THE CAUSES AND CONSEQUENCES OF FISSION-FUSION DYNAMICS IN FEMALE NORTHERN LONG-EARED BATS (*MYOTIS SEPTENTRIONALIS*)

by

Krista J Patriquin

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The undersigned hereby certify that they have read and recommend to the Faculty of Graduate Studies for acceptance a thesis entitled "THE CAUSES AND CONSEQUENCES OF FISSION-FUSION DYNAMICS IN FEMALE NORTHERN LONG-EARED BATS (*MYOTIS SEPTENTRIONALIS*)" by Krista J Patriquin in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

Dated: May 23, 2012

External Examiner: _____

Research Supervisor: _____

Examining Committee: _____

_____

Departmental Representative: _____

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AUTHOR: Krista J Patriquin

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Signature of Author

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ABSTRACT

Individual costs and benefits of living in groups vary with group size, stability, and composition. Investigations of these features of group living have lead to the recognition of a variety of social structures. Although many studies have examined social structure in animals with long-term, stable groups, little is known about groups with highly variable group size and composition, such as fission-fusion dynamics.

In this thesis I examined the causes and consequences of fission-fusion dynamics by exploring the socioecology of female northern long-eared bats, *Myotis septentrionalis*. Like many temperate bats, female northern long-eared bats show natal philopatry to summer areas. During this time, they live in groups with fission-fusion dynamics as individuals move among a network of roosts and roost-groups. To examine the causes of fission-fusion dynamics, I examined why females switch roosts. To address the consequences of these dynamics, I asked whether females could form stable relationships, and what factors might explain these relationships.

I was able to identify the possible causes and consequences of fission-fusion dynamics that had not yet been explored in bats. I demonstrated that fission-fusion dynamics may be explained, at least in part, by changes in ambient conditions that prompt frequent roost-switching. Despite the highly dynamic nature of these groups, females formed long-term social relationships that were based in part on age and genetic relatedness. These findings have potential consequences for the evolution of social behaviour within groups, such as cooperation and nepotism.

My work also raised several questions that require further examination to fully understand the evolution of fission-fusion dynamics. For example, the question remains whether species or sympatric groups of conspecifics with different degrees of roost-switching show the same social structure. By answering these questions, we can gain a better understanding of the causes and consequences of fission-fusion dynamics across species of bats. Once this is achieved, we can then look for parallels with other taxa to answer questions about the evolution of these dynamic systems.

LIST OF ABBREVIATIONS USED

CI	confidence interval
CV	coefficient of variance
df	degrees of freedom
DLPP	Dollar Lake Provincial Park
g	gram
h	hour
ha	hectare
HWI	half-weight index
km	kilometer
kpa	kilopascal
m	metre
PCA	principal components analysis
PIT	passive integrated transponder
RF	roost fidelity index
SD	standard deviation
SE	standard error
SLAR	standardized lagged association rate
QAIC	Akaike's information criterion adjusted for overdispersion and small sample sizes

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CHAPTER 1
INTRODUCTION

1.1 RATIONALE

Most animals form groups at some point in their lives, but the individual costs and benefits of living in groups vary. For instance, as group size increases, individuals suffer a number of costs, such as intra- and interspecific competition, resource depletion, increased conspicuousness, and risk of disease. At the same time, individuals may gain a number of direct benefits, such as reduced predation risk or lower energetic costs associated with flight, swimming, or thermoregulation (Krause and Ruxton 2002). If groups are relatively stable, members may gain an array of additional benefits by cooperating with one another (Kutsukake 2009). If group members are also related, they may gain inclusive fitness benefits by cooperating with relatives (Hamilton 1964). Thus, the benefits individuals receive within groups may depend on who individuals interact with and how often, which are influenced by group size, stability, and composition (Hinde 1976).

Group size, stability, and composition have been quantified for a wide range of taxa, resulting in the recognition of a variety of social structures. For example, considerable information exists about the social structure of eusocial insects and mammals (Choe and Crespi 1997, Burda et al. 2000), cooperatively breeding fish, birds, and mammals (Stephens et al. 2005, Stiver et al. 2005, Rubenstein and Lovette 2007), and bonded primate groups (Kappeler 1997). Much less is known about groups with fission-fusion dynamics, however – presumably because group size and composition vary over space and time as individuals move regularly among a network of social groups. Quantifying who interacts with whom can be challenging in these dynamic groups and has been achieved for only a few species, including African elephants (*Loxodonta africana*, (Wittemyer et al. 2005, Archie et al. 2006), bottlenose dolphins (*Tursiops truncates*; (Lusseau et al. 2006), Connor et al. 2000) and chimpanzees (*Pan troglodytes*; Lehmann

and Boesch 2004). Nonetheless, fission-fusion dynamics are assumed to be relatively widespread, but remain to be properly quantified (Aureli et al. 2008).

Fission-fusion dynamics appear to be particularly common among bats, especially those in temperate regions. For example, following hibernation, female bats typically aggregate in summer roosts, such as trees, rock cavities, caves, and human-made structures, where they give birth and raise offspring (Kunz and Lumsden 2003). Throughout this time, females switch among roosts on an almost daily basis, yet they also form preferred social relationships, roosting more often with particular individuals throughout roost-switching events (Lewis 1995, Kerth 2008). It remains unclear why females switch roosts, and what the consequences of frequent roost-switching might be for long-term social relationships. In addition, what shapes these preferred relationships is also poorly understood. The purpose of my research, therefore, was to examine the causes and consequences of fission-fusion dynamics that have been documented for female northern long-eared bats, *Myotis septentrionalis*. To do this, I determined a possible cause for roost-switching behaviour to understand what may cause fission-fusion dynamics in bats. I also quantified the social and genetic relationships within fission-fusion groups, as outlined below.

Females may gain a number of benefits by frequently switching roosts. For example, roost-switching may reduce ectoparasite loads and predation risk (Lewis 1995, Reckardt and Kerth 2006, Bartonicka and Gaisler 2007, Patterson et al. 2007), minimize distances between roosts and ephemeral prey (Lewis 1995), and facilitate social connections and information sharing among a network of conspecifics (Willis and Brigham 2004, Kerth and van Schaik 2011). However, females use roosts primarily to minimize energetic costs by selecting roosts with optimal microclimates for thermoregulation (Barclay and Kurta 2007). Frequent roost-switching may therefore allow females to select different microclimates according to their varying thermoregulatory needs, which vary with reproductive condition and ambient conditions. Changes in ambient conditions may therefore explain frequent roost-switching, which I explored in Chapter 2.

Fission-fusion dynamics may be a consequence of roost-switching. While a growing body of evidence suggests that females form preferred relationships despite switching roosts frequently (Kerth 2008), it remains unclear whether these relationships are stable over time. Yet, stable relationships may be important for social behaviours to evolve and persist (Trivers 1971). Therefore, in Chapter 3, I determined whether preferred relationships among females persisted throughout a given summer and across summers (Patriquin et al. 2010). What shapes these preferred social relationships is also not fully understood, though it appears they are based in part on reproductive condition. However, evidence that female bats in temperate regions live in groups of overlapping generations suggests relationships may also be based on age, as has been documented for other long-lived mammals with fission-fusion dynamics. Therefore, in Chapter 3, I also tested whether females roosted more often with group members based on their age (Patriquin et al. 2010).

Preferred relationships among bats could also be based to some degree on genetic relatedness (Hamilton 1964). Females of temperate bat species show strong natal philopatry to summer roosting areas, suggesting the potential for social relationships to be based on matrilineal relatedness. However, the potential for kin selection in bat populations with fission-fusion dynamics has often been discounted as average group relatedness at the nuclear level is typically low. Yet, selection acts at the individual level, suggesting that relatedness between interacting pairs, rather than average group relatedness, should be examined. Therefore, in Chapter 4, I examined pairwise relatedness of females to test whether pairwise social relationships may be shaped by genetic relatedness.

Together, the social and genetic structure of populations can have important evolutionary consequences. Culture, for example, is generally defined by group differences in behaviour that can be attributed to social-learning rather than due to genetic differences between groups. The likelihood that culture may exist in groups therefore depends in part on the opportunity to learn from conspecifics, which depends on the social structure of

groups. While culture has not yet been examined in bats, I explored whether there is evidence to suggest they may meet the criteria for culture (Chapter 5).

1.2 THESIS OBJECTIVES

In summary, the primary objective of my thesis was to better understand the causes and consequences of fission-fusion dynamics. To do this, I investigated the socioecology of female northern long-eared bats, *Myotis septentrionalis*. Like many temperate bats studied to date, female northern long-eared bats show natal philopatry to summer areas where they live in groups with fission-fusion dynamics as females move among a network of roosts and roost-groups. Based on the rationale outlined above, I addressed the following objectives:

Chapter 2: Given that fission-fusion dynamics in bats are a result of frequent roost-switching, I examined why female bats switch roosts. I first determined if the characteristics of roosts used by females differed with ambient conditions. I then tested whether the changes in ambient conditions correlated with movement to different roosts and whether these changes also correlated with changes in roost characteristics.

Chapter 3: I investigated the social consequences of frequent roost-switching. I determined whether females formed preferred long-term social relationships despite frequent roost-switching. I also examined whether these relationships could be explained by demographic factors, such as a preference to associate with individuals based on age and reproductive condition. I also assessed the potential consequences of sociality by determining whether females formed long-term bonds, thereby providing the potential for cooperation to evolve despite the highly dynamic nature of fission-fusion groups

Chapter 4: I examined whether social relationships within fission-fusion groups could be explained by genetic relatedness among group members. I first determined whether groups were made up of closely related individuals at the maternal and bi-parental level. I then tested whether pairs of females that roosted together more often were also more closely related.

Chapter 5: I investigated possible consequences of bat sociality by assessing whether bats may exhibit culture. To do this, I reviewed the existing literature to summarize the criteria used to assess culture in other taxa. I then provided examples where bats may meet these criteria.

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CHAPTER 2
ROOST-SWITCHING BY FEMALE NORTHERN LONG-EARED BATS IS EXPLAINED BY CHANGES IN AMBIENT CONDITIONS

2.1 INTRODUCTION

While most vertebrates show fidelity at the landscape level, they may move frequently among sites at smaller spatio-temporal scales (reviewed in Mayor et al. 2009). For example, animals often return to the same winter and breeding areas between large-scale, seasonal migrations due to seasonal changes in habitat quality (Piper 2011). At smaller scales, however, animals may move frequently among sites within an area, potentially revisiting sites, in response to local changes in site quality across the season (Lewis 1995). Site fidelity may therefore vary across spatio-temporal scales in response to changes in site quality at different scales.

Site fidelity by bats in temperate zones varies across several spatio-temporal scales. For example, most bat species move seasonally between hibernacula, where they mate and hibernate, and summer foraging areas, where they roost during the day in rock crevices, tree cavities, or human-made structures. Females show strong philopatry to summer areas, and to particular roosts within these areas, where they form groups to give birth and raise offspring (Kunz and Lumsden 2003). Within a summer, however, females may switch among roosts almost daily. These daily switches are thought to help reduce ectoparasite loads and predation risk (Lewis 1995; Reckardt and Kerth 2006; Bartonička and Gaisler 2007; Patterson, Dick, and Dittmar 2007), minimize distances between roosts and ephemeral prey (Lewis 1995), and facilitate social connections and information sharing among a network of conspecifics (Willis and Brigham 2004; Kerth and Van Schaik 2011). However, the main benefit of switching roosts may be to select roosts that provide optimal thermal conditions for reproduction.

The potential for a roost to help bats maximize their reproductive success may depend on the interaction among a female's thermoregulatory strategies, the thermal properties of the roost, and local ambient conditions. Females use a combination of group warming and torpor to reduce thermoregulatory costs, which are particularly high because of their small size and high metabolisms (Geiser 2004; Willis and Brigham 2007). Torpor, however, reduces body temperature, potentially delaying foetal development and milk production, which may in turn reduce offspring growth and survival (Frick, Reynolds, and Kunz 2010; reviewed in Speakman 2008). While limiting torpor may improve offspring development, it can be particularly costly to females when ambient temperatures exceed thermoneutral zones. Females may therefore select roosts with optimal thermal conditions that allow them to restrict torpor use to periods of particularly unfavourable ambient conditions, and to limit the depth and extent of torpor (Lausen and Barclay 2003; Broders and Forbes 2004; Geiser 2004; Willis, Turbill, and Geiser 2005; Solick and Barclay 2006; Willis,Voss, and Brigham 2006; Bartonička and Řehák 2007; Willis and Brigham 2007; Speakman 2008; Pretzlaff, Kerth, and Dausmann 2010). For example, group warming may be easier in roosts that can accommodate larger groups, or in more exposed roosts that warm quickly in the sun. Torpor use, however, may be easier in more protected roosts that may be cooler than exposed roosts. The types of roosts females select may therefore differ with reproductive and ambient conditions in order to facilitate either group warming or torpor, thereby minimizing thermoregulatory costs while also maximizing offspring development (Callahan, Drobney, and Clawson 1997; Kerth, Weissmann, and König 2001; Chruszcz and Barclay 2002; Lausen and Barclay 2003; Bartonička and Řehák 2007; Pretzlaff, Kerth, and Dausmann 2010; Dietz and Hörig 2011); reviewed in Barclay and Kurta 2007). Females should therefore switch roosts when ambient conditions alter the suitability of particular roosts for thermoregulation.

To test whether females switch roosts in response to changes in ambient conditions, a few studies directly compared daily changes in ambient conditions with day-to-day movements among roosts. Switching to different roosts was not correlated, however, with changes in ambient temperature for pallid bats, *Antrozous pallidus* (Lewis 1996). Several

other species switched roosts when ambient, and presumably roost, temperatures changed, but only when they were exceedingly high (Vonhof and Barclay 1996; Lourenco and Palmeirim 2004; Ellison et al. 2007). Changes in ambient conditions therefore did not appear to have a strong influence on roost-switching. Most of these studies, however, focused on switching within or among buildings where thermal conditions are less affected by ambient conditions and movement is less frequent than in natural roosts (Lausen and Barclay 2003; Evelyn, Stiles, and Young 2004; Trousdale, Beckett, and Hammond 2008). Furthermore, these studies did not consider the reproductive condition of females, or focused solely on lactating females, and therefore may have overlooked possible differences in roost-switching patterns with reproductive condition. Changes in ambient conditions may therefore play a significant role in switching among natural roosts, but has not been adequately investigated.

The purpose of this study was to determine whether female northern long-eared bats (*Myotis septentrionalis*) switch roosts in response to changes in ambient conditions. Though not tested here, I assume that females use roosts that minimize thermoregulatory costs; costs vary with reproductive condition; costs vary with ambient conditions; thermal properties of roosts vary with structural characteristics of roost-trees and ambient conditions. I therefore expect females to switch roost-trees within summers in response to changes in ambient conditions, and that these patterns will vary with reproductive condition. To test this, I first determined whether the characteristics of the roosts used by females differed with ambient conditions and reproductive condition. I then tested whether changes in these ambient conditions correlated with roost-switching behaviour. As I was able to collect roost-use across multiple years, I also characterized inter-annual roost fidelity.

Female northern long-eared bats across their range appear to be flexible in their roost-use. Females are found in a wide range of tree species of varying stages of decay, and in a variety of roosts, including cavities, cracks, and under exfoliation bark, and also use human-made structures (Whitaker and Brack 2006; Barclay and Kurta 2007; Henderson and Broders 2008). However, females roost primarily in cavities found in trees located in

the forest interior with relatively high canopy cover (Barclay and Kurta 2007; Lacki and Schwierjohann 2001; Perry and Thill 2007; Timpone et al. 2007; Garroway and Broders 2008; Henderson and Broders 2008; Henderson, Farrow, and Broders 2008). Similar to other species, females show strong philopatry to particular roost areas, but roost-use varies with reproductive condition and females switch roosts almost daily (Garroway and Broders 2007; Patriquin et al. 2010).

2.2 METHODS

2.2.1 General Methods

I conducted my study in Dollar Lake Provincial Park (DLPP), Nova Scotia, Canada ($44^{o}55'$ N, $63^{o}19'$ W) from early June to mid-August, 2006 – 2007. I combined data collected during this time with those collected by Garroway and Broders (2008) in the same area between early June and mid-August 2005. The park borders a large (27 km^2) lake and is characterized as mixedwood old growth Acadian forest, which consists of uneven-aged stands. Stands are made up primarily of red maple (*Acer rubrum*), eastern hemlock (*Tsuga canadensis*), eastern white pine (*Pinus strobus*), and yellow birch (*Betula alleghaniensis*), as well as some older sugar maple (*Acer saccharum*), younger or regenerating black spruce (*Picea mariana*), red spruce (*Picea rubens*), maple and birch, and dead or dying trees (Loo and Ives 2003).

I captured bats using mist-nets (Avinet, Dryden, New York, USA) and harp traps (Austbat Research Equipment, Lower Plenty, Victoria, Australia). Upon capture, I identified reproductively active females as pregnant, lactating, or post-lactating by palpation of the abdomen, expression of milk from the nipples, or worn fur around the nipples with no expression of milk, respectively (Racey 1988). While I was able to assess individual reproductive condition at the time of capture, I could not confirm an individual's condition throughout the summer. Based on the assumption that the timing of breeding events is relatively synchronous in temperate bats (Racey 1988), I assessed whether roost-use differed with reproductive condition by dividing the summer into reproductive periods. The gestation period was defined from 1 June until the first capture

of a lactating female, which then defined the beginning of the lactation period. The post-lactation period was defined from the first capture of a volant juvenile, or of a post-lactating female, until the end of August. I identified juveniles based on incomplete calcification of the epiphyseal gap on the fourth metacarpal (Anthony 1988).

To locate roost-trees, radio-transmitters (0.39g, model LB-2NT, Holohil Systems Limited, Carp, Ontario, Canada) were attached to 63 captured, reproductively active, females. By removing fur from between the scapula, transmitters were attached with surgical adhesive (SkinBond, Smith and Nephew United Inc., Largo, FL, USA). Females were tracked with a radio receiver (R-1000, Communication Specialists Inc., CA, USA) and a three-element yagi antenna (AF Antronics Inc., Urbana, IL, USA) to locate the trees occupied by bats each day. Bats were tracked daily until the transmitter fell off or the battery died ($\bar{X}$ = 6.7 days; range 1–24 days).

To minimize disturbance to bats, roost-tree and site characteristics were measured for 121 roosts at the end of the summer or when bats had moved to a different tree. Characteristics commonly used as indicators of the thermal properties of roosts were measured as they may affect either direct exposure to sun, wind or rain, or the potential buffering properties against extreme temperatures (Barclay and Kurta 2005). These characteristics included: (1) roost-tree height, (2) roost height, (3) average dominant canopy height, (4) canopy height relative to roost height, (5) average canopy cover, (6) tree species, (7) diameter at breast height (dbh), (8) percent of bark remaining on the tree, and (9) decay stage. Heights were collected using a clinometer (model PM-5/1520, Suunto, Finland) and average dominant canopy height was the average height of five trees representative of the dominant canopy within a 0.1-ha plot centred on the roost-tree. Canopy height relative to roost height was the difference between the average canopy height and the roost entrance; a negative value then suggests the roost was above the canopy and vice versa. Average canopy cover was the average canopy closure in four cardinal directions collected using a spherical densitometer (model-A, Forest Densiometers, Bartlesville, Oklahoma, USA) from the base of the roost-tree. Canopy cover did not vary considerably during the course of my study as foliage had mostly

developed by early June and remained intact well into September. Decay stage was the overall condition of a tree, with the lowest class, 1, representing live, healthy trees, and the highest class, 9, representing decaying debris (see Vonhof and Barclay 1988 for detailed description). Several of these roost characteristics may be highly correlated (e.g., various height measurements), and therefore subsequent models based on these variables may be biased due to multicollinearity (Alpert and Peterson 1972). I therefore performed a principal component analysis (PCA) to remove highly correlated variables (SPSS version 20.0, IBM Corp.).

A PCA produces components which represent the best linear combination of roost characteristics that explain the most variance in the types of roosts used by females. Each component represents an orthogonal combination of roost characteristics that accounts for a different proportion of the variance (Quinn and Keough 2002). Each component therefore explains a different set of roost characteristics that then explain roost selection by females. I examined components with eigenvalues greater than one and that accounted for the greatest proportion of the variance (Quinn and Keough 2002, SAS 2009) to then identify the variables that best described each component (loadings > 0.5 or < -0.5) and used these variables in subsequent tests. By choosing different variables that described different components, I was able to minimize the risk of multicollinearity among variables while still capturing characteristics that are important to roost-use by females. I chose to use the original variables rather than using component scores as new variables in subsequent analyses to simplify the interpretability of subsequent tests (SAS 2009).

Three of the five components had eigenvalues greater than one and cumulatively these explained 74% of the variance (Table 2.1). Variables with high loadings on the first component included roost-tree height, decay stage, percent of bark on the tree, dominant canopy height, and dbh, suggesting these variables best describe the roosts used by females (Table 2.2). Dominant canopy height and canopy height relative to roost height best explained the second component while average canopy cover best explained the third component (Table 2.2), suggesting these variables were also important roost

Table 2.1 Total variance explained by principal components of roost characteristics for subsequent analyses of roost-use by female northern long-eared bats (*Myotis septentrionalis)* in Dollar Lake Provincial Park, NS, Canada, from 2005-2007.

	Initial Eigenvalues		
Principal Component	Total	% of Variance	Cumulative %
1	3.23	40.41	40.41
2	1.40	17.46	57.87
3	1.27	15.87	73.75
4	0.75	9.36	83.11
5	0.69	8.63	91.74
6	0.36	4.47	96.21
7	0.19	2.33	98.53
8	0.12	1.47	100.00

Components with eigenvalue greater than 1.0 were examined further.

