiple roost on a day. Wilkinson (1985) quantitatively demonstrated that tropical female common vampire bats from multiple harems actively associated in non-random fission-fusion societies and further showed that female pairs with strong associations were more likely to share food than randomly chosen individuals thus demonstrating unambiguous benefits of sociality. Similarly, O'Donnell (2000) and Vonhof et al. (2004) demonstrated that temperate long-tailed bats (*Chalinolobus tuberculatus*) and tropical Spix's disc-winged bat (*Thyroptera tricolor*), respectively, live in non-random multi-male multi-female fission-fusion societies. Finally, Kerth and Konig (1999) and Willis and Brigham (2004), and Kozhurina (1993) describe what seems, at least superficially, to be the most similar social system to that described here for northern long-eared bats among Bechstein's bats, big brown bats (*Eptesicus fuscus*), and noctule bats (*Nyctalus noctula*) respectively. Each of these species life histories are characterized by sexual segregation at roosts during the summer with males tending to roost solitarily and only females congregating at maternity roosts and social groups roosted in multiple roost trees on a given day with roost group composition varying daily. Particularly intensive monitoring of Bechstein's bat social-groups have provided interesting insights into possible mechanisms through which this social system could be maintained among temperate bats. Bechstein's bats live in behaviourally and genetically closed matrilineal fission-fusion social-groups (Kerth & Konig 1999; Kerth et al. 2000). Allogrooming and information transfer about suitable roosts has been shown to be common (Kerth & Reckardt 2003) and possible inheritance of foraging sites has also been identified within Bechstein's bat social-groups (Kerth et al. 2001a). Two functions of information transfer about roosts were suggested; the first was to generate a communal knowledge of suitable roosts and the second was to prevent unwanted colony fission.

Our study is the first to quantitatively consider the temporal persistence of relationships for temperate bats. The temporal nature of relationships is an important but often overlooked aspect of Hinde's (1976) framework for social analysis (Whitehead & Dufault 1999). Pairs that spend an uninterrupted period of time together over a short period (perhaps several consecutive weeks) have very different relationships than a pair that may spend the same amount of time together over a year, however an association index value for the period of one year will be equal (Whitehead & Dufault 1999). For temperate bats it seems possible that fitness benefits of sociality occur primarily when individuals are pregnant and lactating. During this period bats synchronize behaviour, possibly forgoing other individually beneficial behaviours to synchronize with the social group (e.g., congregating and locating a tree when it may also be beneficial to continue feeding) because overall fitness is enhanced by being a member of the social group. After offspring have become volant benefits of maintaining social group cohesion may be less important than feeding for an extra time period and group cohesiveness becomes less important.

As discussed previously (Introduction) forms of fission-fusion sociality have been described within and across diverse taxa. As of yet it is not clear whether there are general mechanisms through which fitness is enhanced and in fact the diversity of possible pathways is large. For example, chimpanzee (*Pan troglodytes*) social group size and composition varies with predation pressure (Sakura 1994), the presence of reproductive females (Hashimoto et al. 2001), the quality and patchiness of food sources (Matsumoto-Oda et al. 1998), and whole social unit size (Lehmann & Boesch 2004). Cetaceans may benefit from various group-living situations through communal care of young when other group members protect the offspring of a diving mother from predators while she forages (Arnbom & Whitehead 1989) and coordinated foraging may allow group members to capture prey that have eluded others (Whitehead 1989) and adult female spotted hyena (*Crocuta crocuta*) association patterns are strongly based upon kinship (Holekamp et al. 1997). Also, in some instances young and inexperienced individuals may benefit from associating with older individuals that may, through experience, possess a greater knowledge of ecological situations and settings thus learn from their response (Kerth & Reckardt 2003; Wittemyer et al. 2005). One common feature of these fission-fusion societies is behavioural flexibility. This flexibility allows quick alteration of group size and composition with varying costs and benefits associated accordingly with changing ecological conditions.

It is apparent that the social nature of bat species can be complex, adding behavioural and potentially genetic structure to populations. If there are reproductive consequences for the degradation of social relationships, as has been previously suggested, then social groups may be the appropriate management unit for social bat species (O'Donnell 2000; Vonhof et al. 2004; Willis & Brigham 2004). Also the added structure will be important to consider when interpreting results from other biological questions pertaining to behaviour, resource use, population distributions etc. Finally, due to the ecological and species diversity of bats, comparative studies of bat species social systems have the potential to provide valuable insight into the evolution of ba social systems.