Table 2.2 Principal component loadings and coefficients for the components used to identify roost characteristics for subsequent analyses of roost-use by female northern long-eared bats (*Myotis septentrionalis*) in Dollar Lake Provincial Park, NS, Canada, from 2005-2007.

	Loadings			Coefficients		
Principal Component	1	2	3	1	2	3
roost tree height (m)	**0.86**	-0.22	0.22	0.26	-0.16	0.17
decay stage	**-0.84**	0.31	0.06	-0.26	0.22	0.05
percent bark (%)[a]	0.75	-0.29	-0.31	0.23	-0.21	-0.25
cavity height (m)[b]	-0.28	-0.01	0.74	-0.09	-0.01	0.58
average dominant canopy height (m)[b]	0.77	0.56	0.03	0.24	0.40	0.02
tree diameter at breast height (cm)	**0.60**	-0.03	0.07	0.19	-0.02	0.06
average canopy cover (%)	0.35	-0.01	**0.75**	0.11	-0.01	0.59
canopy height relative to roost (m)[c]	0.27	**0.93**	-0.07	0.08	0.66	-0.05

Component variables with loadings greater than 0.5 were used in subsequent analyses.

[a] excluded from subsequent analyses as it was used to assess decay stage, which is more biologically relevant as it captures more information about tree condition

[b] excluded from subsequent analyses as it was used to derive canopy relative to roost height, which is more biologically relevant as it captures the potential for exposure of cavity to sun or inclement weather

[c] positive values suggest the roost is below the canopy and vice versa for negative values

characteristics. To further reduce the number of variables to ensure sufficient power in subsequent tests (Alpert and Peterson 1972), I excluded percent bark since it is one of the metrics used to assess decay stage, which is more biologically relevant as it better captures roost-tree condition. Similarly, canopy height was excluded as it is used to obtain canopy height relative to roost height, which is more biologically relevant as it more likely reflects exposure of the roost cavity to direct sun or inclement weather. A total of five roost characteristics were therefore included in subsequent analyses: roost-tree height, decay stage, dbh, average canopy cover, and canopy height relative to roost height.

I obtained measures of ambient conditions throughout each summer from an Environment Canada weather station at the Halifax Stanfield International Airport (44°52′ N, 063°30 W), located approximately 20 km from DLPP. Values from the station therefore likely reflect ambient conditions in DLPP. I obtained the following measures of daily ambient conditions, as well as conditions at sunset and sunrise: (1) daily maximum temperature, (2) daily mean temperature, (3) daily minimum temperature, (4) total daily rainfall, (5) temperature at sunset, (6) precipitation at sunset, (7) wind speed at sunset, (8) barometric pressure at sunset, and the same measures at sunrise (9-12). Precipitation at sunset and sunrise represent the presence or absence of precipitation as total precipitation was not available at these times. The daily ambient conditions listed here have been identified in other studies as potential influences on either roost-use, thermal properties of roosts, or bat thermoregulation (Callahan et al. 1993, Lourenco and Palmeirim 2004). Conditions at sunset (emergence) may influence the thermal conditions experienced by non-volant juveniles remaining in roosts at night, and they may restrict bat movement by affecting maneuverability and thermoregulation (Chruszcz and Barclay 2002; Voigt et al. 2011). Though not verified, conditions at sunrise may predict daytime ambient conditions. Changes in barometric pressure may indicate weather change and may affect animal movement, including bat movement (Danhardt and Lindstrom 2001, Baerwald and Barclay 2011).

Based on the same rationale and following the same procedure outlined for roost characteristics, I used a PCA to reduce the number of variables for ambient conditions to be used in subsequent tests (SPSS). Four of the 12 components had eigenvalues greater than one and cumulatively explained 73% of the variance (Table 2.3). Variables with high loadings (> 0.5, or < -0.5) on the first component included maximum, minimum, and mean daily temperature, as well as temperature at sunrise and sunset, suggesting these best explained ambient conditions throughout the summer (Table 2.4). Wind speed and barometric pressure at both sunrise and sunset best explained the second component. Total daily rainfall, and barometric pressure at both sunrise and sunset best explained the third component. Total rainfall, and wind speed at both sunrise and sunset best explained the fourth component (Table 2.4). Because several of these variables described the same component and had similar relationships (e.g., all the variables for temperature described the first component), only: (1) maximum daily temperature, (2) total daily rainfall, (3) temperature at sunset, (4) wind speed at sunset, and (5) barometric pressure at sunset were included in further tests. Maximum temperature and temperature at sunset (which also reflects minimum temperature as indicated by their high loadings on the same principal component) were used to represent ambient temperatures that may be above or below the thermoneutral zone, thereby having the greatest impact on thermoregulation and therefore roost-selection. Ambient conditions at sunset were selected over those at sunrise as previous studies suggest that, during the gestation period, females do not regularly return to roosts throughout the night after they emerge to forage. By contrast, during the lactation period, females regularly return throughout the night, presumably to nurse young (Lučan and Radil 2010). The decision to switch roosts may then be based on information about roost suitability and ambient conditions at night.

2.2.2 Variation in Roost-use with Year, Reproductive Period, and Ambient Conditions

To determine whether characteristics of the roosts used by females varied with ambient conditions, I performed a canonical correlation analysis (SPSS version 20.0). Roost-use is likely explained by relationships among multiple variables, which may not be adequately

reflected in univariate analyses. I therefore used canonical correlation analysis to explore multivariate relationships by comparing the explanatory set of ambient conditions to the response set of roost characteristics to determine if the two sets covary. This is achieved by creating different dimensions that represent orthogonal combinations of variables with the highest covariance (Quinn and Keough 2002). A high covariance between dimensions therefore suggests a strong relationship between the set of ambient conditions and roost characteristics.

Table 2.3 Total variance explained by principal components used to identify components to reduce the number of variables for ambient condition for subsequent analyses of roost-use by female northern long-eared bats (*Myotis septentrionalis)* in Dollar Lake Provincial Park, NS, Canada, from 2005-2007.

	Initial Eigenvalues		
Principal Component	Total	% of Variance	Cumulative %
1	4.028	33.566	33.566
2	2.413	20.109	53.675
3	1.552	12.936	66.610
4	1.147	9.558	76.169
5	.880	7.337	83.506
6	.738	6.147	89.653
7	.511	4.262	93.915
8	.377	3.138	97.053
9	.227	1.890	98.943
10	.068	.563	99.506
11	.059	.494	100.000
12	3.536E-05	.000	100.000

Table 2.4 Principal component loadings and coefficients for the components used to identify ambient conditions for subsequent analyses of roost-use by female northern long-eared bats (*Myotis septentrionalis*) in Dollar Lake Provincial Park, NS, Canada, from 2005-2007.

	Loadings				Coefficients			
Principal Component	1	2	3	4	1	2	3	4
max temperature (°C)	**.821**	-.252	-.271	.189	.204	-.104	-.174	.165
min temperature (°C)	**.908**	.230	.170	-.045	.225	.095	.110	-.039
mean temperature (°C)	**.965**	-.048	-.089	.098	.239	-.020	-.057	.086
daily rain (mm)	-.072	.308	**.597**	**-.491**	-.018	.128	.384	-.428
sunrise temperature (°C)	**.880**	.339	.127	-.099	.218	.140	.082	-.087
sunset wind speed (km/h)	.001	**.555**	.361	**.482**	.000	.230	.233	.420
sunset barometric pressure (kpa)	.106	**-.804**	**.520**	.123	.026	-.333	.335	.107
sunset precipitation (y/n)*	-.062	.436	.384	-.399	-.015	.181	.247	-.348
sunset temperature (°C)	**.852**	.090	-.030	-.205	.212	.037	-.020	-.179
sunset wind speed (km/h)	-.017	**.537**	.311	**.604**	-.004	.223	.201	.527
sunset barometric pressure (kpa)	.133	**-.701**	**.651**	.142	.033	-.291	.419	.124
sunset precipitation (y/n)*	-.244	.390	.010	.120	-.061	.162	.007	.105

* while total daily rainfall accumulation was available, only information about presence/absence of precipitation at sunrise and sunset was available

Only significant canonical dimensions ($p < 0.05$) that explained the greatest amount of variation (25% or more) in roost-use and with high canonical correlations (25% or more) were examined further (Hair et al. 2010). To better understand the relationships between specific ambient conditions and roost characteristics, the variables that best describe each dimension must be identified. Variables with large positive (0.3 or greater) or negative (-0.3 or less) standardized coefficients were considered to best explain each of the significant dimensions (Alpert and Peterson 1972). Therefore, variables with high loadings on the first dimension for ambient conditions best explained those variables with high loadings on the first dimension for roost characteristics, and the same held true across each dimension. Year and reproductive period (as defined above) were also included in the explanatory set to account for possible differences in roost-switching among years and among reproductive periods. Because each variable was measured on a different scale, I used only the standardized coefficients to allow a more direct comparison of the relationships among variables.

To determine whether ambient conditions and the characteristics of the roosts used by females differed among years and reproductive periods, I also performed a series of one-way analysis of variance (ANOVA) analyses and Games-Howell post-hoc multiple comparisons, which account for unequal variance. I performed the following ANOVAS: roost characteristics with year as a factor, roost characteristics with reproductive period as a factor, ambient conditions with year as a factor, and ambient conditions with reproductive period as a factor.

2.2.3 Roost fidelity and switching

I assessed inter- and intra-annual roost fidelity by assessing the degree to which particular roosts were reused each summer, and I assessed the degree to which females switched among roosts for each year and each reproductive period. I obtained a general estimate of inter-annual re-use of particular roosts by calculating the proportion of roosts reused in subsequent years, but not necessarily by the same bat. I then estimated the propensity of each bat to switch roosts within years. For each bat that I observed on two or more

consecutive days, I estimated roost-switching, using a roost fidelity index developed by Chaverri and Kunz (2006):

$$RF = [2(STAY) + 1(RETURN) - 1(MOVE)] / (STAY + RETURN + MOVE),$$

where STAY is the number of days a female remained in the same roost, MOVE is the number of days a female moved to a different roost, and RETURN is the number days a female moved from one roost to return to a roost used previously that year and therefore illustrates fidelity to a particular roost-tree. Therefore, a value of -1 suggests complete roost infidelity, or a high degree of roost-switching, while a value of 2 suggests complete roost fidelity, or a low degree of roost-switching. I calculated an average RF across all females, as well as an average RF for each year and each reproductive period.

I determined whether roost-switching events could be explained by changes in ambient conditions, and whether the degree of roost-switching differed among years and reproductive periods. To do this, I used a backward stepwise logistic regression to examine roost-switching for individuals observed on two or more consecutive days (SPSS). For each day an individual was observed, the response variable was whether the individual had moved to a different roost or remained in the same roost. The predictor variables for movement in the initial model included the changes in ambient conditions, defined as the difference between the variables on the day an individual was located and the previous day. Changes in roost characteristics, defined as the difference between the characteristics of a roost used on the day an individual was located and the roost it had used on the previous day, were also included as predictor variables. Changes in roost characteristics were included based on the assumption that bats would move only if roost characteristics on days prior to moving were no longer suitable when ambient conditions changed. Interaction terms between the ambient conditions and roost characteristics were also included in the initial model. To test for potential differences in roost-switching with year and reproductive period, they were included as categorical variables in the initial model. Because each of the variables was measured on a different scale, they were standardized using z-score transformations (SAS manual). To determine which variables

or interactions best explain roost-switching behaviour, a backward stepwise procedure was used where, at each step, a variable or interaction term that did not significantly explain roost-switching ($p \geq 0.05$) was removed from the model and a new estimate of the fit of the model was obtained. This stepwise process was repeated until the removal of additional variables did not significantly improve the fit, which was assessed as the model with the lowest Akaike's Information Criterion (AIC). A Hosmer and Lemeshow Test was performed to assess the goodness-of-fit of the final model.

2.3 RESULTS

2.3.1 General description of roost characteristics and ambient conditions

Over 3 years, a total of 63 adult females were radio-tracked ($\bar{X}$ = 6.7 days; range 1–24 days) to 121 different roost-trees that were used for a total of 370 bat-roost-days. A bat-roost-day represents the observed presence of a bat in a roost on a particular day. Based on the Chaverri and Kunz (2006) roost fidelity index (RF), females showed very low average roost fidelity ($\bar{X}$ ± SD (standard deviation) = 0.33 ± 1.02), suggesting they switched roosts frequently.

Tests of dimensionality for the canonical correlation analysis suggest that three of the five canonical dimensions were statistically significant (Table 2.5). However, the third dimension explained very little of the variance for the relationship between roost characteristics and ambient conditions and is therefore not considered an important dimension. The two remaining dimensions had high canonical correlations (0.53 and 0.49) between the roost characteristics and ambient conditions, suggesting the two sets were highly correlated. The first canonical dimension for the roost variables was most strongly positively influenced by tree height, dbh, and canopy relative to roost, and negatively influenced by decay stage. The first canonical dimension for the ambient conditions, plus year and reproductive period, was most strongly positively influenced by total daily rainfall and negatively influenced by year, reproductive period, and maximum daily temperature (Table 2.6). Therefore, large diameter trees that were tall and healthy with cavities below the canopy were used more often during cooler and wetter days.

The second canonical dimension for roost characteristics was most strongly positively influenced by dbh and negatively influenced by canopy relative to roost. The second dimension for the ambient conditions was strongly positively influenced by reproductive period, maximum daily temperature, and temperature at sunset, and negatively influenced by year, total daily rainfall, and wind speed at sunset (Table 2.6). Therefore, large diameter trees with cavities near or above the canopy were used more often on warm, dry, and calm days. Also, the relationships between roost characteristics and ambient conditions differed with year and reproductive period, as further discussed below.

2.3.2 Inter-annual roost-use, roost fidelity and ambient conditions

The characteristics of the roosts used by females and ambient conditions differed significantly among years (see Figures 2.1 and 2.2 and Table 2.7 for values and summary of statistics). On average, roost-trees used by bats in 2005 were significantly taller, healthier, with a larger dbh in areas with slightly lower canopy cover, and cavities tended to be below the canopy, compared to roosts used in 2006 and 2007, for which characteristics did not differ significantly between years (see Figure 2.1 for values and Table 2.7 summary of statistics). Ambient conditions also differed significantly among years, as 2005 was significantly dryer, and less windy than 2006 and 2007, and was also warmer than 2007, whereas it was warmer and more windy during 2006 than 2007 (see Figure 2.2 for values and Table 2.7 for summary of statistics). The strong negative influence of year on the canonical dimensions supports the observation that roost characteristics and ambient conditions differed among years (Table 2.6).

The degree of fidelity to particular roosts, and average roost-switching behaviour by bats, differed among years. Twenty-six percent of the 50 roosts located in 2006 were previously used in 2005, while 31 % of the 36 roosts used in 2007 were previously used in 2005 and 2006 (14% were used in 2005 and 17% were used in 2006). Roost-switching behaviour varied, as RF values ($\bar{X} \pm SD$) ranged from 0.33 (0.78), 0.14 (1.06), and 0.63 (1.13) in 2005, 2006, and 2007, respectively. Year, however, was not a significant term in the final logistic regression model (Table 2.8), suggesting the degree of roost-switching did not differ among years.

Table 2.5 Tests of canonical dimensions used to explain the relationship between ambient conditions and the characteristics of roosts used by female northern long-eared bats (*Myotis septentrionalis*) in Dollar Lake Provincial Park, NS, Canada, from 2005-2007.

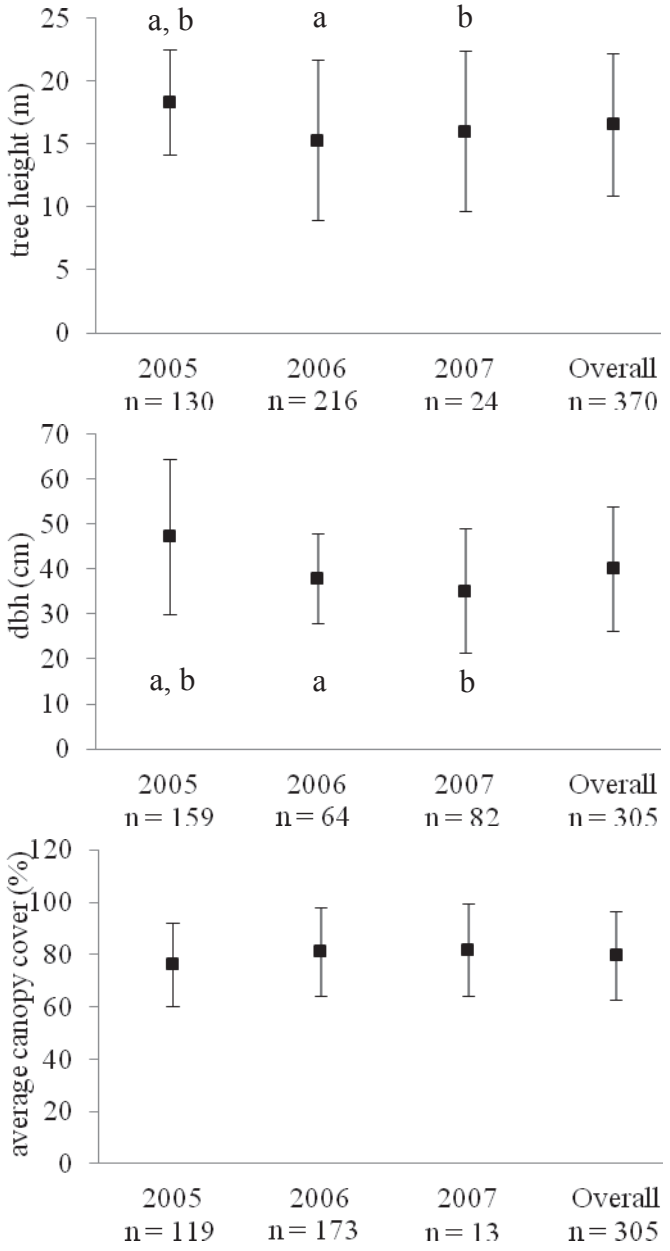
Dimension	% of variance	Canonical correlation	Multivariate F	df1	df2	p
1	48.24	0.53	6.00	35	1138.22	**0.00**
2	38.07	0.49	4.54	24	946.62	**0.00**
3	6.59	0.23	2.03	15	751.27	**0.01**
4	4.34	0.18	1.99	8	546.00	0.05
5	2.76	0.15	2.06	3	274.00	0.11

Dimensions with $p < 0.05$ and that explained > 25% of variance were examined further.

Table 2.6 Canonical variable loadings and standardized coefficients for significant dimensions used to explain the relationship between ambient conditions and the characteristics of roosts used by female northern long-eared bats (*Myotis septentrionalis*) in Dollar Lake Provincial Park, NS, Canada, from 2005-2007.

	Loadings		Coefficients	
Roost Variables	1	2	1	2
tree height (m)	**0.85**	-0.11	0.75	-0.14
decay class	**-0.86**	-0.10	-0.32	-0.06
dbh (cm)	**0.28**	**0.73**	0.06	0.83
average canopy cover (%)	-0.07	-0.19	-0.45	-0.18
canopy relative to roost (m)	**0.29**	**-0.56**	0.14	-0.60
Seasonal and Ambient Condition Variables				
year	**-0.38**	**-0.87**	-0.53	-0.77
reproductive period	**-0.82**	**0.34**	-0.79	0.13
maximum temperature (^{o}C)	**-0.37**	**0.35**	-0.26	0.05
daily rain (mm)	**0.26**	**-0.48**	0.13	-0.26
temperature at sunset (^{o}C)	-0.20	**0.37**	0.00	0.21
wind speed at sunset (km/h)	0.24	**-0.35**	0.07	-0.24
precipitation at sunset (y/n)	0.00	-0.21	0.06	0.08

Canonical variables with loadings greater than, or equal to, 0.3 (rounded up) had the greatest influence on each dimension



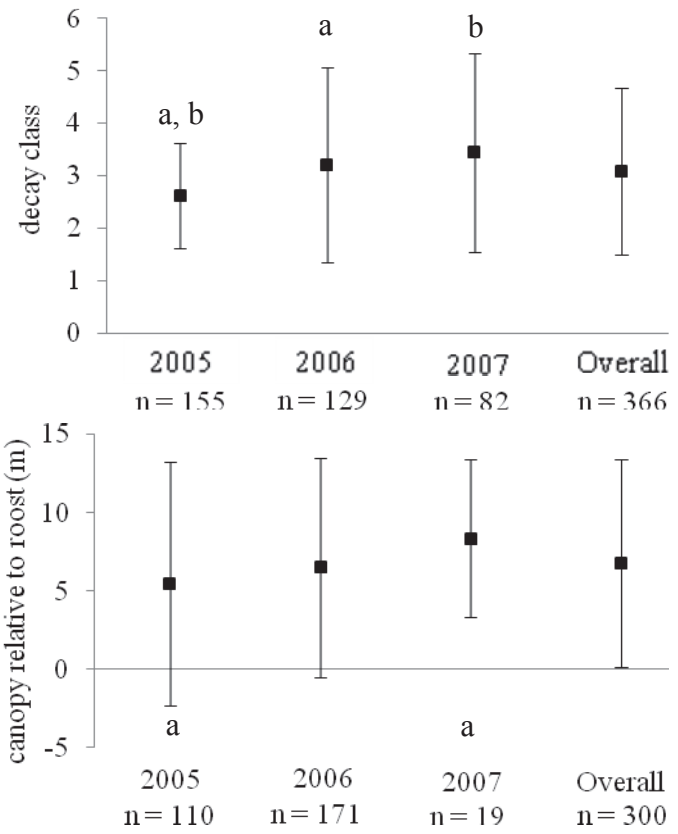


Figure 2.1. Mean (standard deviation) roost tree and site characteristics used to describe roost use by female northern long-eared bats (*Myotis septentrionalis*) during different years in Dollar Lake Provincial Park, NS, from 2005-2007. [a, b] Indicates significant differences ($p < 0.05$) between years based on Games-Howell post-hoc comparisons.