Acknowledgments

We would like to thank Joe Poissant for assistance in the field and Hal Whitehead for valuable comments on an earlier version of this manuscript. This research was funded by the Natural Science and Engineering Research Council of Canada through a Canada Graduate Scholarship to Colin J. Garroway and Discovery and Research Tools and Equipment Grants to Hugh G. Broders. All procedures were approved by the Saint Mary's University Animal Care Committee.

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Table 1. A priori candidate model set of simulated social structures fit to the standardized lagged association rate of northern long-eared bats (*Myotis septentrionalis*) in Nova Scotia, Canada, 2005.

Model Description	**Model Structre**	w_i	Δ_i	**Rank**
Constant Companions	$g(\tau) = a_1$	0.00	110.83	4
Casual Aquantances (CA)	$g(\tau) = a_2 e^{(-a_1 \tau)}$	0.00	1.54	3
CA + CC	$g(\tau) = a_2 + a_3 e^{(-a_3 \tau)}$	0.68	0.00	1
Two levels of CA	$g(\tau) = a_3 e^{(-a_1 \tau)} + a_4 e^{(-a_2 \tau)}$	0.32	0.39	2

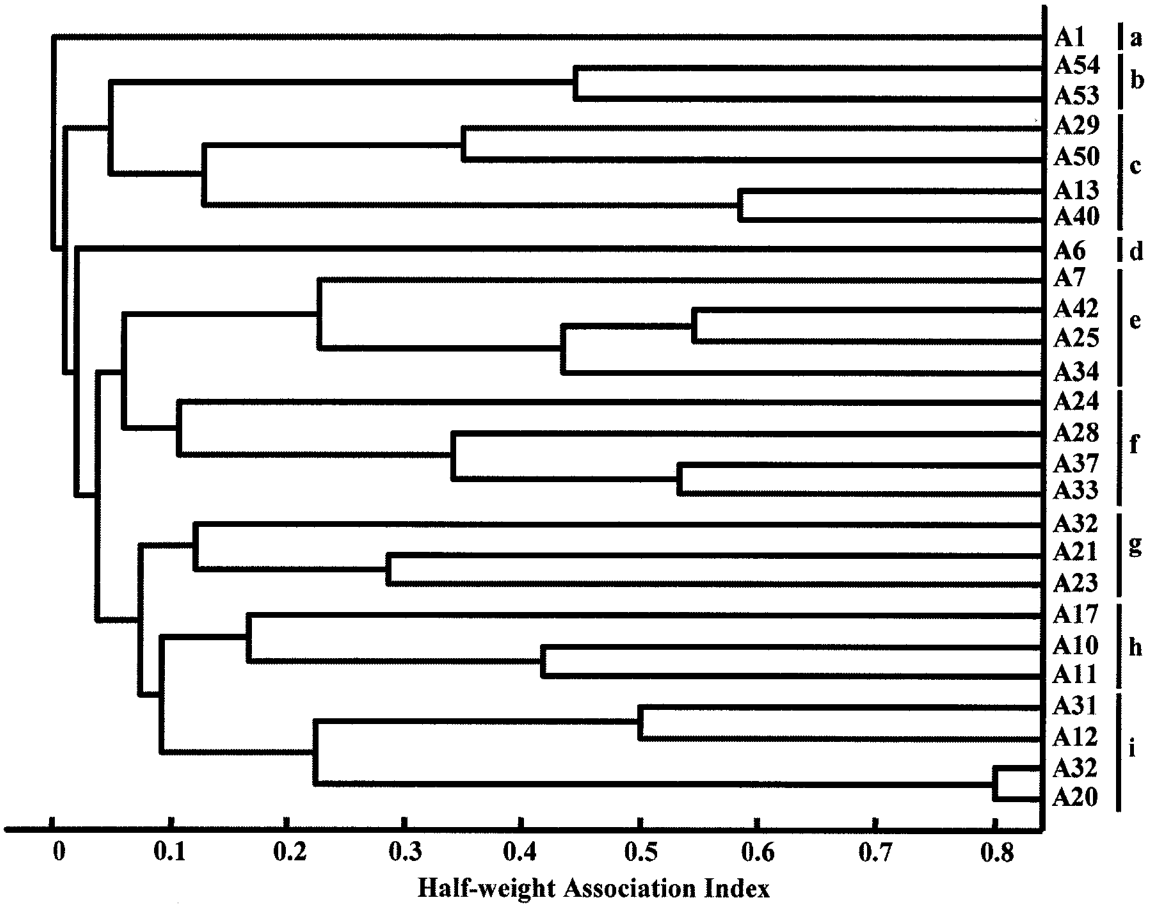

Figure 1. Average linkage cluster analysis diagram of half-weight association index values of female northern long-eared bats (*Myotis septentrionalis*) within maternity roosts at Dollar Lake Provincial Park, Nova Scotia, Canada, 2005. Permutation tests indicated that clustering was different than random. Nine social-groups (a-i) were delineated based upon individuals with index values greater than 0.1 (average plus standard deviation of permuted data).

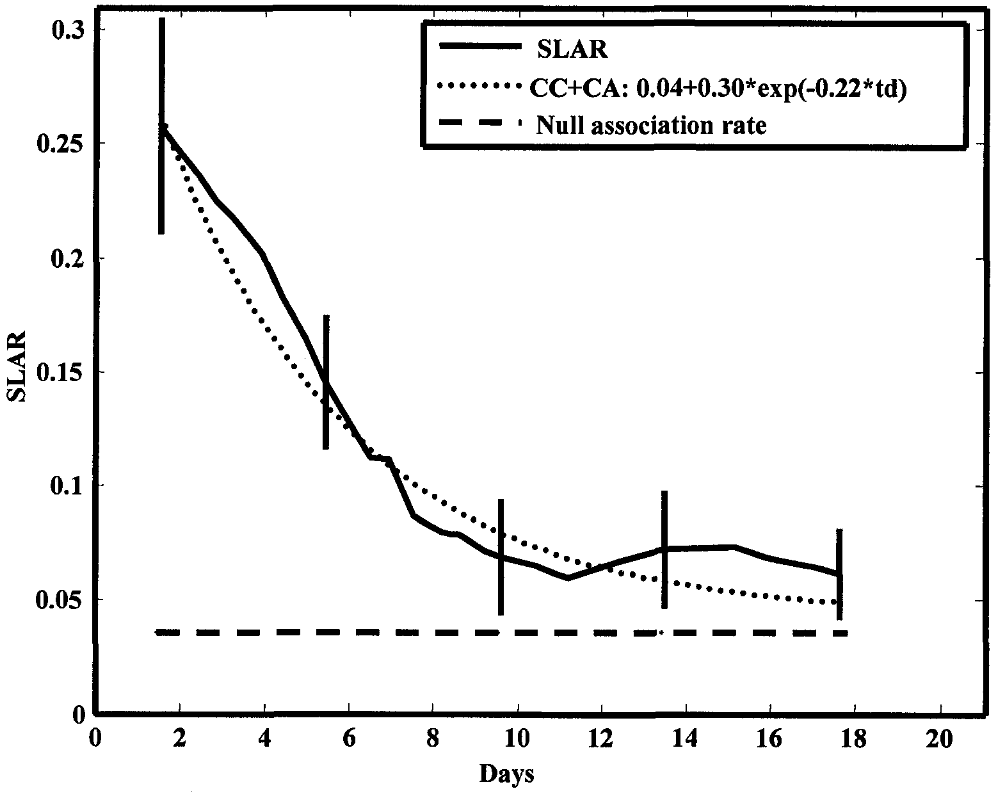

Figure 2. Standardized lagged association rate (SLAR) and jackknifed standard error bars, null association rate, and best fit model (constant companions and casual acquaintances; CC+CA) to the SLAR.

CHAPTER 3:

Intra-annual variation in day-roost characteristics in relation to reproductive season of northern long-eared bats (*Myotis septentrionalis*)

Abstract

During the summer, females of most temperate bat species roost colonially at maternity roost. During this period females gestate, give birth, and wean offspring making the presence of suitable roosts critical to population persistence. Many studies have identified important roost tree characteristics by comparing roost trees to random trees. However, if bats select trees that facilitate either torpor use or maintenance of normothermic body temperatures relative to the energetic demands of reproduction then it follows that roost tree characteristics may vary similarly. We compared variation in roost tree and site selection of lactating northern long-eared bats to pre- and post-lactation periods. Scores from two principal components were the best predictors of the variation in roost selection. Relative to pre- and post-lactation periods lactating bat roost sites had a high and relatively open dominant canopy with low tree density (both coniferous and deciduous); roosts were situated high in tall trees. This study demonstrates that to ensure population persistence, managers should consider roost area level management and seasonal variation in roost tree suitability. The fact that roost tree use during lactation was explained by multivariate variables correlated with a suite of forest characteristics associated with mature forests also suggests the potential utility of this species as an indicator for these forest characteristics.