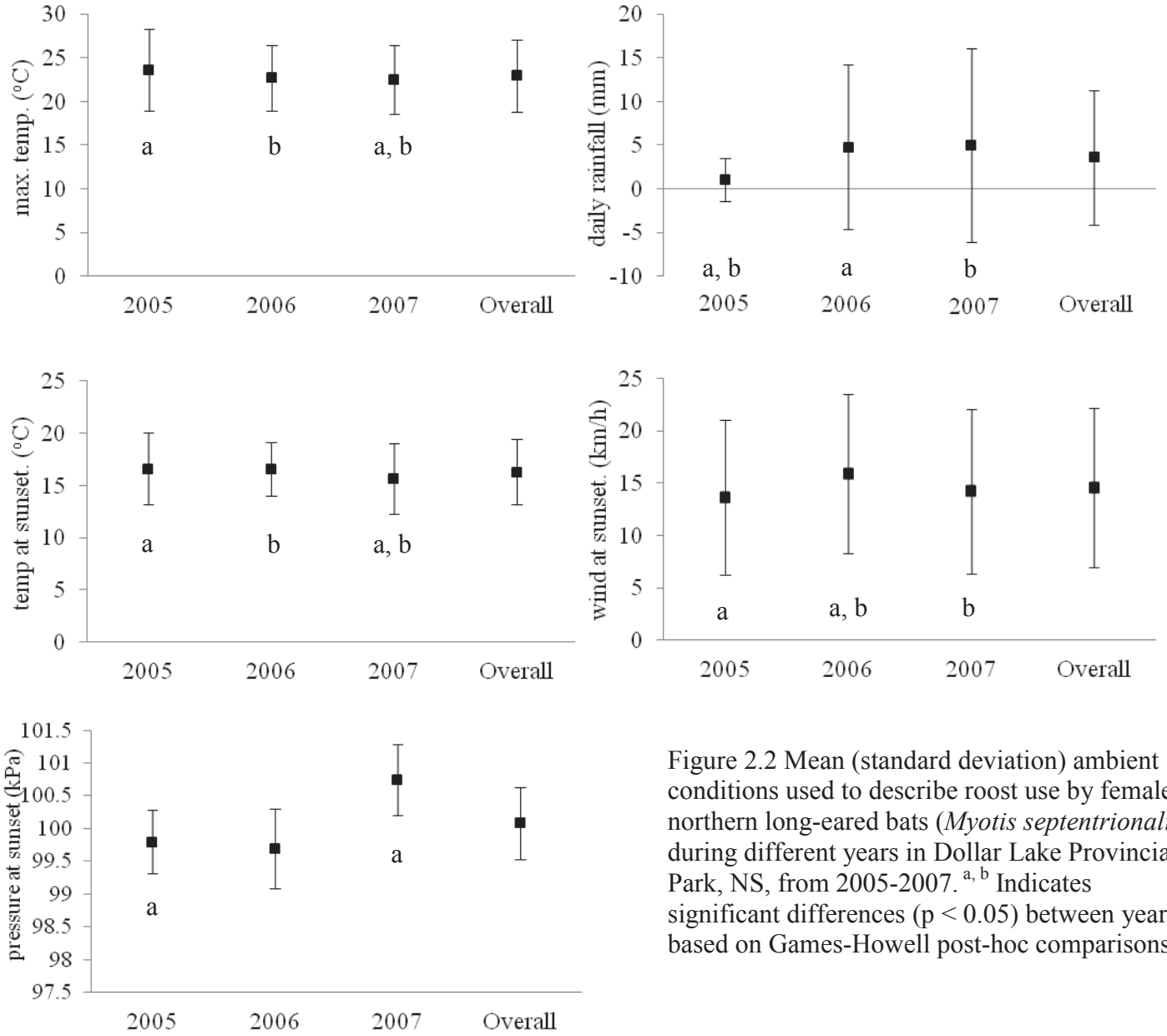


Figure 2.2 Mean (standard deviation) ambient conditions used to describe roost use by female northern long-eared bats (*Myotis septentrionalis*) during different years in Dollar Lake Provincial Park, NS, from 2005-2007. [a, b] Indicates significant differences ($p < 0.05$) between years based on Games-Howell post-hoc comparisons.

Table 2.7 ANOVA results for tests of differences between years in average roost characteristics and ambient conditions in Dollar Lake Provincial Park, NS, Canada, 2005-2007.

Ambient Condition	df	F	p
maximum temperature	2	9.45	< 0.001
total rain	2	14.69	< 0.001
temperature at sunset	2	11.39	<0.001
wind at sunset	2	10.1	<0.001
barometric pressure at sunset	2	3.74	0.025
Roost Characteristic			
tree height	2	11.54	< 0.001
decay stage	2	9.23	< 0.001
dbh	2	3.62	0.028
average canopy cover	2	4.16	0.016
canopy relative to roost	2	25.11	< 0.001

2.3.3 Intra-annual roost-use, roost-switching and ambient conditions

2.3.3.1Reproductive period

The characteristics of the roosts used by females in each reproductive period differed significantly, as did ambient conditions (see Figures 2.3 and 2.4, and Table 2.9 for values and summary of statistics). Females tended to use hemlock (48%) more often than red maple (31%) during the gestation period, while the opposite was true during the lactation period when red maple (62%) were used more often than hemlock (29%). Meanwhile, red maple were used almost exclusively (75%) during the post-lactation period. Females used significantly taller trees in lower decay stages during the gestation period compared to the lactation and post-lactation periods. They also used trees that were smaller in diameter with roosts that were below the canopy significantly more during the gestation period than the lactation period. Females also used significantly taller trees in lower decay stage with larger diameter during the lactation period compared to the post-lactation period. Average canopy cover of the roosts used by females did not differ significantly among any of the reproductive periods (see Figure 2.3 for values and Table 2.9 for summary of statistics). These observations were partially supported by the strong

negative relationship of reproductive period with the first canonical dimension, which suggests that tall, large diameter, healthy trees with roosts below the canopy were more important during early reproductive periods. The strong positive relationship of reproductive period with the second canonical dimension suggests large diameter trees with roosts above the canopy were more important during later reproductive periods (Table 2.6). The gestation period was significantly cooler, with more rain and higher winds than during the lactation period, while the lactation period was significantly warmer than both the gestation and post-lactation periods (see Figure 2.4 for values and Table 2.9 summary of statistics).

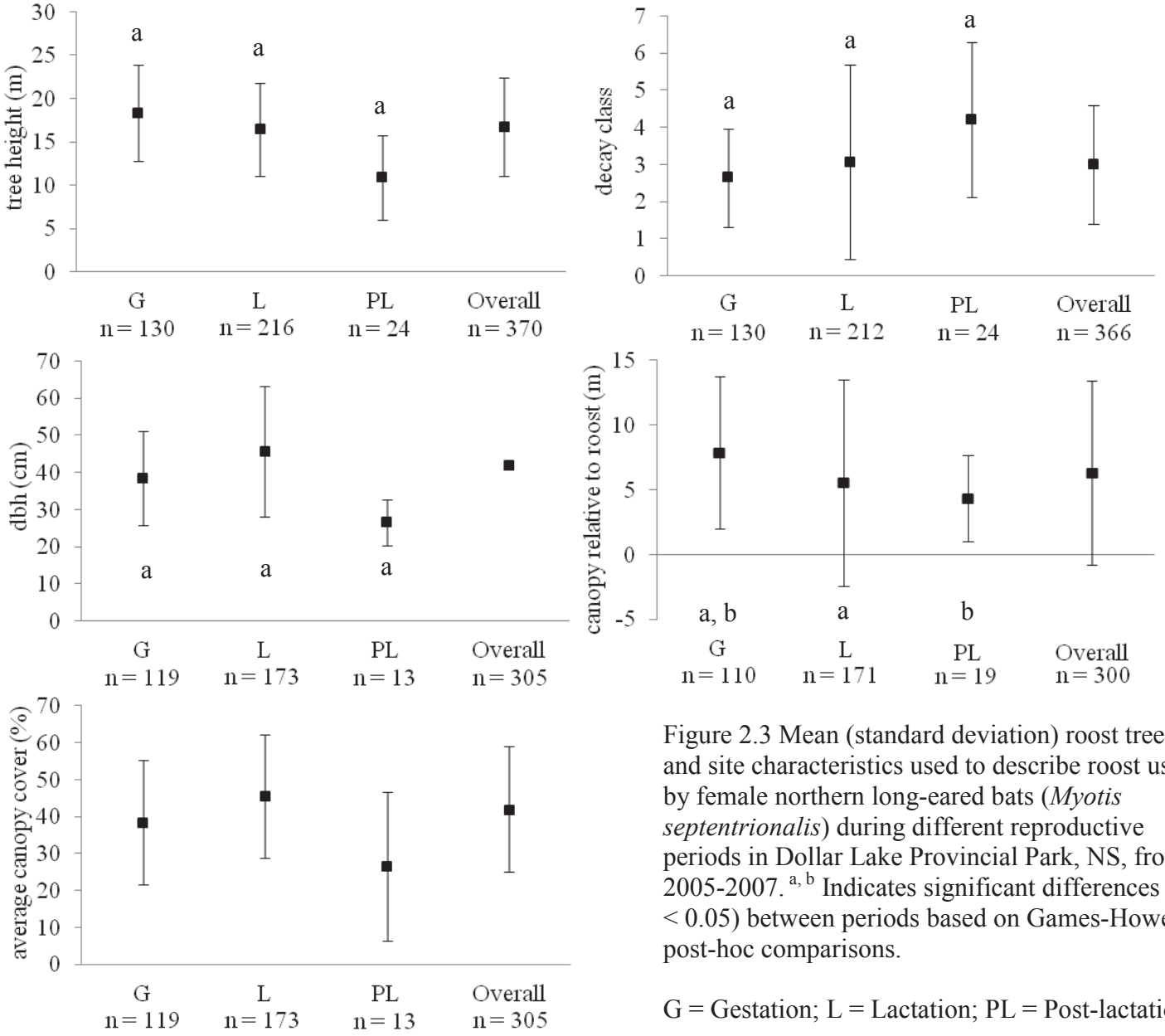


Figure 2.3 Mean (standard deviation) roost tree and site characteristics used to describe roost use by female northern long-eared bats (*Myotis septentrionalis*) during different reproductive periods in Dollar Lake Provincial Park, NS, from 2005-2007. [a, b] Indicates significant differences ($p < 0.05$) between periods based on Games-Howell post-hoc comparisons.

G = Gestation; L = Lactation; PL = Post-lactation

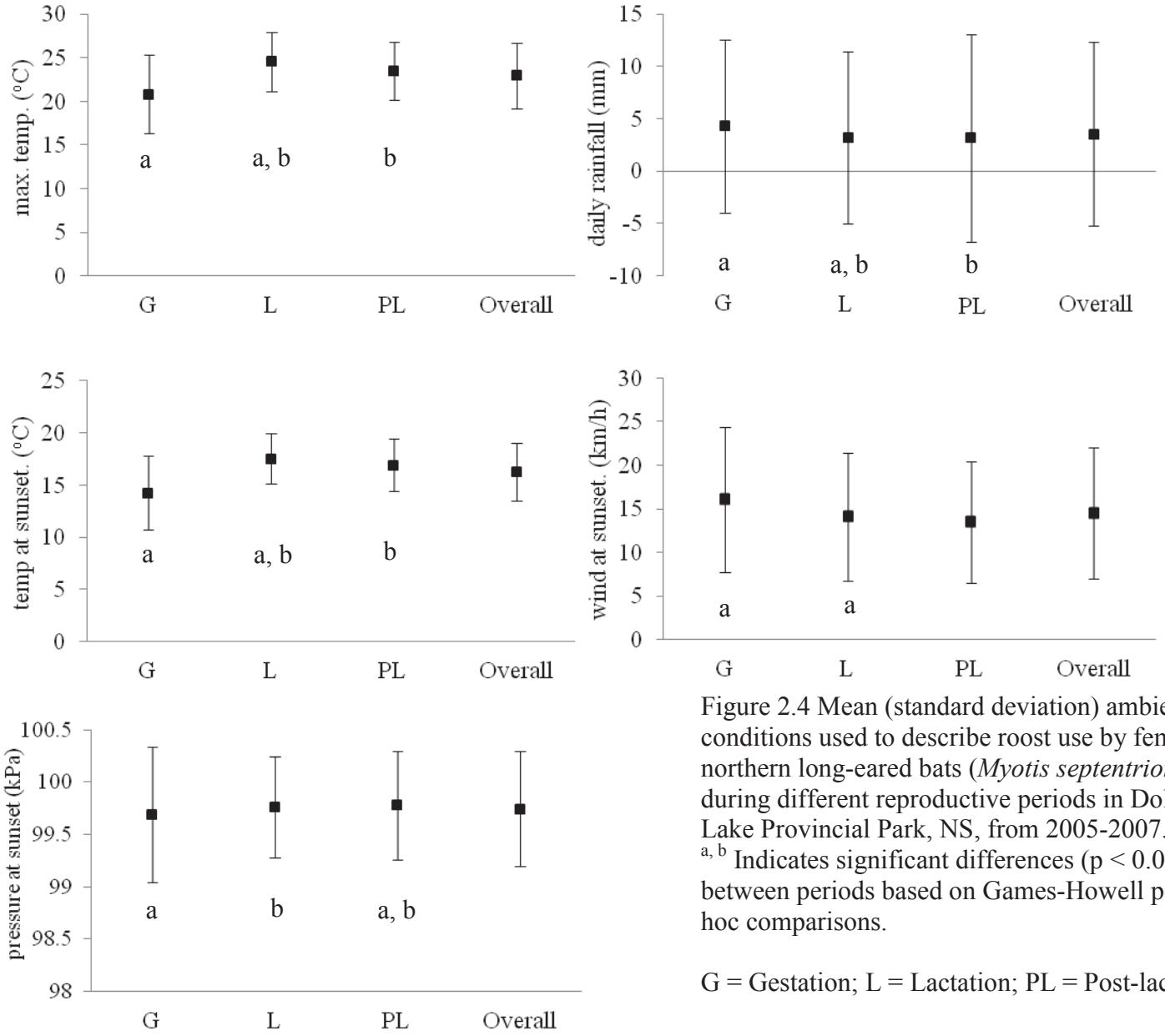


Figure 2.4 Mean (standard deviation) ambient conditions used to describe roost use by female northern long-eared bats (*Myotis septentrionalis*) during different reproductive periods in Dollar Lake Provincial Park, NS, from 2005-2007. [a, b] Indicates significant differences ($p < 0.05$) between periods based on Games-Howell post-hoc comparisons.

G = Gestation; L = Lactation; PL = Post-lactation

Table 2.8 Z-transformed variables included in the final logistic regression model used to explain roost-switching behaviour by female northern long-eared bats (*Myotis septentrionalis*) in Dollar Lake Provincial Park, NS, from 2005-2007.

Variables in the equation*	B	S.E.	Wald	df	Sig.	Exp(B)
Repro			9.965	2	**.007**	
Repro(1)	-.045	.715	.004	1	.950	.956
Repro(2)	-1.079	.680	2.515	1	.113	.340
average canopy cover	.030	.011	7.022	1	**.008**	1.030
total rain	.089	.025	12.582	1	**.000**	1.093
maximum temperature * tree height	-.084	.020	17.867	1	**.000**	.919
maximum temperature * decay stage	-.106	.051	4.375	1	**.036**	.900
total rain *decay stage	.030	.015	3.999	1	**.046**	1.030
wind speed at sunset * decay stage	-.021	.010	4.126	1	**.042**	.979
temperature at sunset * canopy relative to roost	-.013	.008	2.723	1	.099	.987
wind speed at sunset * canopy relative to roost	.008	.003	6.112	1	**.013**	1.008
wind speed at sunset * dbh	.071	.030	5.468	1	**.019**	1.074
Constant	.489	.648	.570	1	.450	1.631

* variables represent the difference in values for roost characteristics and ambient conditions on the day a bat was observed compared to the day prior to observation

Table 2.9 ANOVA results for tests of differences between reproductive periods in average roost characteristics and ambient conditions in Dollar Lake Provincial Park, NS, Canada, 2005-2007.

Ambient Condition	df	F	p
maximum temperature	2	9.45	< 0.001
total rain	2	14.69	< 0.001
temperature at sunset	2	11.39	<0.001
wind at sunset	2	10.1	<0.001
barometric pressure at sunset	2	3.74	0.025
Roost Characteristic			
tree height	2	11.54	< 0.001
decay stage	2	9.23	< 0.001
dbh	2	3.62	0.028
average canopy cover	2	4.16	0.016
canopy relative to roost	2	25.11	< 0.001

The degree to which females switched roosts in each reproductive period also differed, as RF values ($\bar{X}$ ± SD) ranged from 0.34 (1.00), 0.39 (1.05), and -0.25 (1.06) from gestation, lactation, and post-lactation, respectively. This observation was supported by the significant term for reproductive period in the logistic regression (Table 2.8). An investigation of the number of times bats switched roosts compared to when they did not switch roosts in each reproductive period illustrated that bats were least likely to move during the lactation period compared to the gestation or post-lactation period (not shown).

2.3.3.2 Daily roost-switching

By tracking 63 different females, I obtained almost 50 consecutive census days of daily movement and roost-use data each summer, with occasional gaps in recorded movement. During this time, I captured 159 occasions when females switched roosts and 122 occasions when females did not switch roosts, for a total of 281 observations. Females switched roosts almost daily, as evidenced by the low average RF index ($\bar{X}$ ± SD = 0.33 ± 1.02). While some females showed complete fidelity to roosts (RF = 2), many showed complete infidelity (RF = -1). On 12% of the occasions where females moved, they

returned to roosts they had used previously that summer. The final model with the lowest AIC score had an R^2 value of 0.35. The Hosmer and Lemeshow test, which tests the null that there is no difference between the observed and predicted patterns, suggests this model had a low goodness-of-fit (chi-square = 51.73, df = 8, $p < 0.001$), suggesting other variables may better explain roost-switching behaviour. Nevertheless, based on the significant terms in the model it appears switching was influenced by rain, maximum temperature, and wind speed and barometric pressure at sunset, but the likelihood of switching depended on the roost characteristics on the day prior to moving (Table 2.8).

A number of patterns were revealed by investigating plots (Figure 2.5) for roost-switching with respect to each of the significant interaction terms. Females were more likely to switch roosts when maximum temperature decreased to move to taller trees, and to move from trees in higher decay to lower decay, whereas they did not appear to move when maximum temperature increased. They were also more likely to move when wind speeds at emergence decreased to move from trees from high decay to lower decay and to move from below the canopy to above the canopy, whereas they did not appear to move when wind speeds increased. In addition, females were more likely to move when pressure at emergence decreased to move from trees with a small dbh to trees with a larger dbh, whereas they were unlikely to move if pressure increased. Finally, females were more likely to move when rain decreased than when it increased; however, the relationship with decay stage indicated by the interaction term is difficult to interpret.

2.4 DISCUSSION

As expected, roost use by female northern long-eared bats varied with ambient conditions, and roost fidelity varied with spatio-temporal scales. An earlier study illustrated that females showed strong inter-annual fidelity to roost areas (Patriquin et al. 2010). Here I demonstrated that within these areas, females also exhibited a moderate degree of inter-annual fidelity to particular roosts, yet they showed very low intra-annual fidelity as they switched frequently among roosts throughout the summer. This high degree of roost-switching can be explained in part by changes in the types of roosts that females prefer to use in different reproductive periods. Most importantly, however,

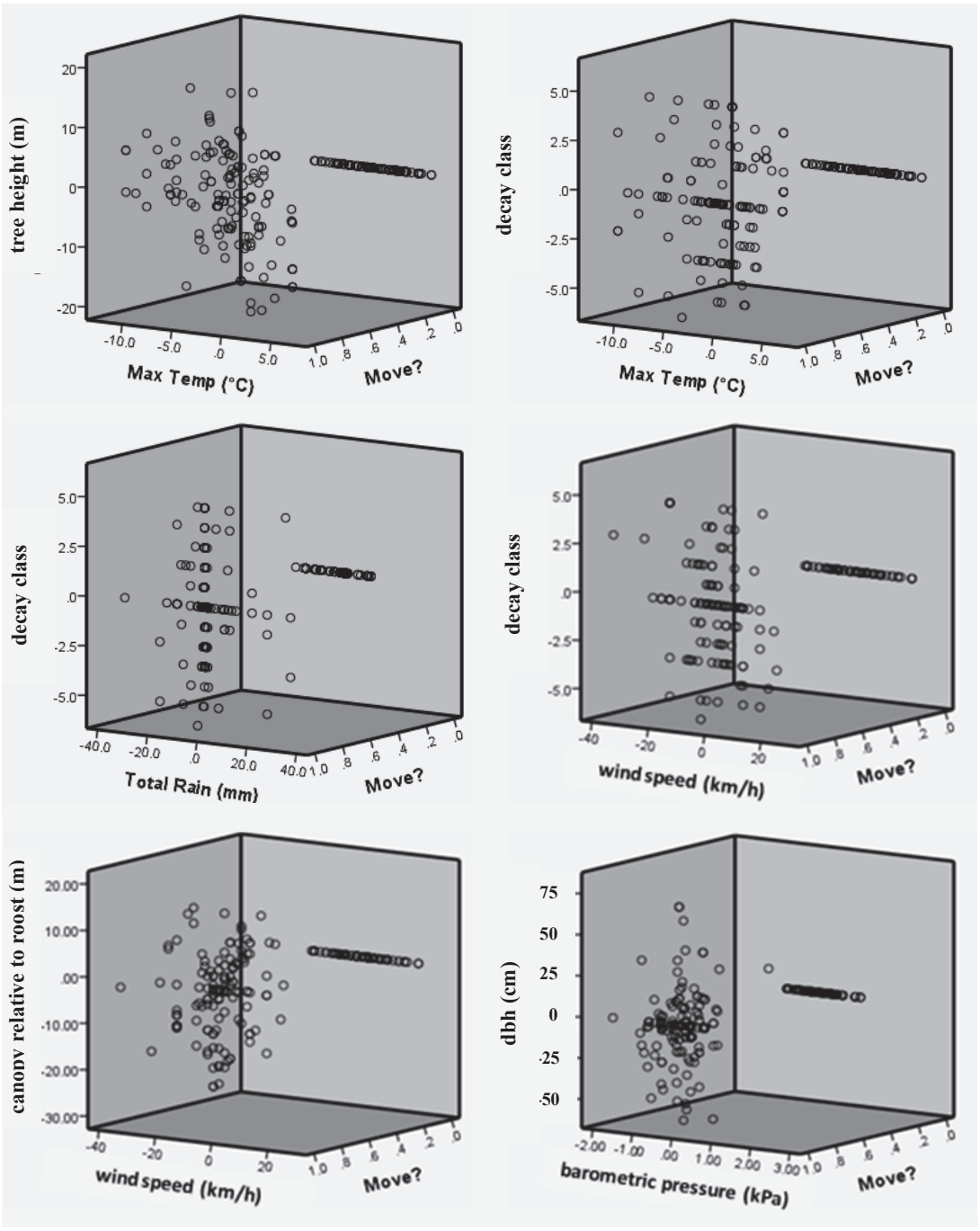


Figure 2.5 Significant interactions from the logistic regression model used to describe the influence of changes in ambient conditions and roost characteristics on the likelihood of roost-switching behaviour by female northern long-eared bats (*Myotis septentrionalis*) in Dollar Lake Provincial Park, NS, from 2005-2007.

frequent roost-switching within summers appears to be due to changes in ambient conditions that may influence roost suitability. Generally, the types of roosts used by females differed with temperature, precipitation, and wind. Though I do not have direct information about the thermal properties of roosts and thermoregulation by bats within roosts, I can propose mechanisms favouring the patterns I detected based on earlier studies in similar systems.

Consistent with several other studies (Callahan, Drobney, and Clawson 1997; Kerth, Weissmann, and König 2001; Chruszcz and Barclay 2002; Lausen and Barclay 2003; Bartonička and Řehák 2007; Pretzlaff, Kerth, and Dausmann 2010; Dietz and Hörig 2011); reviewed in Barclay and Kurta 2007), female northern long-eared bats in my study used different roosts under different ambient conditions. On cold, wet, windy days, females tended to use large, healthy trees where they typically roosted below the canopy. On warmer, drier, and calmer days, females also tended to roost in large trees, but instead they roosted near or above the canopy. Though it is not possible to confirm with these data, these patterns suggest females may be selecting roosts that offer protection from unfavourable ambient conditions. For example, thermal conditions in larger, living trees may be more stable than in smaller or decaying trees and therefore may offer a buffer against cold or hot temperatures that may exceed the thermoneutral zone of bats (Callahan et al. 1997). Similarly, conditions below the canopy may be more stable during unstable weather conditions as the canopy cover prevents heat loss on cooler days and offers protection against wind and rain (Chen, Franklin, and Spies 1993). It is also possible that females are selecting larger trees that may provide more space for group warming, which plays a strong role in thermoregulation by female bats (Foster and Kurta 1999; Lacki and Schwierjohann 2001; Lausen and Barclay 2002; Willis and Brigham 2004; Solick and Barclay 2006; Bartonička and Řehák 2007; Pretzlaff, Kerth, and Dausmann 2010). However, I was unable to obtain sufficient data on group size to test this hypothesis.

Selecting roosts that offer protection against thermal extremes is likely critical to survival and reproductive success. Thermoregulatory costs are greatest when temperatures exceed

thermoneutral zones, and selecting sub-optimal roosts can have significant negative fitness consequences (Geiser 2004; Lausen and Barclay 2006). Familiarity with roosts, and therefore their suitability under different conditions, may then minimize potential costs of searching for roosts or selecting suboptimal roosts. Strong inter-annual fidelity to particular roosts across multiple consecutive years suggests females may in fact develop familiarity with roosts. Within years, however, females showed low fidelity to roosts as they switched roosts frequently.

Consistent with other studies, including an earlier study on female northern long-eared bats in the same study area (e.g., Chaverri et al. 2007; Garroway and Broders 2008), roost characteristics and the degree of roost-switching by female northern long-eared bats during the lactation period differed from other reproductive periods. During the lactation period, females appeared to use more exposed roosts by using cavities above the canopy, which suggests they may be selecting exposed roosts that offer warmer microclimates to minimize thermoregulatory costs and compensate for the high energetic demands of nursing young (McComb and Noble 1981; Wilde, Knight, and Racey 1999; Kerth, Weissmann, and König 2001; Garroway and Broders 2008). During this time, females appear to switch roosts less frequently, which has typically been attributed to minimizing the costs of transporting young (Cryan, Bogan, and Yanega 2001). However, I propose that because ambient conditions during the lactation period were generally more favourable, as it was typically warm, dry, and calm, females were not required to move as frequently to accommodate thermoregulatory demands. While roost-switching of female western long-eared bats (*Myotis evotis*) did not change with lactation (Nixon, Gruver, and Barclay 2009), it is likely they are under different energetic constraints as they are typically solitary (Chruszcz and Barclay 2002), and therefore may show different roost-use patterns. While female northern long-eared bats generally used different roosts during different reproductive periods, roost use also varied on a daily basis.

Consistent with several other studies, female northern long-eared bats showed very low roost fidelity within years as they frequently switched roosts. Most studies of roost fidelity use different indices, or make qualitative inferences, making comparisons across

studies difficult. Nevertheless, it appears most insectivorous temperate species show low roost fidelity, as they tend to switch roosts almost daily (Chaverri et al. 2007). It is widely accepted that females switch roosts to seek optimal microclimates (e.g., Bartonička, Řehák, and Gaisler 2007), yet until now it has not been clearly demonstrated that changes in ambient conditions prompt roost-switching. Here I demonstrate that females appear to move primarily when conditions become unfavourable (i.e., decrease in temperature and pressure), particularly if they were roosting in small trees in higher decay stages prior to changes in ambient conditions. At the same time, females are more likely to move when wind speeds decrease, particularly if they were roosting below the canopy on days prior to changes in ambient conditions. This, together with evidence that females prefer to roost in tall, healthy trees in cavities below the canopy during inclement weather, and above the canopy during favourable conditions, suggests females move in response to changes in ambient conditions in order to move to more optimal roosts. However, consistent with other studies, movement appears to be restricted by precipitation (Vonhof and Barclay 1996) and wind, as females do not move when precipitation levels and wind speeds increase. This suggests that the costs of moving under high rain and wind outweigh the benefits of moving to different roosts, likely because rain and wind can interfere with echolocation and flight, as well as increase thermoregulatory costs (Voigt et al. 2011). Roost-switching behaviour by female northern long-eared bats therefore appears to be shaped by changes in ambient conditions.

An alternative hypothesis for frequent roost-switching suggests it may be related to the relative permanence of roosts. It has been argued that a high degree of roost switching may reflect low roost permanence (Lewis 1995), which appears to be supported by the observation that species, and different populations within the same species, typically show higher fidelity to relatively permanent roosts, such as caves and human-made structures, than to natural roosts (Trousdale, Beckett, and Hammond 2008; Chaverri and Kunz 2010). Interestingly, in a study using the same index used here, tent-making bats (*Artibeus watsonii*) had a much higher average roost fidelity ($\bar{X} \pm SD = 0.99 \pm 0.82$; Chaverri and Kunz 2006) than female northern long-eared bats. Yet, it is expected that tent-making species will switch roosts more frequently than tree roosting species as tents

are generally more ephemeral (Chaverri and Kunz 2010). It therefore appears that frequent roost-switching by female northern long-eared bats observed here is not likely because roosts are ephemeral.

Bats may also switch roosts to minimize predation-risk where predators may pose a significant threat. However, potential predators, such as owls, were rarely detected in my study area (pers. obs.), suggesting frequent roost-switching was not a response to predation-risk. I therefore conclude that the most parsimonious explanation for frequent roost-switching by female northern long-eared bats in my study area is that it is a response to changes in ambient conditions. Though not tested here, roost microclimate varies with ambient conditions and roost-characterisitics (Barclay and Kurta 2005). Therefore, females likely switch roosts to locate to more suitable microclimates that allow them to minimize changing thermoregulatory costs with changing ambient conditions.

Regardless of the mechanisms shaping roost-switching, the degree of roost fidelity or switching can influence the genetic and social structure of populations, as well as social behaviour within groups (Kerth 2008). For instance, strong natal site fidelity to summer roost areas characteristic of many temperate bats often results in matrilineal groups, thus providing the opportunity for kin selection to favour nepotism among matrilineal kin (Hamilton 1964). When females also show strong fidelity to particular roosts, rarely switching among them, group structure tends to be more stable (Chaverri and Kunz 2010), thus potentially favouring reciprocity among familiar group members. In areas with low roost fidelity, however, frequent roost-switching results in changing group size and composition within roosts over time. This pattern is characteristic of fission-fusion dynamics described for variety of taxa, such as elephants, cetaceans, and primates, where females form strong social relationships despite the variable nature of groups (Conradt and Roper 2000; Lehmann and Boesch 2004; Cross, Lloyd-Smith, and Getz 2005; Wittemyer, Douglas-hamilton, and Getz 2005; Archie, Moss, and Alberts 2006; Lusseau et al. 2006; Kerth 2008b). Fission-fusion dynamics have also been quantified for several bat species, including female northern long-eared bats (Garroway and Broders 2007,

Patriquin et al. 2010, Kerth 2008). As such, it has been suggested that frequent roost-switching, and the resultant changes in group composition, may also serve a social function by allowing females to maintain social connections across a larger social network spread among multiple roosts (Willis and Brigham 2004). This may then be important for facilitating social behaviours, such as information transfer about suitable roosts and foraging habitat (Wilkinson 1992; Kerth and Reckardt 2003).

My findings also have potential management implications. Females appear to require a network of trees to accommodate changing energetic demands with changes in reproductive condition and ambient conditions. Therefore, conserving trees with "average" characteristics will not likely provide adequate roost habitat for bats. Though other studies have highlighted the importance of conserving different types of trees to accommodate changes with reproductive condition (e.g., Garroway and Broders 2008), my results suggest individual needs vary on a much finer scale. As suggested for managing forests in other parts of its range, to properly manage Acadian forests to support northern long-eared bats, a habitat mosaic should be created to provide a variety of roost types (Ethier and Fahrig 2011).

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CHAPTER 3
DO SOCIAL NETWORKS OF FEMALE NORTHERN LONG-EARED BATS VARY WITH REPRODUCTIVE PERIOD AND AGE?

The work presented in Chapter 3 also appears in:
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3.1 INTRODUCTION

Social structure is described by the frequency, temporal patterns and nature of interactions among individuals (Hinde 1976). Fission-fusion societies, for example, are characterized by non-randomly associating individuals moving regularly among multiple, interconnected groups. These dynamics result in variable group size and composition and have been most notably described for ungulates, marine mammals, primates, elephants, and, more recently, bats (Archie et al. 2006; Connor et al. 2000; Conradt and Roper 2005; Cross et al. 2005; Kerth 2008; Lehmann and Boesch 2004; Lusseau et al. 2006; Whitehead 2003; Wittemyer et al. 2005). The factors that shape these dynamic groups are not well known, but they likely involve an interaction between the costs and benefits of social living and ecological constraints (Alexander 1974; Komdeur 2006) associated with individual characteristics, such as sex, age, reproductive condition and relatedness (Conradt and Roper 2000; Hinde 1976; Ruckstuhl and Neuhaus 2002; Silk 2007; Wolf et al. 2005; 2007). Understanding how these factors influence the dynamics of fission-fusion societies is necessary if we are to understand the consequences for population dynamics, such as dispersal patterns (Blanco and Cortes 2007), disease transmission (Vicente et al. 2007) and population genetics (Krause et al. 2007).

Sociality is taxonomically and geographically widespread among the roughly 1200 described bat species (Kerth 2008; Kunz and Lumsden 2003; McCracken and Wilkinson 2000). Fission-fusion societies, for example, have been documented in temperate regions

where females typically gather in summer roost trees to give birth and raise their young. During this time, females switch roosts almost daily and group size and composition change with each switch (Kunz and Lumsden 2003; Lewis 1995). However, particular females consistently roost together more often than expected by chance throughout switches, forming preferred associations that are not explained by mutual roost preferences (Garroway and Broders 2007; Kerth and König 1999; O'Donnell 2000; Popa-Lisseanu et al. 2008; Rhodes 2007; Willis and Brigham 2004).

Reproductive condition has been proposed to influence preferred associations among female bats. For example, reproductively active female Bechstein's (*Myotis bechsteinii*) and big brown (*Eptesicus fuscus*) bats roost more often with reproductive conspecifics than with non-reproductive conspecifics (Kerth and König 1999, Willis and Brigham 2004). In addition, female northern long-eared (*M. septentrionalis*) and big brown bats are more likely to repeatedly roost with the same individuals during lactation than other periods (Garroway and Broders 2007; Willis and Brigham 2004, 2007). Female association preferences may differ with reproductive stage due to differences in energetic demands and strategies to minimize costs during each stage. For example, social thermoregulation and large group sizes during lactation likely reduce the need to use torpor, which negatively impacts milk production and thus offspring survival (Racey 1973; Racey and Swift 1981; Speakman 2008; Tuttle and Stevenson 1982; Wilde et al. 1999; Willis 2006; Willis and Brigham 2007). Larger group sizes and stronger associations during lactation may also facilitate cooperative care of young, such as allonursing (Eales et al. 1988; McCracken 1984; Wilkinson 1992a). By contrast, smaller group sizes during gestation may facilitate torpor use, which may function to delay parturition until conditions are suitable for offspring (Willis et al. 2006). Nevertheless, non-reproductive and reproductive females do roost together (Kerth and König 1999), which suggests reproductive condition alone cannot explain all association patterns.

Age might also influence social interactions among bats as it does in a variety of other animals, although this is yet to be examined. In many species, from birds to primates, younger individuals preferentially associate with older individuals, presumably to benefit

from information transfer or to learn socially appropriate behavior (Bourjade et al. 2008; Cockburn et al. 2008; Durant 2000; Galef and Laland 2005; McComb et al. 2001). Like other long-lived mammals, young female bats roost in groups of overlapping generations (Barclay and Harder 2003; Podlutsky et al. 2005) and therefore may also learn from older, or more experienced, females (Jones and Ransome 1993; Kerth and Reckardt 2003; Page and Ryan 2006; Ratcliffe and ter Hofstede 2005; Wilkinson and Boughman 1998).

According to Hinde's (1976) framework of quantifying sociality, in addition to identifying who associates with whom and why, the temporal patterning of these relationships is also necessary to understand how long associations may persist. Only two studies to date have explicitly quantified the temporal patterns of associations among bats. Spix's disc-winged bats (*Thyroptera tricolor*), a tropical species that roosts in unfurling leaves, maintained preferred associations for at least 100 days, and up to four years (Vonhof et al. 2004). Similarly, female northern long-eared bats, a temperate species, maintained preferred associations for an entire summer breeding season and temporal models predicted these associations could persist across multiple years (Garroway and Broders 2007). However, the predictions generated by the models in Garroway and Broders (2007) have yet to be tested and it remains unclear whether these relationships can persist across years in temperate regions where females move from summer breeding areas to winter hibernation sites (Fleming and Eby 2003). Females of some species exhibit inter-annual fidelity to summer roosting areas and, in some cases, to specific roost trees (Arnold 2007; Barclay and Brigham 2001; Entwistle et al. 2000; Kerth and König 1999; O'Donnell 2000; Veilleux and Veilleux 2004; Willis and Brigham 2004) and, so, could reestablish preferred associations upon their return.

We tested the hypotheses that association patterns among female northern long-eared bats vary with reproductive period and age and that females form long-term associations. Specifically, we tested the predictions that preferred associations and social network metrics of female northern long-eared bats vary with reproductive period and age and that preferred associations persist across years. Female northern long-eared bats live in fission-fusion societies where individuals switch roosts almost daily (Broders and Forbes

2004; Foster and Kurta 1999; Garroway and Broders 2007; Lacki and Schwierjohann 2001; Sasse and Perkins 1996) and subsets of individuals maintain preferred associations for at least an entire summer (Garroway and Broders 2007). However, the results and subsequent predictions of the latter study that preferred associations would persist across years were based on data from a single summer and therefore require empirical testing with a multi-year dataset. Moreover, it is not known how reproductive period and age influence social networks in this species. Network analysis permits exploration of the role individuals, or groups of individuals, play in a population by summarizing their direct and indirect connections (via common associates) with others (for recent reviews see Croft et al. 2008; Krause et al. 2009). Therefore, we used network analyses to test the prediction that pairwise associations among females differ between reproductive periods and among age classes. We also calculated the standardized lagged association rate over three summers to test the prediction, made by Garroway and Broders (2007), that females would maintain preferred associations across years.

3.2 METHODS

We conducted our study in Dollar Lake Provincial Park (DLPP), Nova Scotia, Canada ($44^{o}55'$ N, $63^{o}19'$ W; see Garroway and Broders 2007 for site description) between early-June and mid-August, 2006 and 2007. We combined data from these years with those collected by Garroway and Broders (2007) from the same site between early-June and mid-August, 2005.

3.2.1 Capture and Marking

We caught bats in mist nets (Avinet, Dryden, New York, USA) and harp traps (Austbat Research Equipment, Lower Plenty, Victoria, Australia) placed along corridors and gaps in the forest interior, as well as roost traps (modified harp traps; Kunz and Kurta 1988) placed over roost cavities. Following capture, we recorded the sex, mass (g) and forearm length (mm) of all bats. We also assessed reproductive condition of females as either pregnant, by palpation of the abdomen; lactating, by expression of milk from the nipples;

or post-lactating, by the presence of worn patches around the nipples in the absence of milk expression (Racey 1988).

We identified bats as either juvenile (young of the year) or adult by examining the epiphyseal gap of the fourth metacarpal for calcification, which is incomplete in juveniles (Anthony 1988). For a finer resolution of adult age, we ranked individuals based on canine tooth wear. Tooth wear provides an index of relative age, with older bats having greater wear than younger bats (Anthony 1988). We placed individuals into one of three age classes, similar to those of Davis et al. (1962), and adapted from Holroyd (1993), which was derived from Christian (1956): YOUNG: no longer pinpoint sharp, starting to round. INTERMEDIATE: tips could range from obviously rounded but not yet flat to obviously flat and beginning to wear on an angle. OLD: tips obviously worn flat and on an angle, but more than two-thirds of the canine remain. Although we based our classification on a system developed for big brown bats, which feed on more hard-bodied insects than do northern long-eared bats, tooth wear or damage does not appear to differ consistently with diet, especially among vespertilionids (Evans and Sanson 2005). Based on blind ad-hoc comparisons of known-aged individuals, tooth wear classification is a reliable means of aging Mexican free-tailed bats (*Tadarida brasiliensis*; Perry and Herreid II 1969). In addition, in our population, estimates of wear are fairly repeatable as 73% of recaptured individuals received the same tooth wear score. Scores for misclassified recaptured individuals never differed by more than one.

To identify individuals, we implanted passive integrated transponders (0.09 g), which contain unique alphanumeric codes (EID-ID100 implantable transponders, EIDAPInc, Sherwood Park, Alberta, Canada), subcutaneously between the scapula of all new captures (56 and 9 in 2006 and 2007, respectively). PIT-tags have been used to study a variety of small mammals, including bats, with no reported cases of mortality, morbidity or impact on behavior (Garroway and Broders 2007; Gibbons and Andrews 2004).

To locate roost trees, and ultimately groups of females, we glued (SkinBond, Smith and Nephew United Inc., Largo, Florida, USA) a radio-transmitter (LB-2N, Holohil Systems

Ltd., Carp, Ontario, Canada) between the scapula of a subset of females (n=57). Radio-tagged females were typically gestating or lactating and had been previously captured and PIT-tagged and thus known to associate with a group. We used a radio receiver (R-1000, Communication Specialists Inc., California, USA) and 3-element yagi antenna (AF Antronics Inc., Urbana, Illinois, USA) to track females daily during the battery life of transmitters or until they fell off (mean=6.7 days; range:1-24 days).

Once we located roost trees, we placed PIT-tag scanner antennas (LID650, Trovan Electronic Identification Systems, UK) at roost entrances to record the date and time PIT-tagged individuals entered or exited the roost. These data were later used to assess associations between individuals. We typically moved scanners to new roosts when radio-tagged animals moved. However, three scanners were left permanently at roosts that appeared to be used regularly. Group size is a fundamental characteristic of social structure (Wilson 1975), yet not all individuals in groups were tagged. Therefore, on 59 evenings we also visually counted the number of individuals emerging from roosts to estimate group sizes.

3.2.2 Analyses

3.2.2.1 Associations

To increase sample sizes and provide a longer-term dataset for temporal analyses, we combined our data with those obtained in 2005 by Garroway and Broders (2007) as there were no significant differences among years in associations among individuals observed across all three years (Mantel's $p>0.50$ in all cases). It was not possible to directly observe interactions among bats in roosts; therefore, we assumed that, due to their close proximity to one another, females that roosted together also interacted (Whitehead 1995, Whitehead and Dufault 1999). To determine how often females roosted together, we used SOCPROG 2.3 (Whitehead 2008a) to calculate the half-weight association index (HWI) of all pairs. The HWI is an estimate of the proportion of days pairs roosted together relative to the total number of days each individual in a pair was observed, whether together or separate, and standard deviations indicate the reliability of these estimates (Cairns and Schwager 1987). The HWI is appropriate for our system because it

is less biased than the other commonly used indices, such as simple-ratio or twice-weight, when not all individuals in a group can be identified (Whitehead 2008b). In our study, not all individuals were identified when bats exited roosts from multiple locations and if several tagged individuals simultaneously passed through the antenna, which cannot record multiple codes simultaneously. Moreover, the HWI was used previously for this population (Garroway and Broders 2007) and is computationally similar to other indices used for studies of bat sociality (Kerth and König 1999; Wilkinson 1985), which facilitates comparisons.