Introduction

Beginning in late spring and continuing through early autumn, females of most temperate bat species roost in groups ranging in size from a few to several hundreds of individuals within which offspring are gestated and nursed until weaned (Kunz and Lumsden, 2003). These roost sites are critical for population persistence as they provide a microclimate suitable for offspring development and act as a centre for social interactions (Kalcounis-Ruppell *et al.*, 2005). Accordingly, it is important to understand how bats use roosts if these features are to be maintained in a landscape.

Roosts with microclimates that either facilitate the use of torpor or reduce the costs of maintaining normothermic body temperature may be selected depending upon the energetic demands of reproduction. For example, reproductive individuals may select warm roosts because low temperatures may delay gestation (Racey and Swift, 1981) and decrease milk production (Wilde *et al.*, 1995; Wilde *et al.*, 1999). Alternatively, pregnant individuals may sometimes select cooler roosts to facilitate entering torpor in order to mediate the added energetic costs of flight associated with carrying a fetus (Kerth *et al.*, 2001) or possibly to delay parturition until environmental conditions and resources are favorable for meeting the added energetic demands associated with lactation (Willis *et al.*, 2006b).

Furthermore, evidence is accumulating that suggests social interactions between individuals at maternity roosts conform to the fission-fusion social model and may provide important fitness benefits (Kerth and Konig, 1999; O'Donnell, 2000; Vonhof *et al.*, 2004; Willis and Brigham, 2004; Garroway and Broders, 2006). Within the fission-fusion social setting colony members roost in multiple roost trees on a given day and switch roost trees often (Kerth and Konig, 1999; O'Donnell, 2000; Vonhof *et al.*, 2004;

Willis and Brigham, 2004; Garroway and Broders, 2006). Therefore, it may also be important to manage for a large network of suitable roosts for the maintenance of a colony.

Kalcounis-Ruppell et al. (2005) performed a meta-analysis of studies that explicitly compared random trees with known roost trees. They found that in general, both foliage and cavity roosting species roosted in tall trees with a large diameter at breast height that were located in stands with a high density of snags. Cavity roosting bats selected trees in open canopy stands that were closer to water relative to those selected by foliage roosting species. The used versus random paradigm for assessing roost characteristics of bat species has been popular and informative, but there are some important and often unstated assumptions that may limit inferences when this study design is applied to bat roost tree studies (Willis *et al.*, 2006a). A particularly common assumption that is of interest here is that roost tree data from individuals across reproductive stages of the roosting season can be combined. Energetic constraints (Gittleman and Thompson, 1988) and social group cohesion (Garroway and Broders, 2006) vary with reproductive stage and so it seems likely that roost tree characteristics could co-vary reflecting these constraints.

To assure the persistence of forest dependent bat populations it is important to have easily measured characteristics from which to judge the suitability of a tree and site as a bat roost. Despite the potential for variation in roost tree selection, few studies have examined intra-annual variation in roost tree and site level characteristics in temperate bats. Studies that have looked at roost microclimate variation in relation to reproductive period (rock-crevice roosting female *Eptesicus fuscus* and *Myotis evotis* (Chrusczc and Barclay, 2002; Lausen and Barclay, 2002); cavity roosting *M. bechsteinii* (Kerth *et al.*, 2001)) have demonstrated that reproductive bats (at varying stages) select different roost microclimates than bats during non-reproductive periods. Willis et al. (2006a) found that roost cavity shape varied with reproductive season and suggested that this too was related to the association between cavity shapes and roost microclimate. However, it is often difficult to measure microclimatic characteristics of cavities used by forest roosting bats. To our knowledge, only Veilleux et al. (2004) investigated intra-annual variation in roost tree and site characteristic in forest dwelling bats. They showed the characteristics of day roosts selected by foliage-roosting female eastern pipistrelles (*Pipistrellus subflavus*) vary with 'reproductive season' and the putative energetic constraints associated with reproductive periods.

We hypothesized that for female temperate bats to maximize energy efficiency during the different stages of reproduction, roosts that they select should vary in microclimates among the different stages. This is because of the variation in: 1) energetic constraints associated with the various stages of reproduction and 2) the fitness benefits of torpor during these stages. To assess this hypothesis we tested its prediction that roost characteristics associated with the lactation period would be distinguishable from those used both before and after the lactation period. To test this we studied variation in roost tree selection by female northern long-eared bats (*M. septentrionalis*) in relation to reproductive season in Nova Scotia, Canada. Northern long-eared bats are forest dependant for roosting and foraging and typically roost in cavities or under loose bark (Sasse and Pekins, 1996; Foster and Kurta, 1999; Jung *et al.*, 1999; Lacki and Schwierjohann, 2001; Broders and Forbes, 2004; Broders *et al.*, 2006). Males roost solitarily while females most often roost in maternity roosts. In Nova Scotia, maternity roosts are comprised of members from multiple, relatively stable interacting social groups with individuals from social groups roosting in multiple roost trees that together form a colony (Garroway and Broders, 2006). Social group cohesion is positively related to reproductive status (lactation) but not related to minimum temperatures from the previous night (Garroway and Broders, 2006). This suggests that roost selection rather than social clustering behaviour may be the primary means through which the energetic costs of thermoregulation relative reproduction are mediated.

Methods

Field work was conducted at Dollar Lake Provincial Park (44°55’ N, 63°19’ W) in Nova Scotia, Canada 1 June- 31 August, 2005. Capture, marking, and radio-tracking protocol are described in Garroway and Broders (2006). When no bats were known to be roosting within roost trees, we measured both roost tree and site characteristics for a 0.1 ha plot (17.8 m radius) centred of roost trees. The variables measured were chosen for their potential influence on roost microclimate and structural characteristics of the surrounding forest (e.g., clutter) that may influence roost selection. We measured tree height with a clinometer (model PM-5/1520, Suunto, Finland) and canopy closure (average of four cardinal directions measured from the base of the roost tree) using a spherical densitometer (model-A, Forest Densiometers, Bartlesville, Oklahoma). The dominant canopy height was calculated from the average of five trees judged to be representative of the dominant canopy within the plot. Canopy height relative to roost was calculated as the distance between the dominant canopy height and the roost. We also measured roost tree diameter at breast height (dbh), distance to the nearest tree as tall as the roost within a 180° arc centered on the roost entrance, and counted the number of deciduous trees, coniferous trees (trees higher than 2 m), and potential roost (defined as trees decay class ≥ 2 with evidence of defects; (sensu (Broders and Forbes, 2004)) trees within the plot. Finally we included a variable for the total number of trees within the plot.

Analysis was conducted using a logistic regression with lactation period (from first evidence of lactation to capture of the first volant juvenile) trees coded as 1 and pre- and post-lactation trees coded as 0. To test whether bat roosts are associated with multiple tree and site level characteristics multivariate components were constructed using a correlation matrix based principal components analysis. Principal component scores were used as independent variables within the logistic regression analysis (Aguilera *et al.*, 2006). We included components with eiganvalues >1 as variables within the logistic regression model because components with values below 1 explain less variation than single variables (Kaiser, 1960). The dependent variable was permuted (keeping the number of trees in each category constant) and parameter estimates calculated 999 times. Components were considered to have a significant effect if the parameter estimate was greater than 97.5% or less than 2.5% (two-tailed test) of permuted values and the confidence interval of the parameter estimate did not overlap zero. Goodness of fit was assessed using Hosmer and Lemeshow's goodness of fit test and McFadden's rho^2 (Hosmer and Lemeshow, 2000). McFadden' rho^2 values are interpreted similarly to the linear regression R2 however values tend to be lower (Hosmer and Lemeshow 2000) with values between 0.20-0.40 indicating a high proportion of variation in the data are explained by the model (Wrigley 1985REF). Variables highly correlated (loadings < -0.5 and > 0.5; arbitrarily chosen) on important components were considered to have important effects.

Results

We located and recorded tree and site measurements for 44 day-roost trees (pre- and post lactation n= 22, lactation n= 22). Tree species used included red maple (*Acer rubrum;* n= 20), eastern hemlock (*Tsuga Canadensis*; n=15), yellow birch (*Betula alleghaniensis*; n=4), red spruce (*Picea rubens*; n= 2), sugar maple (*A. saccharum*; n=2), and white birch (*B. papyrifera*; n=1).