To determine whether the observed HWI differed from random expectations, we compared the coefficients of variation (CV) for observed and random association matrices of all possible pairwise associations (Bejder et al. 1998; Whitehead 1997). Random matrices were generated by permuting observed matrices, where pairwise associations were altered but the total number of individuals and the number of groups from the original matrix were conserved (Bejder et al. 1998; Manly 1995; Miklós and Podani 2004; Whitehead 1999; Whitehead et al. 2005). Associations were considered non-random and significant if the CV of the observed matrix was greater than the random CV in more than 95% of the permutations ($p>0.95$). In addition, as recommended by Whitehead (2008c), we used SOCPROG 2.3 to obtain a measure of correlation between our estimated association indices and the true pattern. We also obtained an estimate of social differentiation (S) and the average number of associations per individual (H) to ensure our data were sufficient to reject the null hypothesis that individuals associated randomly, which is true when $S^2 * H > 5$ (Whitehead 2008c).

To graphically illustrate pairwise associations and groups, we used average linkage clustering analyses to create dendograms that linked individuals based on HWI. Individuals with higher HWI were clustered together and these clusters were considered distinct groups if they clustered at or above twice the randomly permuted mean. The dendogram was considered a good representation of the data if the cophenetic correlation coefficient (the correlation between pairwise HWI and the dendogram linkages between pairs) was 0.8 or greater (Whitehead 2008b).

3.2.2.2 Temporal patterns of associations

The HWI does not indicate whether the proportion of days a pair roosted together was continuous or whether associations were interrupted by periods of separation. Thus, to characterize temporal patterns, we used a standardized lagged association rate (SLAR) to calculate the average probability that pairs roosting together on a particular day were still together on subsequent days. The precision of the estimated SLAR was determined using jackknifing and the pattern was compared to the null association rate, which is the inverse of the number of observed individuals minus one (Whitehead 1995, 2008b). Because females disperse to hibernacula at the end of the breeding season, we only collected summer association data from early-June until mid-August (approximately 75 days) in each of three years. Our goal was to assess association patterns among females at summer roosts; therefore, we treated the three summers as one continuous period.

Four exponential decay models were fitted to the observed SLAR to provide a quantitative means of describing temporal patterns of associations. The four models described different levels of permanence in the associations among individuals in the group, they included: 1) constant companions, where all pairs associate permanently; 2) casual acquaintances, where all pairs disassociate over time; 3) constant companions and casual acquaintances, where some pairs associate permanently and others disassociate over time; 4) two levels of casual acquaintances, where pairs disassociate over time, but at two different rates (Table 3.1; Whitehead 1995; 2008b). To determine which model best fit the observed temporal pattern, we chose the model with the lowest Akaike's information criterion adjusted for overdispersion and small sample sizes (QAICc; Whitehead 2007, 2008b). We then ranked each model based on the following: Δ_i, the difference in QAICc between each model and that with the lowest QAICc ; w_i, Aikake weights, which are the probability that the given model is the best among all candidate models (Burnham and Anderson 2002); K, the number of estimatable parameters. From the best fit model, we divided the value when the model reached an asymptote by the y-intercept to obtain an estimate of the proportion of individuals found roosting together

that were likely to be together for the maximum number of days defined by the SLAR (Garroway and Broders 2007).

Table 3.1 Candidate exponential decay models fit to the standardized lagged association rate of female northern long-eared bats (*Myotis septentrionalis*) observed from June to August, 2005-2007, in Dollar Lake Provincial Park, Nova Scotia, Canada.

Model description	Model structure	Δ_i	w_i	K	Rank
Constant companions (CC)	$g(r) = a_1$	39.11	0	0	4
Casual acquaintances (CA)	$g(r) = a_2\exp(-a_1 r)$	2.65	0.21	1	2
CC + CA	$g(r) = a_2+a_3\exp(-a_1 r)$	16.16	0	2	3
2 levels of CA	$g(r) = a_3\exp(-a_1 r) + a_4\exp(-a_2 r)$	0	0.79	3	1

Note: Based on the Akaike's information criteria adjusted for overdispersion and small sample sizes (QAICc), models were ranked according to the following: Δ_i, the difference between each model and the best ranked model, w_i, the probability that each model was the best of all candidate models, and K, the number of estimatable parameters.

3.2.2.3 Network analyses

Network analysis provides an analytical framework for linking individual behaviors, such as associations, with higher level phenomena, such as age, at the group or population level. Within a social network, individuals are represented by nodes and associations among individuals are represented by valued edges, or connections. We used weighted networks which assign values to edges according to estimated proportion of time individuals spent together, in this case the pairwise HWI values. Weighted networks, therefore, provide information about the variation in the proportion of time individuals associated in contrast to unweighted networks which provide information about whether or not individuals associated (Boccaletti et al. 2006, Croft et al 2008, Lusseau et al. 2008). We used Netdraw 2.081 (Borgatti 2002) to graphically illustrate a spring-embedded network, which arranges individuals with more similar associations more closely together.

We calculated three metrics that quantify various aspects of an individual's (node) position within the social network; specifically, strength, reach and betweenness. Strength is the sum of all edges directly connected to a node (Croft et al. 2008; Whitehead 2008b). Thus, strength is a measure of the proportion of time a female was found roosting with specific individuals and how many other individuals she roosted with. Reach is the sum of the product of a node's strength and the strength of each of the nodes it is directly connected to (Flack et al. 2006; Croft et al. 2008; Whitehead 2008b). Thus, reach is a measure of how closely females associate directly with one another and indirectly via common roost associates. This metric offers some insight into the potential for indirect transfer of information or disease, for example, between females that do not roost together (Flack et al. 2006). Both strength and reach were calculated using SOCPROG 2.3 (Whitehead 2008a). Betweenness is the number of shortest paths (or smallest total edge weight) between an individual node and other nodes in the network (Brandes 2001). For the calculation of betweenness on weighted networks, the distance between nodes is calculated as the smallest sum of edge weights between a pair of nodes. Thus, edges need to represent distances rather than similarities, so, for this calculation edges were weighted as the proportion of time individuals spent apart (1–HWI). Many individuals connected to one another via a particular female yields a high betweenness for that female. Thus, betweenness could offer insight into which individuals play a central role in connecting females that do not roost together directly or how information or disease could transfer between females that may not roost together directly. Because we were more interested in identifying how characteristics, rather than specific individuals, influence preferred associations, we calculated network metrics averaged across individuals pooled for each reproductive period and age class. In addition, because network analyses are sensitive to missing data, interpretations based on group level metrics rather than individuals is more robust (see James et al. 2009 for more discussion).

3.2.2.4 Nature of associations: Effects of reproductive period and age

Because most of the captured females were reproductive (70%) and reproduction tends to be highly synchronous in temperate bats (O'Donnell 2002; Racey 1982; Racey and

Entwistle 2000), we had few pairwise data to compare association patterns between pairs in different reproductive condition as has been done in other studies (e.g., Kerth and König 1999; Willis and Brigham 2004). Thus, to determine how reproductive period influenced association patterns in our study, we compared associations among individuals observed during the gestation period to those observed during the lactation period. For our purposes, the gestation period began June 1 and ended with the first capture of a lactating female. The lactation period began with our first capture of a lactating female and ended with the first capture of a post-lactating female. We had insufficient data to consider the post-lactation period in our analyses.

To determine the potential effects of reproductive period on association patterns, we compared the mean (±95% confidence intervals (CI) HWI, strength and reach between gestation and lactation periods. We did not compare betweenness values during different reproductive periods as we used this measure to determine whether certain classes of individuals played a more important role in connecting other individuals in the population. This measure, therefore, has no biological relevance in this context because reproductive period is temporally separated and cannot play a role in maintaining connections at the group level. Because the same individuals were not necessarily observed during the two reproductive periods we could not use test statistics, such as Mantel's test, to determine whether association patterns differed between the two periods (Croft et al. 2008). In addition, because association indices and network metrics are based on pairwise observations between each individual and all other individuals in the population, the same individual was observed repeatedly within a given association matrix and network. Thus observations within a single network are not independent, making traditional statistical analyses of means invalid (Croft et al. 2008). Therefore, we relied on comparing the CIs of observed means and concluded means were different when CIs did not overlap. Generally, comparisons of means in this way should also be avoided for networks because differences in the number of individuals and connections within networks can strongly influence measures. However, such an approach is appropriate where sample sizes are similar (Croft et al. 2008), as was the case for our data.

To determine whether age class affected association patterns among female bats, we compared mean (±95% CI) HWI and weighted networks statistics, including strength, reach and betweenness (see above), for young, intermediate and old age classes (described above).

3.3 RESULTS

Capture and marking methods may impact animal movement, and different methods may have different impacts. In recognition of this, we limited disturbance resulting from trapping at roosts such that individual females were rarely captured at roosts on more than one occasion (mean±SD=1.30±0.61; range=1–5). In addition, we reduced trapping effort in 2007; however, roost-switching behavior of females did not appear to differ between 2006 (mean±SD residency time=1.26±0.40 consecutive days in a roost) and 2007 (1.20±0.49), suggesting that trapping at roosts had minimal impact on movement patterns. Additional weight associated with PIT-tags and radio-transmitters may have also affected movement. However, PIT-tag mass (0.09 g) represented only 1.2% of female body mass (mean±SE=7.20±0.14 g), which is considerably lower than the accepted "5% rule" (Aldridge and Brigham 1988). Average transmitter mass (mean±SE=0.41±0.004 g) and PIT-tag mass together represented 6.9% of body mass. Previous studies demonstrated that PIT-tags had little impact on the morbidity, mortality and behavior of small mammals, including bats, (Gibbons and Andrews 2004) and we found no apparent difference in movement patterns between individuals with only PIT-tags (mean±SD residency time=1.20±0.33 days) and those with PIT-tags and radio-tags (1.34±0.59 days) in our study. This suggests that although transmitter mass exceeded the 5% rule, this had little impact on movement. Moreover, PIT-tagged and radio-tagged females continued to forage and reproduce, and roughly a third (34.1%) were recaptured or observed in subsequent years.

We captured 69 and 24 adults in 2006 and 2007, respectively, 13 and 15 of which had been caught in previous years. The lower capture rate in 2007 was due to reduced trapping effort at roosts because it appeared we were recapturing or recording many

females that had already been PIT-tagged; therefore, we chose to limit disturbance at roosts. Based on nights where both emergence counts and PIT-tag data were obtained from the same roosts, PIT-tagged individuals represented 51-100 % (median=92%) of the total number of individuals observed emerging from roosts. We radio-tracked 19 females to 53 roost trees in 2006, and 21 females to 46 roost trees in 2007. Females switched roosts almost daily (mean±SD residency time=1.40±0.64 days) and roosted in groups of variable sizes (range 1-67, mean=20, n=59 emergence counts).

3.3.1 Associations

The 83 females located on two or more occasions (mean±SD=8.60±6.40; range=2–33) formed non-random associations, as the CV of the observed matrix (1.88) was greater than the random CV (1.87) on more than 95% of the permutations (1,000 permutations; $p>0.999$). Based on Whitehead (2008c), our data were sufficient to reject the null hypothesis that females associated randomly ($S^2*H=1.03^2*47.23=49.80>5$) and our estimates of association indices were a good representation of the true pattern ($r=0.62$).

On average, pairs roosted together on 9% (range=0–100%) of the total number of days they were located over the three summers (mean±SD observed HWI=0.09±0.16), though not necessarily on consecutive days. Although there were no significant differences between years (Mantel's $p>0.50$ in all cases), the mean HWI was lower in 2005 (0.06±0.12) than in 2006 (0.26±0.29) and 2007 (0.24±0.28).

Cluster analysis assigned 64 of the 83 females to 11 groups within which individuals roosted more regularly with one another than with individuals assigned to other groups (Figure 3.1). Two females were never seen associating with other individuals, and others did not cluster at or above twice the randomly permuted mean HWI; therefore, these females were not assigned to a distinct group. This clustering was a good representation of the observed patterns (cophenetic correlation coefficient=0.86). Although there were 11 groups, the high HWI for linkages between clusters suggest individuals of different clusters also roosted together. However, the six individuals in group 1 (observed on average five times each) and the two individuals in group 2 (observed five times each)

appeared to roost exclusively with members of their respective groups as they were not linked to any other group (Figure 3.1).

3.3.1.1 Temporal pattern

The SLAR dropped until day 10 at which point it reached an asymptote above the null association rate (Figure 3.2). This pattern, together with the best fit decay model [0.024245*exp(-0.0014345*td)+0.032077*exp(-0.40395*td); Figure 3.2; Table 1], suggests two levels of casual associates, where some pairs roosted together for as many as 10 consecutive days after first observation, while some may have roosted together for 75, or more, days after first observation. In fact, dividing the value of the model at day 10 (0.026) by the y-intercept at time lag 0 (0.056) suggests that approximately 45% of pairs roosted together for at least 10 consecutive days. Similarly, dividing the value when the model

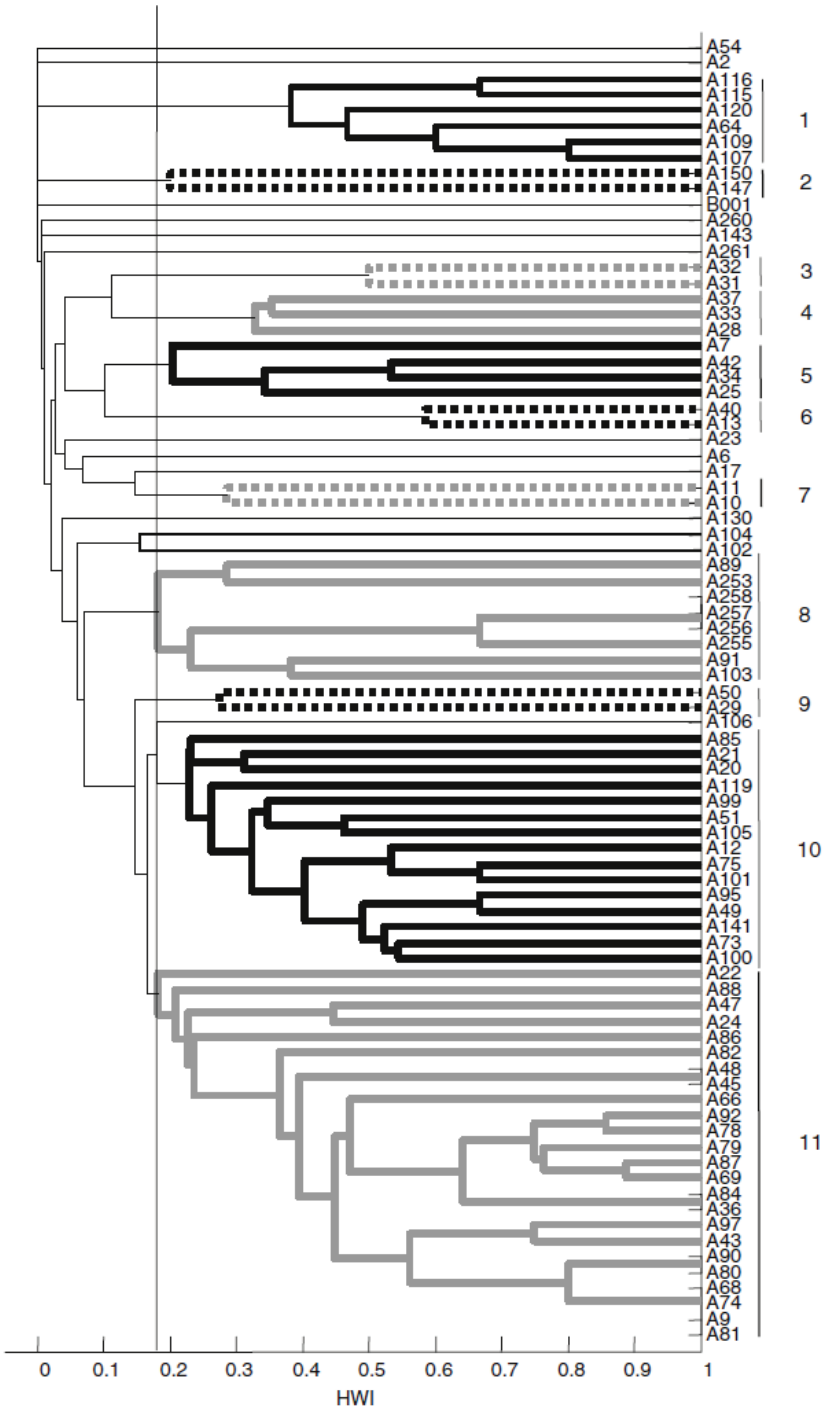

Figure 3.1 Average linkage cluster analysis of mean half-weight association index (HWI) values for female northern long-eared bats (*Myotis septentrionalis*) observed from June to August, 2005-2007, in Dollar Lake Provincial Park, Nova Scotia, Canada. (cophenetic correlation coefficient = 0.86). Eleven groups (demarked by bold solid and hashed black and grey lines) were identified based on individuals with HWI values greater than twice the mean random HWI (> 0.18; indicated by vertical line).

reached an asymptote (0.024) by the y-intercept at time lag 0 (0.056) suggests that approximately 43% of pairs roosted together for at least 75 days.

3.3.2 Reproductive Period

Females switched roosts almost daily during gestation (mean residency time±95% CI=1.47±0.40 days) and lactation (1.34±0.24). Based on emergence counts, average group size was smaller, although not significantly, during gestation (mean±95% CI=12.91±4.96; n=24) than lactation (16.42±5.83; n=17; Figure 3.3). We located 56 and 63 adult females on two or more occasions during gestation and lactation, respectively. We first confirmed that females in these subsets (i.e. gestating or lactating groups) also formed non-random associations (1,000 permutations; $p>0.98$ in both cases). On average, pairs roosted together significantly more often during gestation (mean±CI observed HWI=0.22±0.04) than lactation (0.10±0.02). However, the maximum time pairs spent together did not differ between gestation (mean±CI maximum HWI=0.66±0.09) and lactation (0.62±0.07). We do not present an illustration of the networks obtained for each of the reproductive periods as the number of individuals and connections between them make the networks cluttered and uninformative. Instead we present a summary of network statistics, which suggests that females had significantly higher strength and reach during the gestation period (mean strength±95% CI=12.09±2.90; reach=219.79±124.56; Figure 3.3) than lactation (strength=6.30±1.27; reach=67.45±33.50; Figure 3.3).

3.3.3 Age

We assigned age class scores to 58 adult females (14 young, 31 intermediate, 13 old) observed on two or more occasions (mean±CI observations: 6.93±2.86 young, 7.23±2.26 intermediate, 8.15±2.71 old). As above, we first confirmed that these females also formed non-random associations (1,000 permutations; $p=0.99$), that the data were sufficient to reject the null hypothesis that females associated randomly ($S^2*H=1.05^2*46.81=51.4>5$) and that our estimates of association indices were a good representation of the true pattern ($r=0.62$). A comparison of mean HWI between pairs of

similar and different age revealed that individuals of all age classes roosted more often with young individuals. Based on non-overlapping CIs, mean HWI was higher when young individuals were paired with other young females than when old individuals were paired with other old individuals.

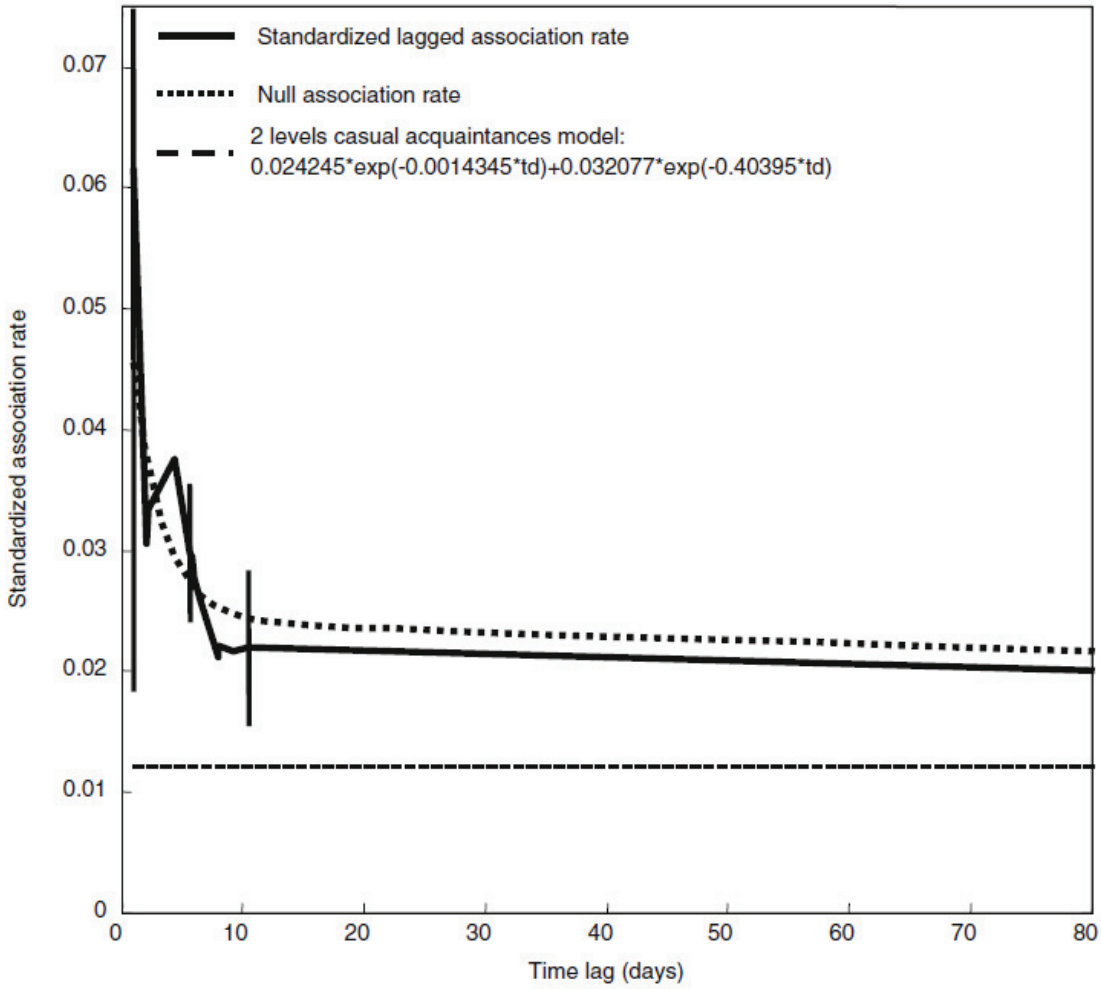

Figure 3.2 Standardized lagged association rate (SLAR), calculated as the average probability that pairs roosting together on a given day are still found roosting together on subsequent days, with jackknifed standard error bars, null association rate and the best fit model (2 levels of casual acquaintances) for female northern long-eared bats (*Myotis septentrionalis*) observed from June to August, 2005-2007, in Dollar Lake Provincial Park, Nova Scotia, Canada.

In fact, although not significant in most cases, mean HWI was highest when each age class was paired with young individuals and decreased with increasing age of their roosting partner (Figure 3.4). Individuals of all age classes were highly interconnected, as

evidenced by the spring-embedded network (Figure 3.5). Although not significant based on overlapping CIs, young females had higher strength, reach and betweenness (mean strength±95% CI=8.43±2.78; reach=85.94±55.66; betweenness=23.04±23.55; Figure 3.6) than did intermediate (strength=6.67±2.16; reach=63.70±41.44; betweenness=10.75±8.04; Figure 3.6) and old females (strength=5.97±1.86; reach=61.72±38.18; betweenness=9.32±8.33).

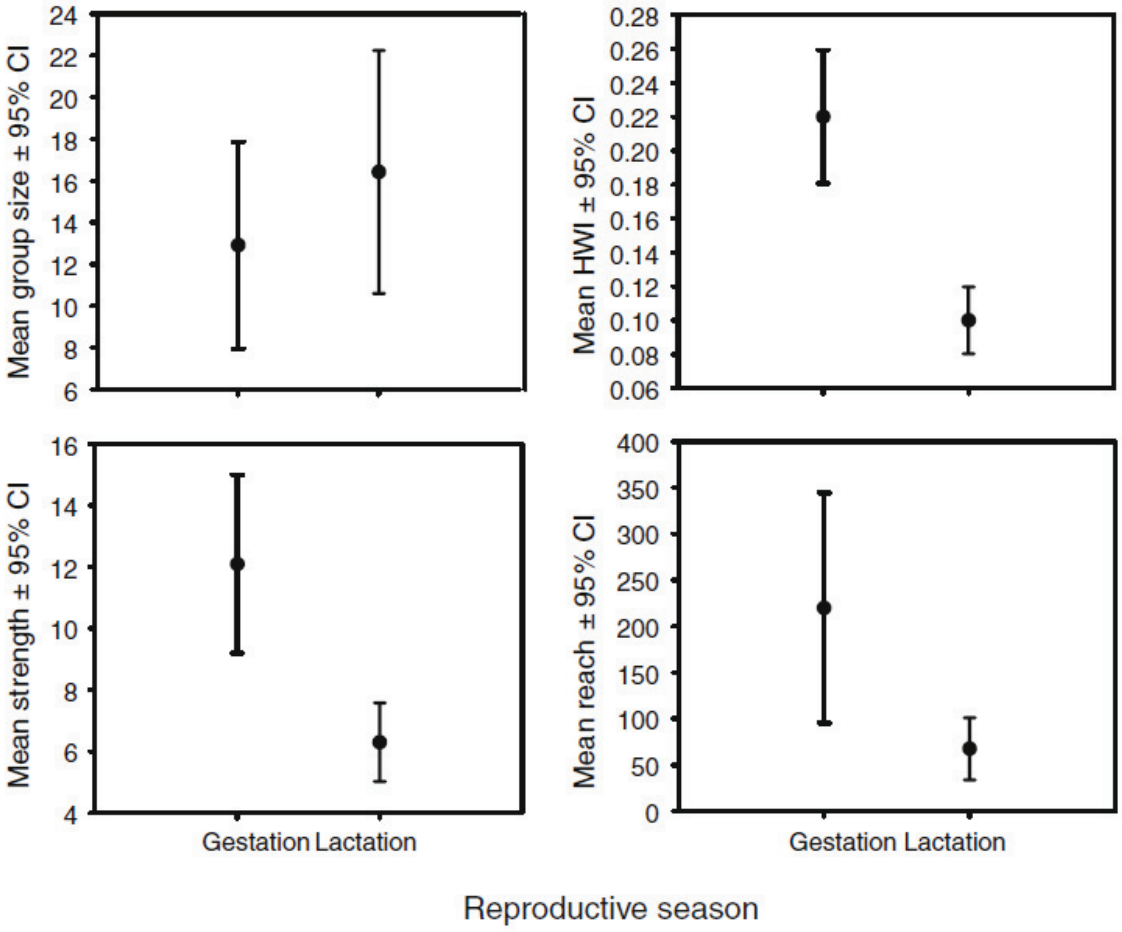

Figure 3.3 Mean (± 95% confidence intervals) group size, half-weight index (HWI), strength and reach during the gestation and lactation periods for female northern long-eared bats (*Myotis septentrionalis*) observed from June to August, 2005-2007, in Dollar Lake Provincial Park, Nova Scotia, Canada.

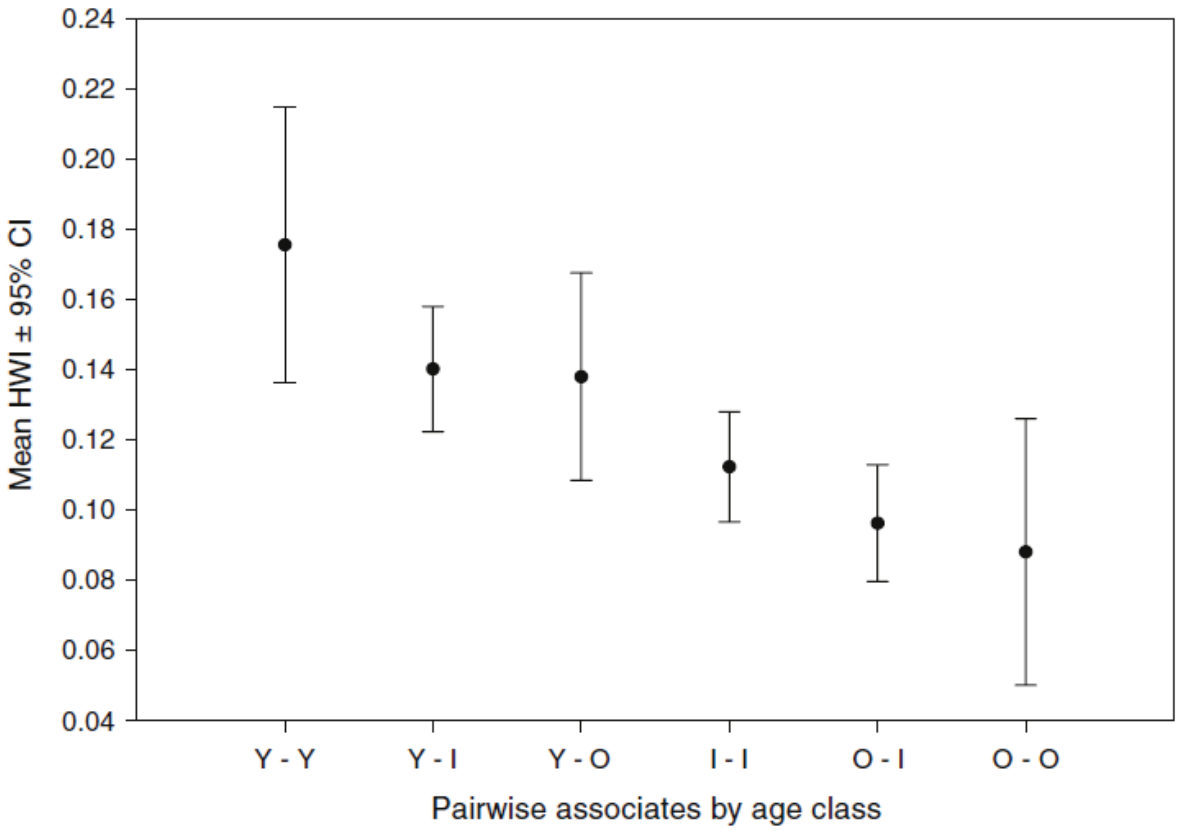

Figure 3.4 Mean (± 95% confidence intervals) half-weight index (HWI) of young (Y), intermediate (I) and old (O) female northern long-eared bats (*Myotis septentrionalis*) paired with either young, intermediate or old females observed from June to August, 2005-2007, in Dollar Lake Provincial Park, Nova Scotia, Canada.

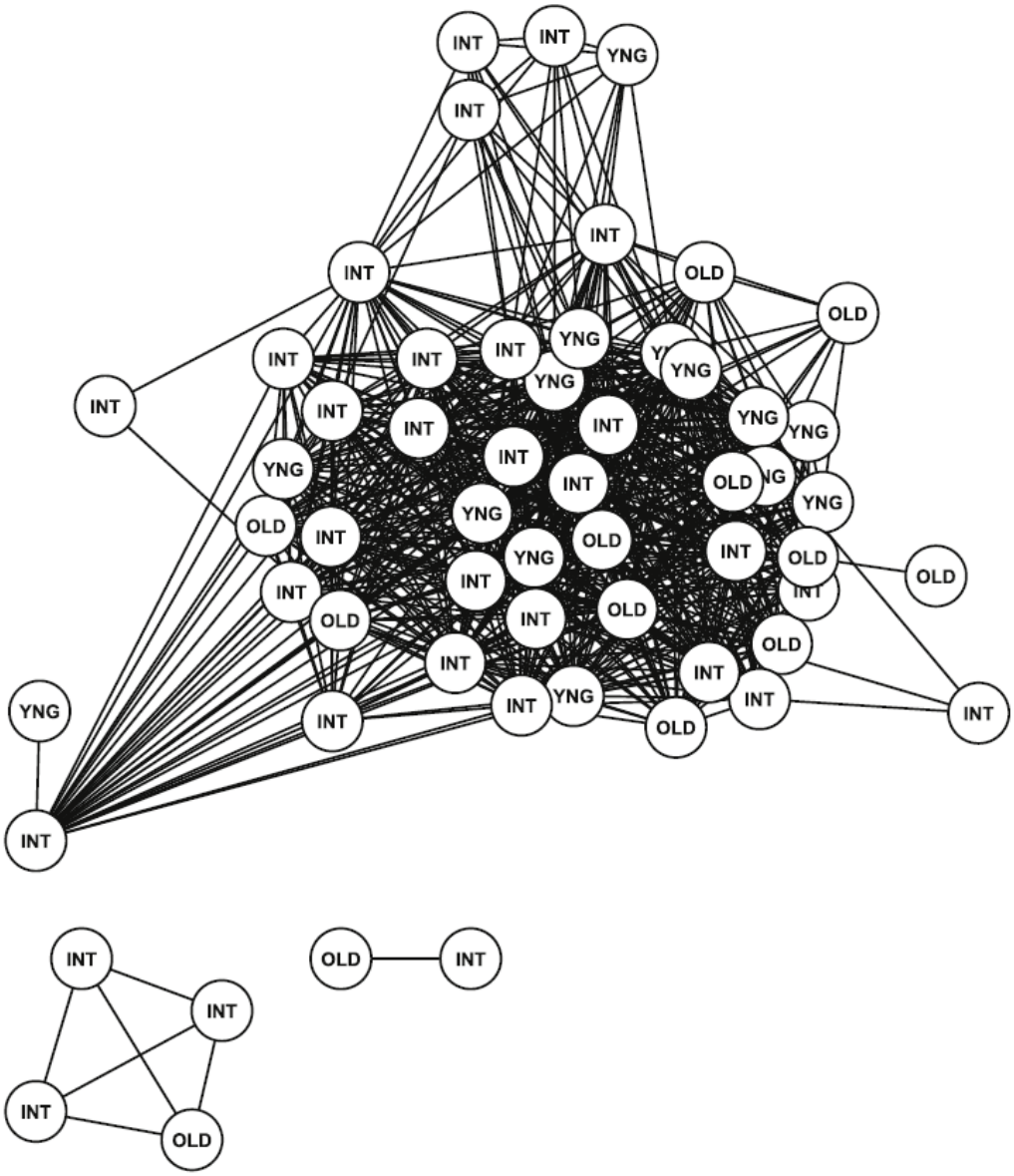

Figure 3.5 Network diagram illustrating associations among individuals of young (YNG), intermediate (INT) and old (OLD) age classes for female northern long-eared bats (*Myotis septentrionalis*) observed from June to August, 2005-2007, in Dollar Lake Provincial Park, Nova Scotia, Canada.

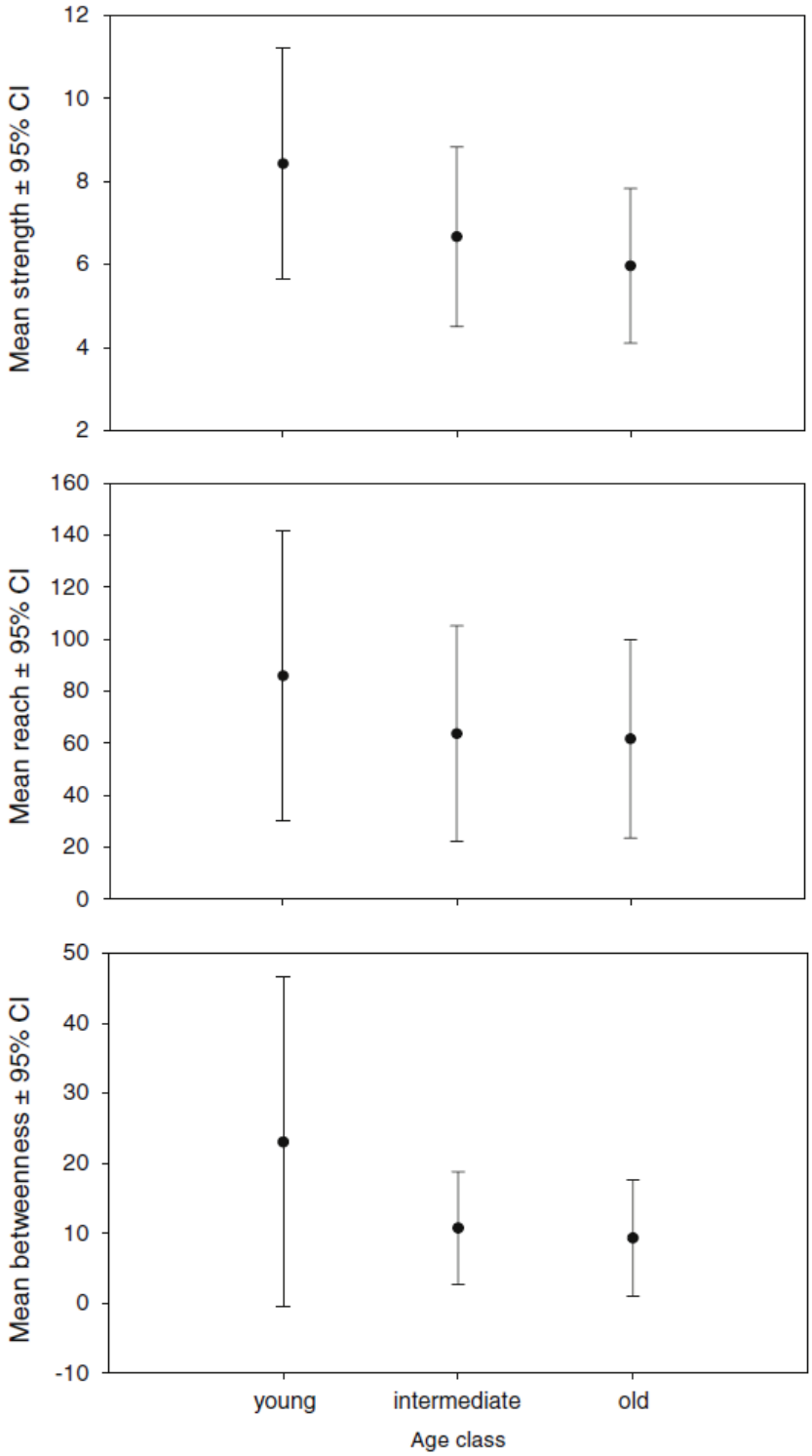

Figure 3.6 Mean (± 95% confidence intervals) strength, reach and betweenness for young, intermediate and old age classes for female northern long-eared bats (*Myotis septentrionalis*) observed from June to August, 2005-2007, in Dollar Lake Provincial Park, Nova Scotia, Canada.

3.4 DISCUSSION

Female northern long-eared bats showed inter-annual site fidelity to Dollar Lake Provincial Park where they formed preferred roosting relationships within dynamic groups. During the summer, females switched roosts almost daily but not all individuals moved together, resulting in labile group size and composition. Permutation tests, cluster analysis and network analysis showed that there were at least two distinct colonies (sensu Kerth 2008), or roosting areas (sensu Willis and Brigham 2004), in DLPP where females formed 11 groups. Similar to Bechstein's and big brown bats (Kerth and König 1999; Willis and Brigham 2004), females in one of these groups were located in a geographically distinct area of the park and were never observed roosting with members of the other groups and therefore may represent a distinct colony (Kerth and König 1999). The remaining groups, however, were interconnected via shared associations, and therefore belong to a single colony. Despite the dynamic nature of roost group composition, permutation tests indicated that females formed preferred associations. In fact, based on the larger sample sizes from 2006 and 2007 (53 and 42 individuals, respectively) in comparison to 2005 (26), pairs spent on average 25% of their days roosting together.

Within dynamic roosting groups, we found that preferred associations and social networks of female northern long-eared bats varied with reproductive period. Females spent proportionately more days roosting together and formed closer associations during gestation than lactation, as evidenced by higher HWI and strength. These patterns could arise either because females roost (a) infrequently with many individuals, (b) regularly with only a few individuals, or (c) regularly with many individuals. Average group size did not differ significantly between gestation and lactation, yet females were more closely associated, both directly and indirectly, during gestation. Thus, it appears females roosted regularly with fewer individuals during gestation. Willis and Brigham (2004) and Garroway and Broders (2007) found that big brown and northern long-eared bats, respectively, were more likely to associate with conspecifics during lactation than

gestation. Both studies compared specific pairwise associates observed during both reproductive periods whereas we compared group level averages obtained during the two periods. Thus, specific pairs of female northern long-eared bats may indeed be more likely to form preferred relationships during lactation while roosting with more individuals overall.

Because females have greater energetic demands during lactation (Speakman 2008) there should be more constraints on roost selection, and thus the number of suitable roosts, during this time (Garroway and Broders 2008; Willis and Brigham 2004). Therefore, passive mutual roost preferences for limited roosts, combined with preferences to roost with particular individuals, may produce differences in associations during gestation and lactation (Willis and Brigham 2004). However, roost switching, which is correlated with relative roost availability based on occupied roosts (Chaverri et al. 2007), did not differ between gestation and lactation in our study. This suggests that constraints on roost selection do not likely account for observed differences in association patterns. We suggest that additional mechanisms shaped these patterns. For instance, individual big brown bats save more energy from social thermoregulation than roost microclimate (Willis and Brigham 2007). It is possible that during lactation, when energetic constraints are highest, multiple groups come together, perhaps to benefit passively from social thermoregulation (Garroway and Broders 2007, 2008).

Preferred associations and social networks of female northern long-eared bats, may also vary with age, although the results were not significant based on non-overlapping 95% confidence intervals. Nevertheless, all of our measures, including HWI, strength, reach and betweenness, were higher for young females than for intermediate and old females. These patterns suggest that females of all age classes roosted more often with young individuals than other age classes and, consequently, young females had more direct and indirect connections. These patterns suggest that groups consisted primarily of many young individuals roosting with a few older individuals. These patterns cannot be explained by differences in the number of captures or PIT-tag records or the ability to detect different age classes due to differences in mortality. We only measured

associations among adults which typically experience low mortality (e.g., 11%) that does not vary over years (Tuttle and Stevenson 1982; Sendor and Simon 2003). Moreover, the strongest differences in association and network measures were between young and old age classes, which had roughly equal sample sizes and observations per individual.

Based on similarities between other studies and our observation that females of all ages associate more with younger individuals, we cautiously speculate about the biological meaning of these patterns in female northern long-eared bats to offer potential hypotheses for further testing. For example, this structure is consistent with some matrilineal societies, where groups consist of one or more matrilines comprised of an older female and multiple generations of her descendants, similar to those documented in other fission-fusion societies, such as elephants (Archie et al. 2006, 2008). Similarly, genetic evidence for Bechstein's bats suggests they may live in matrilineal groups (Kerth et al. 2000, 2002). In addition, while maternal relatedness does not appear to explain preferred associations among female big brown bats, it does play a role in dispersal events as related females disperse together to new areas (Metheny et al. 2008a,b). If female northern long-eared bats also live in matrilineal societies, we predict that maternal relatedness among individuals in groups would be greater than expected by chance.