Five principal components explaining 87% of the variance in the data were included as variables in the logistic regression analysis. Component 1 ($\beta_{\text{component1}}$: 1.664 95% CI: 1.01, 2.32, p=0.024) and component 2 ($\beta_{\text{component2}}$: -1.478, 95% CI: -0.05, -2.91, p=0.012) had significant effects in the logistic regression analysis. Hosmer and Lemeshow's goodness of fit test indicated that the model adequately fit the data (p=0.416)

Component 1 was correlated with roost tree height, average dominant canopy height, canopy relative to roost, the number of coniferous trees, and the total number of trees (Table 1). The positive logistic regression parameter estimate suggests that during the lactation period, bats are most likely to roost in taller trees with a higher dominant canopy, a greater distance between the roost and the canopy, and in areas with a lower density of coniferous trees and total number of trees in general relative to pre- and post-lactation periods.

Component 2 was correlated with roost height, canopy relative to roost, the number of deciduous trees, and canopy cover (Table 1). The negative logistic regression parameter estimate and direction of variable correlation with component 2 indicate that when bats are lactating, roosts are higher in trees, closer to the dominant canopy, in areas with a lower proportion of deciduous trees, in an area with lower canopy cover relative to pre- and post lactation periods.

Discussion

Roost tree and site characteristics selected by female northern long-eared bats varied with the stage of reproduction. Relative to pre- and post lactation periods, northern long-eared bat roosts were situated high in tall trees during the lactating period. Roost tree sites (0.1 ha plots) were characterized by a high and relatively open dominant canopy and lower tree density (both coniferous and deciduous). Roost locations while lactating were not affected by the distance from the nearest tree to the roost, the diameter at breast height of the roost tree, nor the number of potentially suitable roost trees within the plot. Correlations between the important variables and each principal component were in the same direction except for the variable for the distance between the roost and the canopy. The relationship between component 1 and the distance between the roost site and the dominant canopy suggest that roost sites selected by lactating bats are positively correlated with increasing distance between the dominant canopy and the roost while the relationship between component 2 and the same variable suggests the opposite. This indicates that correlations between the principal components and this variable may be an artifact of strong correlations between other variables and the components.

There are at least two non-exclusive explanations that remain to be tested for the importance of these features to lactating bats. High roosts in tall trees that are in areas with open canopies increase exposure of the roost to the sun during the day possibly reducing the costs of maintaining a normothermic body temperature during lactation when torpor would most impact offspring development and survival (Racey and Swift, 1981; Wilde *et al.*, 1995; Wilde *et al.*, 1999). These features may also provide areas with minimal clutter that allow newly volant offspring to practice flying and foraging. Offspring must be able to forage on their own shortly after being born (three weeks for the congeneric little brown bat, *M. lucifugus* (Fenton and Barclay, 1980)) and so an uncluttered area for the development of flight and foraging proficiency may be important.

Many previous studies have examined the characteristics that differentiate bat roosts from other trees. Willis et al. (2006a) highlight some of the limitations associated with roost versus random tree comparisons. Our results support one point made by these authors in particular in that we demonstrate that within a roosting season, not all roost trees are used equally at all times of the year and so they cannot necessarily be grouped into one category, as is often done in used verses random tree studies. It is therefore important to control for within season variation in roost selection (e.g., Brigham *et al.*, 1997; Kalcounis and Brigham, 1998). The lactation period is the most energetically demanding time period for both mothers and offspring (Racey and Swift, 1981; Wilde *et al.*, 1995; Wilde *et al.*, 1999) and roost tree and site characteristics seem to be reflect these costs. The used versus random tree study design remains a valuable tool for examining what and how forest features are used by bats as roosts. If the observed variation in roost selection is a function of roost microclimate selection in relation to the energetic constraints of reproduction then we expect that torpor use will vary concurrently with roost tree selection.

Few studies have explicitly examined within season variation in roost tree and site selection. Lausen and Barclay (2002) and Chruszcz and Barclay (2002) have described intra-annual variation in roost microclimates for rock crevice roosting female big brown bats (*Eptesicus fuscus*) and long-eared bats (*M. evotis*), respectively. Kerth et al. (2001) have also experimentally shown that female, cavity-roosting Bechstein's bats (*M. bechsteinii*) preferred warmer roosts when lactating than both prior to parturition and post-lactation. In each case these authors hypothesized that the functional roost characteristics selected by individuals reflected putative energetic trade-offs associated with torpor and reproduction. Although roost microclimate has been demonstrated to be an important factor determining whether a roost is selected (Kerth *et al.*, 2001) it is often difficult or impossible to measure microclimatic condition within natural cavities. It is therefore useful to have an understanding of externally measurable features that are related to suitable roost trees. Here we show that easily measured external tree and site level characteristics are associated with suitable roost trees of cavity dwelling bats.

There are some interesting implications for the fact that roost tree use by lactating bats was explained by multivariate principal components that are correlated with a suite of forest characteristics. First, managing for individual forest features (e.g., legacy trees within a harvested stand) alone may be inadequate for populations of this and likely other forest dependent bat species to persist if roost requirements are related to multiple interdependent forest characteristics. It is therefore likely necessary to maintain intact forest stands within which there is minimal disturbance if these features are to be maintained. The social nature of this and other bat species adds another layer of complexity to managing forests for roost tree maintenance which further suggests the need for stand level management (O'Donnell, 2000; Vonhof *et al.*, 2004; Willis and Brigham, 2004; Garroway and Broders, 2006). Bats switch roosts often yet maintain long term associations with specific colony members. This result suggests that there may be fitness benefits to maintaining these associations and the need to maintain a network of trees to facilitate roost switching and social interactions. For social species, roost areas (minimally) may be the appropriate scale for managing for the maintenance of summer bat colonies.

The characteristics of the forest stands used by bats for roosting in this study could be classified as late successional to old-growth Acadian forests (based upon (Mosseler *et al.*, 2003)). There is no consensus on a single definition of old-growth for all forest types however in relation to wildlife the term is generally used to describe a large-scale functional system within which biotic and abiotic processes create unique features that support a high biodiversity. If the roosts used by northern long-eared bats during lactation are associated with the multivariate characteristics of late successional and old growth forests then their presence within a forest may indicate the presence of other mature forest associated species and the forest characteristics of an area. Northern long-eared bats are common throughout much of their range (Caceres and Barclay, 2000) and so in areas where they are present they are likely to be captured. They roost and forage within the forest, are resource limited (suitable roost trees), and roost tree and site level features may be indicative of a suite characteristics associated with mature forests, but this remains to be tested. Although the efficacy of this species as an indicator of forest integrity was not the focus of this study our results suggest that it may be an appropriate candidate species.

Acknowledgements

We would like to thank Joe Poissant for assistance in the field and the Nova Scotia Department of Natural Resources and the staff at Dollar Lake Provincial Park for the use of park facilities and hospitality. This research was funded by the Natural Science and Engineering Research Council of Canada through a Canada Graduate Scholarship to Colin J. Garroway and Discovery and Research Tools and Equipment Grants to Hugh G. Broders. All procedures were approved by the Saint Mary's University Animal Care Committee.

Table 1. Principal component loadings and coefficients of the two principal components that explain intra-annual variation in roost tree selection of northern long-eared bats (*Myotis septentrionalis*). Only variables with loadings <-0.5 or >0.5 were considered important.

	Loadings		**Coefficients**	
Principal Component	***1***	***2***	***1***	***2***
Tree height	0.62	-	0.20	0.14
Nearest tree as tall as roost	-	-	-0.20	-0.02
Roost height	-	-0.61	0.07	-0.26
Average dominant canopy height	0.88	-	0.29	0.14
Canopy relative to roost	0.54	0.66	0.18	0.28
Number of deciduous trees	-	0.69	-0.07	0.29
Number of coniferous trees	-0.85	-	-0.28	0.08
Total number of trees	-0.82	-	-0.27	0.21
Diameter at breast height	-	-	0.01	0.17
Average canopy cover	-	0.60	0.03	0.26
Number of potential roost trees	-	-	-0.10	0.10

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CHAPTER 4:

Social ecology of northern long-eared bats: synthesis

Within maternity roosts northern long-eared bats roosted in non-random social-groups. The model that best described the pattern of association showed a society of constant companions and casual acquaintances. Associations among all individuals at maternity roosts decayed for approximately 10 days after which approximately 14% of individuals remained associated throughout the entire summer. These associations persisted despite individuals changing roosts almost daily, further suggesting that their associations are social and not random. However, the proximate social behaviours from which fitness benefits are derived remain unknown. I do show however that social groups were most cohesive during the lactation period, suggesting that at least some of the fitness benefits of sociality for this species are related to mediating the increased energetic demands during this time period.