Another possible interpretation of our observation that younger females had higher associations is that, regardless of whether they are matrilineal, young females may play a role in maintaining connections among individuals spread across multiple roosts, possibly facilitating information transfer or learning from older individuals (Boujarde et al. 2008; Cockburn et al. 2008; Durant 2000; Galef and Laland 2005; McComb et al. 2001). Similarly, it has been suggested that young individuals play a stabilizing role in response to changing group composition among bottlenose dolphins (*Tursiops* spp.; Lusseau and Newman 2004), Campbell's monkeys (*Cercopithecus campbelli*; Lemasson et al. 2005) and yellow-bellied marmots (*Marmota flaviventris*; Wey et al. 2008). Alternatively, young individuals may have little impact on the nature of the overall social structure as they may simply be more socially exploratory in an attempt to establish relationships.

Regardless of reproductive period or age, female northern long-eared bats formed both short and long-term relationships. Because winter behaviors were beyond the scope of our study, we treated the three summers as a continuous period and found that nearly half of all pairs likely remained together for as many as 75 consecutive days after they were first located. This, coupled with repeated observations of the same pairs over multiple summers, demonstrates that females maintain preferred associations across years and that hibernation does not disrupt preferred relationships among female bats. Maintaining short and long-term preferred relationships in a system where group composition is changing daily may be important in facilitating cooperation (Wilkinson 1987, 1992a; 1992b). Although we could not directly observe cooperative behaviors, evidence from other bat species that exhibit food sharing, allogrooming, allonursing and information sharing about suitable foraging and roosting sites demonstrates that cooperation does occur in this group of mammals (Bradbury 1977; Kerth and Reckardt 2003; Kerth et al. 2003; Kunz and Lumsden 2003; McCracken and Wilkinson 2000; Page and Ryan 2006; Ratcliffe and ter Hofstede 2005; Wilkinson 1984; 1986; 1992a,b; 1995; Wilkinson and Boughman 1998).

In general, our results were consistent with those of Garroway and Broders (2007) who used the same techniques to study the same population in 2005. Subtle differences can likely be attributed in part to differences in sampling and analyses. For example, in 2005, the proportion of days pairs roosted together was lower and fewer females maintained associations for an entire summer. Garroway and Broders (2007) had equally strong support for the two levels of casual acquaintances model, as well as the constant companions and casual acquaintances models. These differences are not likely biological, but instead are likely a result of fewer repeated observations among known individuals (26) over a shorter period in 2005 in comparison to 2006 (53) and 2007 (42). Despite these subtle differences between the studies, the overall interpretations remain the same – females live in dynamic groups where they form long-term preferred associations.

Among those studies that have quantified associations among bats, our analyses were most similar to those used to study Bechstein's bats (Kerth and Konig 1999). In comparing the two, our association values were lower (0.26 and 0.24 in 2006 and 2007, respectively) than those obtained for Bechstein's bats (0.39, 0.50, 0.46 across three years). The stronger associations among Bechstein's bats may be due in part to the fact that observations were based on fewer individuals (16, 17, 18 across three years) in comparison to our study (83 individuals). Nevertheless, despite differences in methodologies and absolute association values, the conclusions remain the same across studies – female bats form preferred relationships even though they live in dynamic groups (Garroway and Broders 2007; Kerth and König 1999; O'Donnell 2000; Popa-Lisseanu et al. 2008; Rhodes 2007; Vonhof et al. 2004; Willis and Brigham 2004).

As we gain a better understanding of sociality at summer roosts, it is clear that there is also a need to explore patterns of associations among bats at hibernacula to understand sociality of temperate bats at all life-history stages. A more detailed understanding of patterns of associations can then offer insight into population dynamics, such as dispersal patterns (Blanco and Cortes 2007) and disease transmission (Vicente et al. 2007). The potential spread of information and disease among giant noctule bats (*Nyctalus lasiopterus*), for example, depends on scale, where it may spread quickly within groups but less quickly between groups (Fortuna et al. 2009). These insights may be particularly important for northern long-eared bats which are currently facing extirpation in northeastern United States, and likely Canada, due to the recent outbreak of a poorly understood disease known as White Nose Syndrome (Blehert et al. 2009).

In conclusion, our data together with the literature from other bats and taxa reveal some emerging properties of fission-fusion societies. First, individual variation in characteristics, such as reproductive condition and age, influences interactions or association patterns among individuals. Individuals face different costs (e.g., disease transmission; Vicente et al. 2007) and benefits (e.g., nepotism, reciprocity and information transfer; Hamilton 1964a,b; Krützen et al. 2005; Ohtsuki et al. 2006; Trivers 1971; Wu et al. 2004), which also vary with group size and composition, thus affecting

individual tradeoffs of social living (Alexander 1974). Because groups are not homogenous, individuals seeking to maximize their own fitness by joining groups in accordance with their own demands will ultimately impact the tradeoffs for existing group members. This in turn will result in dynamic group structure as individuals join and leave groups in an effort to maximize their own fitness. Second, despite the highly dynamic nature of fission-fusion societies, relationships within them are stable over time, which likely facilitates cooperation among individuals. Of course, the interactions between these and environment likely also play an important role in shaping fission-fusion societies (Aureli et al. 2008; Chapman and Rothman 2009; Couzin 2006; Kerth 2008).

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CHAPTER 4
FEMALE NORTHERN LONG-EARED (*MYOTIS SEPTENTRIONALIS*) THAT ROOST TOGETHER ARE RELATED

The work presented in Chapter 4 is currently under revision:
Patriquin, KJ, Palstra, F, Leonard, ML, and Broders, HG. Submitted March 28, 2012. Female northern long-eared (*Myotis septentrionalis*) that roost together are related. Behavioral Ecology.

4.1 INTRODUCTION

Quantifying the social structure of animal groups, by determining who interacts with whom and how often, can help to identify the benefits gained by group living and provide insight into the evolution of sociality (Hinde 1976). Until recently, much of our understanding of animal sociality was restricted to stable kin groups (Hughes 1998). Some animals, however, have fission-fusion dynamics where individuals move freely between multiple small groups that periodically fuse to form larger social units that in turn separate (reviewed in (Aureli et al. 2008)). Unlike stable kin groups, the size and composition of groups with fission-fusion dynamics vary over space and time. Quantifying the type and frequency of associations can therefore be challenging, but necessary for understanding the causes and consequences of sociality and social diversity (Aureli et al. 2008; Kutsukake 2009).

While considered rare among most animals (Aureli et al. 2008), fission-fusion dynamics appear to be relatively widespread among the roughly 1,100 species of bats (Kunz and Lumsden 2003; Simmons 2005; Kerth 2008), making them good models for exploring the evolution of these dynamics. For instance, during the summer, females of many temperate species form maternity colonies in tree cavities where they roost during the day and raise offspring (Lewis 1995; Kunz and Lumsden 2003). The few studies that have quantified the social structure of these maternity colonies show that a single colony is composed of multiple roost-groups that vary in size and composition as females move among roosts on a daily basis. Yet, despite frequent roost-switching, some female pairs

roost together more often than expected by chance, often for months or years (Garroway and Broders 2007; Kerth 2008; Patriquin et al. 2010; Kerth, Perony, and Schweitzer 2011). Opportunities for cooperation are more likely between these relatively stable, familiar pairs that may interact regularly in an otherwise dynamic system (Trivers 1971). If these pairs are also kin, there may be opportunities to also gain inclusive fitness benefits through nepotism (Hamilton 1964; Maynard Smith 1964).

The focus in the few studies examining relatedness among bats with fission-fusion dynamics has been on determining average relatedness within colonies and roost-groups. Evidence from mtDNA markers (i.e., maternally inherited) indicates that colonies typically consist of only a few matrilines that differ from neighbouring colonies (Kerth, Mayer, and König 2000; Kerth, Safi, and König 2002; Vonhof, Strobeck, and Fenton 2008; Kerth and Van Schaik 2011). Evidence from nuclear markers (i.e., bi-parentally inherited) also shows that individuals within colonies are not more closely related than individuals in adjacent colonies and that average nuclear relatedness within roost-groups is generally low (Burland et al. 1999; Kerth, Safi, and König 2002; Rossiter et al. 2002; Metheny, Kalcounis-Rueppell, Willis, et al. 2008). Comparatively little is known, however, about relatedness of familiar pairs within these roost-groups.

Familiar pairs offer stable social relationships over time, which may be especially important in fission-fusion systems where group composition changes almost daily. It is at this level, therefore, that selection for cooperation is most likely to occur in these highly dynamic systems (Hamilton 1964; Maynard Smith 1964; Trivers 1971). Thus, to fully understand the potential for cooperation and hence gains to inclusive fitness, relatedness between familiar pairs must be determined. Only two studies to date have examined genetic relatedness between familiar female pairs within bat fission-fusion groups instead of focusing solely on average relatedness at the colony or roost-group level. Both studies found that familiar pairs were not more closely related than random pairs of females (Kerth and König 1999; Metheny, Kalcounis-Rueppell, Willis, et al. 2008). These studies, however, had some limitations as they had genetic samples from

relatively few group members. Also, in one instance (Kerth and König 1999), all possible pair-wise relationships were not examined for those females that were sampled.

Our main goal was to determine the genetic relationships between familiar pairs of female northern long-eared, *Myotis septentrionalis*, by directly correlating the time pairs spent together with their estimated pair-wise relatedness for all known pairs. In addition, keeping in part with previous studies of fission-fusion dynamics in bats and other taxa, we also examined the genetic relationships among females at broader social levels, including colonies and social groups. Females in our study area show fission-fusion dynamics and appear to live in at least two independent colonies, each composed of multiple groups of females that roost together during the day (Garroway and Broders 2007; Patriquin et al. 2010). While roost-group size and composition change daily, over the long-term some females are found in the same roost-groups more often than expected by chance (hereafter referred to as social groups). Within these social groups, some pairs form relatively stable relationships that can last for months or years (Garroway and Broders 2007; Patriquin et al. 2010). Based on samples collected from most of the known females in the study area, we use nuclear and mtDNA markers to determine the genetic relationships among females within colonies and social groups, and between pairs.

4.2 METHODS

4.2.1 Capture and marking

We conducted our study in Dollar Lake Provincial Park (DLPP), Nova Scotia, Canada (44°55' N, 63°19' W; see (Garroway and Broders 2007) for site description) from June to August, 2005 – 2007. We captured bats using mist-nets (Avinet, Dryden, New York, USA) and harp traps (Austbat Research Equipment, Lower Plenty, Victoria, Australia). We used a sterilized 3 mm biopsy punch to obtain a tissue sample from both wings of all captured adult females, including those whose social relationships were previously quantified, as described above. Biopsies were stored in 95 % ethanol and refrigerated. Previous studies have successfully used similar methods with no reported cases of mortality, morbidity, or impact on behaviour (Kunz and Parsons 2009).

4.2.2 DNA Extraction and genotyping

We successfully extracted DNA from 71 of the 83 females from the known social groups described in (Patriquin et al. 2010), 64 of which had complete genotypes at each of four microsatellite loci used previously for other *Myotis* species (Table B1; Kerth et al. 2002), including *M. septentrionalis* in other regions (Arnold 2007) and were also tested for use in another study with *M. septentrionalis* in our region (L Burns, personal communication). We also sequenced the hypervariable II portion of the control region (HVII) of mitochondrial DNA (mtDNA) using previously developed primers (Fumagelli et al. 1996, Castella et al. 2001). Samples were not available for the remaining 12 of the 83 individuals. DNA was extracted from an additional 43 females for which we had no social information (see (Patriquin et al. 2010)) but were sampled within the same study area to establish baseline allele frequencies (see below). For details on DNA extraction, genotyping, and sequencing, see Appendix B.

4.2.3 Statistical analyses

To quantify bi-parental relatedness, we used Ritland's kinship coefficient to estimate the probability that two alleles are identical by descent based on allelic frequencies from nuclear loci of the 114 females sampled from our study area (SPAGeDi 1.3f, (Hardy and Vekemans 2009)). Although most studies have typically used Queller and Goodnight's (1989) coefficient of kinship to investigate relatedness in bats (e.g., Wilkinson 1992, Burland et al. 2001, Kerth et al. 2002, Rossiter et al. 2002, Veith et al. 2004, Metheny et al. 2008, Bohn et al. 2009), we argue Ritland's coefficient is more appropriate for these types of studies. By using Ritland's estimator and reference allele frequencies from within our study area, we improved our power to detect structure in small samples compared to other estimates of relatedness and minimized the likelihood of artificially high estimates of relatedness (Ritland 1996; Lehmann and Rousset 2010). Nevertheless, we also used this estimator to assess relatedness in our population to allow comparison across studies. However, to determine which estimator was appropriate for our study, we performed a series of simulations to compare different estimators (see Appendix B for details). Ritland's coefficients of kinship are based on weighted probabilities and therefore range from -1 to +1, rather than yielding values that would be easily translated

into relationship-types such as half-siblings (0.25) or full siblings (0.5) (Van de Casteele, Galbusera, and Matthysen 2001). Thus, it is speculative to assign a particular relationship-type to any observed kinship coefficients.

Because individuals were not sampled randomly, we performed a series of randomization tests (SPAGeDi 1.3f) to test whether average relatedness among the 64 females that were successfully genotyped at all loci deviated from random. Genotypes were permuted (10,000 times) among individuals. For this and all subsequent permutation tests, observed values were significantly greater than random ($p < 0.05$, one-tailed) if they were greater than the randomized values on 95% or more permutations.

To determine whether females within colonies and social groups were more related at the nuclear level than expected by chance, individuals were permuted (10, 000 times) either among colonies or social groups, respectively. Nine of the 64 females were excluded from the permutations between colonies as they were not previously identified as belonging to either of the two suspected colonies (Patriquin et al. 2010). In addition, solitary individuals and social groups that consisted of only pairs were excluded from the permutations among social groups, leaving 4 groups with 3, 6, 11, and 19 females, for analysis. While many studies assess the significance of F or R statistics (Fst and Rst) which estimate variance in relatedness between groups, these estimates of population structure are less informative when using microsatellites, particularly for populations where migration rates are low relative to mutation rates (Balloux and Lugon-Moulin 2002). Fst and Rst estimates are thus not likely suitable for addressing population structure of summer populations of non-migratory species of bats in temperate regions as they show strong site fidelity and thus have lower than average migration rates (Burland et al. 1999; Rossiter et al. 2002; J.P. Veilleux and S.L. Veilleux 2004; Perry 2011).

To determine whether females within colonies and social groups were more related at the maternal level than expected by chance, we used ClustalX 2.1 (Thompson et al. 1997) to first group individuals by haplotype according to shared mtDNA sequences; different haplotypes, and hence matrilines, were defined by base substitutions in the consensus

sequence. We then used a chi-square test to compare the observed proportion of haplotypes within each colony or social group to that expected under a random distribution. The expected proportion for each haplotype within a colony or social group was calculated by dividing the number of individuals that possessed each haplotype by the total number of individuals within each colony or social group. In addition, we determined whether females belonging to the same matriline were also closely related at nuclear loci using permutation tests, as described above, except here individuals were permuted among matrilines.

Finally, to determine whether familiar pairs were closely related at the nuclear level, we used SOCPROG 2.4 (Whitehead 2009) to test whether there was a relationship between a matrix of average pair-wise association values (half-weight index, HWI; see (Patriquin et al. 2010) for details) across all pair-wise combinations for the 64 genotyped females and the matrix of pair-wise kinship coefficients for all 64 individuals. We determined correlation coefficients between matrices and compared these to a randomly permuted distribution of correlations (10, 000 permutations). To determine whether pairs that spent more time together were more closely related at the maternal level, we performed a two-group randomization test in SAS version 9.2 (SAS 2008). We calculated the time each individual spent with females from the same matriline and compared that to the time they spent with females from different matrilines. We then compared the observed difference between the average of these two values to a permuted distribution (10, 000 permutations).

4.3 RESULTS

Simulation tests indicated that Ritland's (1996) coefficient of kinship performed marginally better than Queller and Goodnight's (1989) relationship coefficient (Table 4.1). Though absolute estimates of relatedness differed between the two estimators of relatedness, the general trends were the same (Tables 4.2 and 4.3), with the exception of patterns among familiar pairs (see below). Therefore, because patterns were similar for both estimators, and because Ritland's outperformed Queller and Goodnight, we will

discuss only the results obtained using Ritland's estimator. We will, however, discuss the differences between the two estimators when we address relatedness of familiar pairs.

Although average pair-wise relatedness among all 64 females was greater than zero, indicating that some individuals likely shared alleles through common descent, it was not significantly greater than expected by chance (p = 0. 088, Table 4.2). Pair-wise relatedness was highly variable, as the matrix of all pair-wise kinship coefficients for all 64 females showed values ranging from -0.046 up to +0.393 (Figure 4.1). There were four haplotypes distributed among females: Haplotype A was shared by 43% of the females, while Haplotype B and C were shared by 38% and 17% of the females, respectively. Haplotype D was found in only one female, which was omitted from further analyses of maternal relationships (Figures 4.2; see Appendix Tables B2 and B3 for consensus sequence and haplotypes).

Average pair-wise nuclear relatedness across all individuals in both colonies (n= 55 individuals) and across all four social groups (n = 39 individuals) was negative and zero respectively, indicating that the likelihood of shared alleles through common descent was low in both cases. Similarly, average nuclear relatedness within each colony and social group was not significantly higher than between colonies or among social groups (colony: p = 0.260; social group: p = 0. 068; Table 4.2), suggesting that females within each colony or social group were not more closely related to one another than expected by chance. At the maternal level, there was overlap in haplotype distribution between the two colonies, but each colony also had a unique haplotype and the proportion of haplotypes within each of the two colonies differed significantly (χ^2= 16.42, d.f. = 3, upper critical value = 7.82, p = 0.001; Figure 4.2). There was, however, no significant difference in the proportion of haplotypes shared by the females within each social group (χ^2= 7.14, d.f. = 6, upper critical value = 12.59, p = 0.308). Average nuclear relatedness across matrilines was low but greater than zero, indicating that some females within matrilines shared alleles. Average nuclear relatedness also differed for each matriline and was significantly higher within than among matrilines (p = 0.007; Table 4.2), indicating females within the same matriline were more likely to share alleles.

Based on Ritland's coefficient of kinship, there was a small but significant and positive correlation between pair-wise association and pair-wise nuclear relatedness (matrix correlation coefficient = 0.048; p = 0.019; Figure 4.1). However, based on Queller and Goodnight's relationship coefficient, there was no significant correlation between pair-wise association and pair-wise nuclear relatedness (matrix correlation coefficient = 0.031; p = 0.134; Figure 4.1). Pairs of females from the same matriline spent significantly (18 permutations greater than observed mean difference in HWI, p = 0.0018) more time together ($\bar{X}$ HWI ± SD = 0.14 ± 0.26) than did pairs of females from different matrilines ($\bar{X}$ HWI ± SD = 0.10 ± 0.18).

Table 4.1 Correlation coefficients of each relatedness estimator compared to the true value for each simulated structure.

Simulated structure	Ritland	QuellerGt
Twins	0.694	0.615
Parent-offspring	0.458	0.385
Full-siblings	0.468	0.403
Half-siblings, grandparent-grandchild	0.337	0.224
Double-first cousins	0.199	0.179
First cousins	0.099	0.082
Second cousins	-0.008	-0.003
Unrelated	0.564	0.478
Combination 1*	0.564	0.478
Combination 2**	0.327	0.303
Combination 3***	0.321	0.238

Simulations with the highest correlation coefficient are the best estimators for that structure.
* 0.25 twins + 0.25 parent-offspring + 0.25 full siblings + 0.25 half siblings
** 0.25 parent-offspring + 0.25 full siblings + 0.25 half siblings + 0.25 unrelated
***0.187 parent-offspring + 0.156 full siblings + 0.156 half siblings
+ 0.156 first cousins + 0.156 second cousins + 0.187 unrelated

Table 4.2 Observed and permuted average pair-wise kinship coefficient (Ritland 1996)) for all genotyped female northern long-eared, *Myotis septentrionalis*, in Dollar Lake Provincial Park, Nova Scotia (2005-2007), as well as those within colonies, social groups, and matrilines.

		Kinship coefficient		
Comparison	n	Observed (SE)	Permuted	p
all individuals	64	-0.002 (0.001)	-0.003	0.088
among colonies	55	-0.003 (0.001)	-0.003	0.260
within colony 1	49	0.008 (0.008)	n/a	n/a
within colony 2	6	0.010 (0.115)	n/a	n/a
among social groups	39	0.000 (0.001)	-0.004	0.068
within group 8*	6	-0.013 (0.008)	n/a	n/a
within group 10*	11	-0.008 (0.004)	n/a	n/a
within group 11*	19	0.004 (0.001)	n/a	n/a
among matrilines	55	0.002 (0.002)	-0.003	0.007
within matriline A	11	0.012 (0.007)	n/a	n/a
within matriline B	26	0.006 (0.003)	n/a	n/a
within matriline C	28	-0.002 (0.003)	n/a	n/a

* group labels refer to those used in (Patriquin et al. 2010); these represent a subset of groups (those with larger sample sizes) included in the among group analysis and are presented here to illustrate variation in within group estimates

n/a = permutation tests of significance are irrelevant at this level as we are not interested in differences between specific groups.

Table 4.3 Observed and permuted average pair-wise relationship coefficient (Queller & Goodnight 1989) for all genotyped female northern long-eared, *Myotis septentrionalis*, in Dollar Lake Provincial Park, Nova Scotia (2005-2007), as well as those within colonies, social groups, and matrilines.