Similar to social group cohesion, roost tree and site characteristics differed between lactating and non-lactating periods. Relative to pre- and post-lactation periods lactating bat roost sites had a high and relatively open dominant canopy and low tree density (both coniferous and deciduous) with roosts located in high in tall trees. I hypothesised that roosts that were high in tall trees with lower canopy cover may provide a warm roost microclimate which would be important during the lactation period if the detrimental effects of torpor use during this time are to be avoided. The fact that bats used many roost trees (likely >>44) indicates that, if social colonies are to be conserved, areas containing networks of roost trees need to be maintained. The interdependence of the tree and site characteristics selected during this time period has other potentially important implications. These characteristics are related to late successional to old-growth Acadian forest (Mosseler et al. 2003). If the presence of northern long-eared bats indicates the presence of these characteristics, which are also important to many other mature/old-growth dependant species (e.g., woodpeckers (Imbeau and Desrochers 2002)), northern long-eared bat females could be good indicator species for the presence of a suite of other species.

As discussed in chapter 2 forms of fission-fusion sociality have been described within and across diverse taxa which indicates that it has independently evolved on many occasions. This leads to speculation that there may be general beneficial features associated with the evolution of fission-fusion sociality that may be common across these taxa. As of yet it is not clear whether there are general mechanisms through which fitness is enhanced and in fact the diversity of possible pathways is large. However, one overriding common feature of fission-fusion sociality is its flexibility. This flexibility allows quick alteration of group size and composition with varying costs and benefits associated with changing conditions (intrinsic and extrinsic). For bats it seems possible that fitness benefits of sociality occur primarily when individuals are pregnant and lactating. During this period bats synchronize behaviour, possibly forgoing individually beneficial behaviour to synchronize with the social group (e.g., congregating and locating a tree when it may be more beneficial for an individual to continue feeding) because overall fitness is enhanced by being a member of the social group. After offspring have become volant benefits of maintaining social group cohesion may be less important than feeding for an extra time period and group cohesiveness becomes consequently less important. Similarly, chimpanzee social-group size and composition varies with predation pressure (Sakura 1994), the availability of reproductively available females (Hashimoto et al. 2001), and the quality and availability of food sources (Matsumoto-Oda et al. 1998). In these cases group size and composition variation may be considered adaptive traits that are allowed to vary quickly and easily within fission-fusion societies.

The results of chapter 2 demonstrate that social structuring can have important implications for the interpretation of what and how important habitat features are used by animals. The fact that these northern long-eared bats are social implies that there are fitness benefits to sociality and the social colony is the functional reproductive unit. Given near daily roost switching and minimal within season reuse of trees, it is apparent that networks of suitable roost trees are necessary for colony maintenance. Roost trees and sites used by individuals during the lactation period were different than those used prior to and after lactation indicating that all roost trees are not equally available throughout the summer. That multivariate components differentiated trees used during the lactation period from others indicates that it is not likely any one particular forest or tree feature that is important but a suite of interrelated features. Furthermore, features associated with the multivariate components were also features of the late successional/old growth forest of the area (Mosseler et al. 2003). The large number of trees spread over a wide spatial scale (2.4 km^2) used by this species, the abundance of northern long-eared bats in this area of their range, their reliance on the forest for both foraging and roosting, and the fact that roost trees are related to a suite of important forest characteristics may make northern long-eared bats a particularly valuable indicator species for forest age and structure.

Taken together, these results demonstrate the utility of this and likely other bat species as model systems for studying the evolution of sociality and many characteristics associated with environments of high ecological integrity. It also demonstrates the importance of considering the implications of sociality when examining other biological questions. At this point for northern long-eared bats we can only speculate the manner and mechanisms in which this social system impacts individual fitness. However, as discussed in previous chapters, information transfer (Wilkinson and Boughman 1998; Kerth and Reckardt 2003), social learning (Boughman 1998), individual/social-group recognition (olfactory; Bloss et al. 2002; Safi and Kerth 2003, tactile; Wilkinson 1986), vocal; (Boughman 1997) have been demonstrated in other species which hint at potential fitness benefits of sociality and the mechanisms through which it can evolve.

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