		Relationship coefficient		
Comparison	n	Observed (SE)	Permuted	p
all individuals	64	0.004 (0.006)	0.004	0.497
among colonies	55	0.004 (0.003)	0.003	0.348
within colony 1	49	0.004 (0.005)	n/a	n/a
within colony 2	6	0.032 (0.036)	n/a	n/a
among social groups	39	0.008 (0.006)	-0.002	0.132
within group 8*	6	-0.026 (0.034)	n/a	n/a
within group 10*	11	-0.023 (0.025)	n/a	n/a
within group 11*	19	0.020 (0.006)	n/a	n/a
among matrilines	55	0.017 (0.008)	0.004	0.019
within matriline A	11	0.054 (0.019)	n/a	n/a
within matriline B	26	0.021 (0.008)	n/a	n/a
within matriline C	28	0.008 (0.014)	n/a	n/a

* group labels refer to those used in (Patriquin et al. 2010); these represent a subset of groups (those with larger sample sizes) included in the among group analysis and are presented here to illustrate variation in within group estimates

n/a = permutation tests of significance are irrelevant at this level as we are not interested in differences between specific groups.

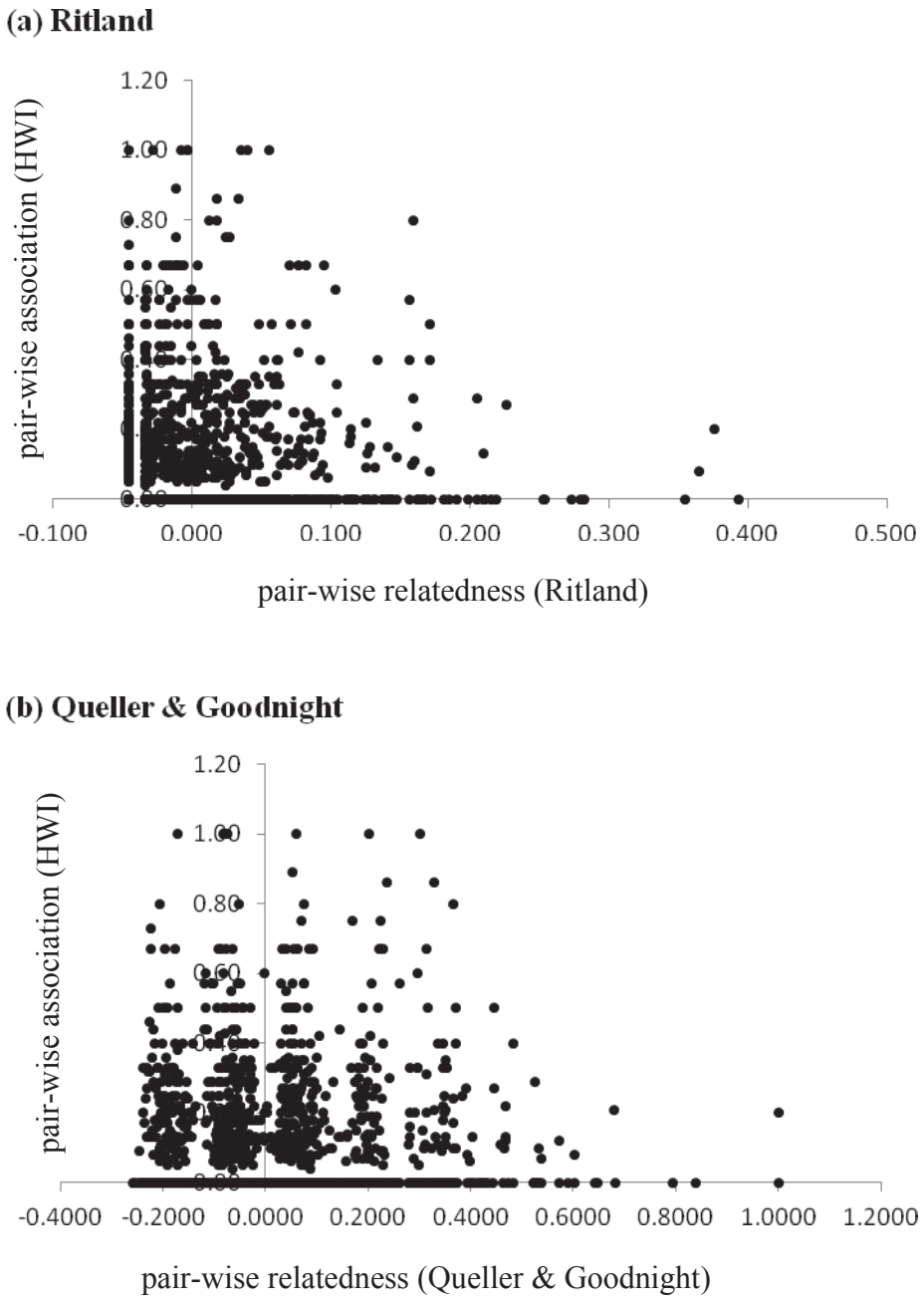

Figure 4.1 Relationship between pair-wise relatedness and pair-wise association among female northern long-eared bats (*Myotis septentrionalis*) in Dollar Lake Provincial Park, Nova Scotia (2005-2007).

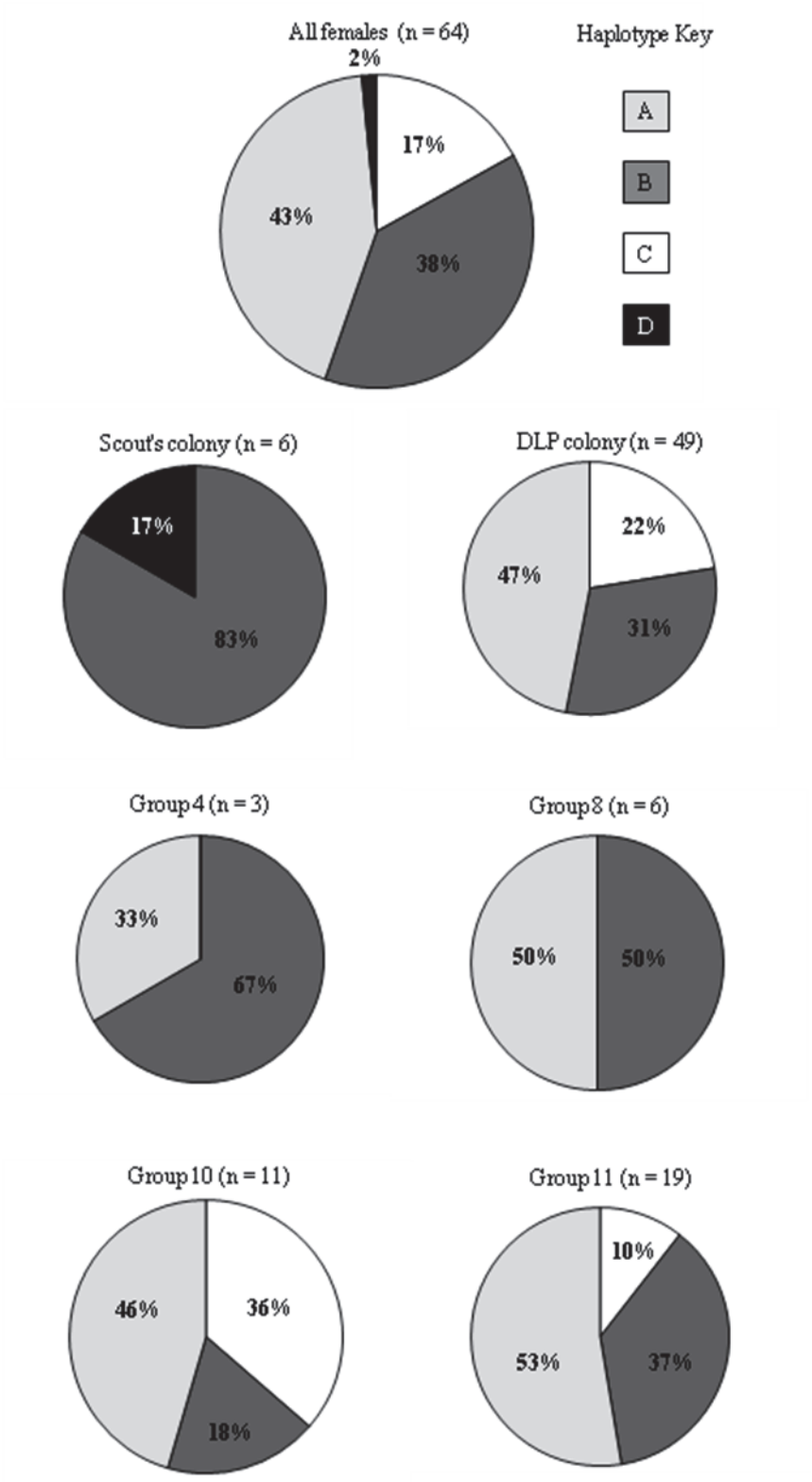

Figure 4.2 Haplotype distribution of female northern long-eared, *Myotis septentrionalis*, within Dollar Lake Provincial Park, Nova Scotia, colonies, and social groups (2005-2007).

4.4 DISCUSSION

Overall, female northern long-eared bats at our study site were not more related to one another than expected by chance at the nuclear level and the same held true across colonies and social groups. Failure to detect genetic structure in this case is not likely a result of limited power because our simulation results suggest that the high allelic richness at four loci gives sufficient power to detect genetic structure, if it exists.

Females within each of our two colonies were no more closely related to one another at the nuclear level than to females in the neighbouring colony, but they were in fact more closely related at the maternal level. Colonies appear to be founded by females that share a matriline and are therefore more likely to be genetically distinct at the maternal level (Metheny, Kalcounis-Rueppell, Bondo, et al. 2008), supporting the behavioural observation that there are at least two distinct colonies in DLPP (Patriquin et al. 2010). It is difficult to compare values of relatedness across studies because they are calculated in different ways (Lehmann and Rousset 2010). However, the pattern in our study is consistent with low differentiation among colonies at the nuclear level but strong differentiation at the maternal level found in several other temperate bats with fission-fusion dynamics (Wilkinson 1992; Burland et al. 1999; Castella, Ruedi, and Excoffier 2001; Kerth, Safi, and König 2002; Metheny, Kalcounis-Rueppell, Willis, et al. 2008; Flanders et al. 2009; Kerth and Van Schaik 2011). This has been attributed to a high level of mixing during mating at hibernacula before hibernation and strong female natal philopatry to summer areas following hibernation (Kerth, Mayer, and König 2000; Burland and Worthington Wilmer 2001; Kerth, Mayer, and Petit 2002; Kerth and Morf 2004; Veith et al. 2004; Metheny, Kalcounis-Rueppell, Willis, et al. 2008). Female philopatry may then promote a high degree of maternal relatedness within colonies where average nuclear relatedness may otherwise be low (Storz 2009).

While previous studies have considered relatedness within roost-groups, we have instead examined relatedness in social groups (Burland et al. 1999; Kerth and König 1999;

Rossiter et al. 2002; Metheny, Kalcounis-Rueppell, Willis, et al. 2008). Social groups differ from roost-groups in that roost-groups represent females that are found in the same roost on a particular day whereas social groups represent females that are repeatedly found in the same roost-groups over time (Patriquin et al. 2010). Genetic relationships within social groups may then provide a better understanding of longer-term social relationships compared to roost-groups, which change on a daily basis. We found that females within social groups were not more closely related than across social groups, either at the nuclear or maternal level, suggesting that relatedness may not be important to longer-term social relationships at this level. By contrast, sperm whales, *Physeter macrocephalus*, and African elephants, *Loxodonta africana*, within comparable social units are related at the maternal level, and, in the case of elephants, are also closely related at the nuclear level (Archie, Moss, and Alberts 2006; Archie et al. 2008). It is not clear why female northern long-eared form social groups, but they may benefit from information sharing about suitable roosts and foraging sites, as suggested for females within roost-groups (Wilkinson 1992; Kerth and Reckardt 2003; Metheny, Kalcounis-Rueppell, Willis, et al. 2008). Alternatively, social groups may reflect shared preferences for roosts that provide optimal conditions for gestation, nursing, and pup development (Metheny, Kalcounis-Rueppell, Willis, et al. 2008).

Perhaps most importantly, by looking at relatedness between all genotyped pairs, we were able to demonstrate that, while average relatedness among group members was low, familiar pairs of females (i.e., particular females that frequently roosted together) were indeed more closely related than expected by chance at both the nuclear and maternal level according to Ritland's (1996) kinship coefficient. By contrast, when using Queller and Goodnight's (1989) relationship coefficient, we found that familiar pairs were not more closely related at either level, which is consistent with other studies that used the same estimator (Kerth and König 1999; Metheny, Kalcounis-Rueppell, Willis, et al. 2008). However, simulation tests suggested Ritland's estimator is more appropriate for our data than Queller and Goodnight's estimator. These results suggest that had previous studies performed simulation tests and perhaps selected a more appropriate estimator for their populations they may have also found that familiar pairs were closely related.

Our findings, however, are consistent with those found for pairs of African elephants that also showed a strong correlation between relatedness and time spent together (Archie, Moss, and Alberts 2006). Our results suggest that the potential exists for cooperation between related female pairs in this dynamic system (Hamilton 1964). While we did not directly observe interactions between females, examples of cooperation among bats exist, including food sharing, allogrooming, allonursing, pup guarding, as well as information sharing about suitable foraging and roosting sites (Kerth 2008).

Our findings illustrate the biological and practical importance of investigating genetic relationships between familiar pairs in fission-fusion systems and for selecting appropriate estimators to addess these questions. That familiar pairs are indeed related suggests the potential for kin selection to play a role in shaping these systems; a result that may have been overlooked had only average nuclear relatedness at the colony or social group level been considered. Because colonies and groups are comprised of a mixture of related and unrelated individuals, averages across this variation will not be high and will lose information about the strength of relatedness of specific pairs. As a result, the potential for kin selection may not be detected. In addition, relationships at the pair-wise level may be overlooked when inappropriate estimators or relatedness are selected. Because selection acts on individuals, rather than at the group level, we encourage future studies exploring fission-fusion dynamics to explicitly address pair-wise relationships and to perform relevant tests to determine appropriate estimators for their populations.

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CHAPTER 5
THE POTENTIAL FOR CULTURE IN BATS

Many of us have an intuitive sense of what it means to have culture and would agree that it is observed in humans; yet, whether nonhuman animals (animals hereafter) also have culture is much debated. Humans are considered to have culture because groups differ in traditions (learned behaviours that persist over time, McGrew 2009), such as different hunting strategies, religions and languages (Richerson & Boyd 2005). There are also examples of traditions in animals, such as potato-washing by Japanese macaques, *Macaca fuscata*, found only in groups on Koshima Island (de Waal 2001). However, there is considerable debate over whether animals, like humans, also display culture and, if so, whether it is analogous or homologous to human culture (Laland & Galef 2009). Much of this debate stems from a lack of consensus on how to define culture (Laland & Galef 2009, Wagner & Danchin 2010).

Definitions of culture vary from general to specific, which, in turn, can significantly influence whether animals are considered to have culture. More general definitions state that animals have culture when groups differ in learned behaviours (Table 1). By these definitions, Japanese macaques have culture because only those living on Koshima Island perform the potato-washing behaviour and naive individuals learn through observation of other group members (de Waal 2001). Alternatively, more specific definitions maintain that animals have culture if groups differ in repertoires of learned behaviours that are performed stereotypically (Table 1). According to these definitions, then, macaques would not have culture if potato-washing was the only learned behaviour that differed between groups. As it turns out, though, Japanese macaques stereotypically perform a repertoire of learned behaviours, including wheat washing and eating, bathing, and fish-eating (deWaal 2001, Hirata et al. 2002) and therefore would also meet the more specific definitions. Clearly, defining culture is a necessary first step before determining whether it occurs in animals.

Animal culture was recently reviewed in Laland & Galef (2009); yet, a consensus on how to define culture was never reached and one particular group of animals, bats, was noticeably absent from the review. Thus, the purpose of my paper is to first review several proposed definitions of culture, drawing primarily from Laland & Galef (2009) and supplementing with additional examples from recent studies focusing on mammals. Based on this review, I will then provide a working definition of culture with which to explore the potential for culture in bats.

Bats share a number of similarities with the more common subjects of animal culture studies, namely primates and cetaceans. For example, all three taxa show group differences in behaviours and a capacity to learn from conspecifics, along with other features often associated with culture, including long life spans and fission-fusion societies (e.g., Whiten et al. 1999, Rendell & Whitehead 2001, Barclay & Harder 2003, Fragaszy & Perry 2003, Perry et al. 2003, van Schaik et al. 2003, Krützen et al. 2005, Kerth 2008). Yet, despite these similarities, the question of whether bats have culture has yet to be explored. Determining whether bats have culture can in turn offer insight into its influence on their fitness, population structure and evolution, all of which will be discussed below.

5.1 DEFINING CULTURE

To test whether animals have culture and to make informative standardized comparisons across species, it is first necessary to establish a clear definition (Whiten 2005). A review of the animal literature reveals nearly 50 definitions of culture, ranging from general to specific (Table 1). Within this range of definitions, there are key reoccurring conditions that are associated with culture, including: (1) groups differ in socially-learned behaviours, (2) behaviours are social, and (3) behaviours are learned specifically through teaching and imitation (Table 1). Below, I critically review each condition and indicate if and how it will be included in the definition of culture that I will use. Certainly some definitions of culture include a fourth condition that behaviours must ratchet (Table 1), whereby new generations build on existing traditions (i.e., cumulative cultural evolution, Boyd & Richerson 1995, or the ratchet effect, Tomasello 1994; reviewed in Caldwell &

Millen 2008). However, this condition is much less common in definitions of animal culture and is therefore not included in my review and the importance of ratchet-effect in culture has been reviewed by several others (e.g., Caldwell & Millen 2008, Marshall-Pescini & Whiten 2008, Tennie et al. 2009, Whiten et al. 2009).

5.1.1 Groups Differ in Socially-Learned Behaviours

Group differences in socially-learned behaviours is one of the few conditions consistently included in definitions of culture (Table 1). Here, the behaviour must be performed by most individuals within a group, or subgroup (e.g., "cliques"), rather than be idiosyncratic (restricted to only a few individuals). Group members perform the same behaviours because they have learned them from each other (through social facilitation, local enhancement, mimicking, emulation learning or imitation, for example) and not because they share genes which code for those behaviours, or because they all independently converged on behaviours that were optimal under particular ecological conditions (Kummer 1971, Whiten & Ham 1992, Heyes 1994, deWaal & Bonnie 2009, McGrew 2009). Group differences in behaviours should then occur because different groups learn different behaviours, rather than because they have different genetic structures or different ecologies. In reality, however, teasing apart the influence of social learning, genetics, and ecology on behaviour is difficult. One approach has been to exclude the influence of genetics and ecology on behaviour, leaving social learning as the logical explanation for behavioural differences between groups (McGrew 1998, van Schaik 2003, van der Post & Hogeweg 2009).

A variety of animals show group differences in behaviour that appear to be due to social learning because the alternative influences of genetics and ecology have been ruled out. For example, bottlenose dolphins (*Tursiops* spp) living in Shark Bay, Australia, but not elsewhere in their range, carry sponges on their noses, presumably to help "ferret prey from the sea floor" (Mann et al. 2008). A single matriline performs this behaviour, which suggests a possible genetic influence. Yet, not all individuals within the matriline carry sponges and a few individuals from other matrilines also carry sponges (Krützen et al. 2005), suggesting that genetics may explain some of the behaviour but it does not

adequately explain group-level differences (Mann & Sargeant 2003, Sargeant et al. 2007). Individuals also generally carry sponges in deep channels, which suggests that the behaviour may be correlated with channel depth and thus influenced by the environment; yet, they do not carry sponges every time they are in channels, thus suggesting environment cannot explain the use of sponges in this group (Krützen et al. 2005, Sargeant et al. 2007). Indeed, a multivariate analysis of the relationship between foraging strategies and ecology, genetics, and social relationships of dolphins in Shark Bay showed that social learning, rather than ecology and genetics, best explained sponge carrying in this population (Sargeant & Mann 2009). Thus, because genetics and ecology do not adequately explain group behaviour, social learning is the most likely explanation for this behaviour. A similar approach has been used to explain group differences in behaviour in other species, such as tool use in chimpanzee groups (*Pan troglodytes*) (Goldberg & Ruvolo 1997, Goldberg & Wrangham 1997, Gruber et al. 2009).

Although the influence of genetics and ecology on group behaviour may be ruled out in some cases, in reality it is often difficult to disentangle the influence of these three factors because they are often inextricably linked. For example, individuals may possess a genetic predisposition to learn, and to engage in, a particular behaviour (e.g., Scharff & White 2004), which may in turn be influenced by ecological conditions; different forms of a behaviour, however, may spread within a group through social learning. The grooming handclasp, for instance, is a specific grooming posture that occurs in both wild and captive chimpanzee populations (McGrew & Tutin 1978, deWaal & Seres 1997), which suggests the behaviour may be influenced by genetics. Ant-retrieval techniques in the same species appear to have been partially influenced by differences in the ecology of their ant prey (reviewed in Galef 2009). Both behaviours, however, have spread within chimpanzee groups through social learning, resulting in group differences in behaviour (deWaal & Seres 1997, McGrew 1998, Möbius et al. 2008, Schöning et al. 2008).
In summary, genetics and ecology may influence the likelihood that a behaviour is learned. However, learning may determine whether a behaviour spreads within one group and not others. Therefore, I accept the first condition of culture that there must be group differences in behaviour and that these differences must be shaped by social

learning. However, I relax the more specific requirement that these behaviours cannot be correlated with genetics and ecology (Perry et al. 2003, Kendal et al. 2009).

5.1.2 Behaviours are Social

A second condition of culture is that learned-behaviours must be social; yet, defining what constitutes "social" in a cultural context is nearly as challenging as defining culture itself. Generally, social behaviours are defined as interactions among conspecifics (Wilson 1975), whereas some definitions of culture specify that social behaviours must also be arbitrary, normative, and symbolic of group identity (Table 1). While normative and symbolic behaviours are likely important to culture, as discussed below, whether behaviours must in fact be arbitrary is a matter of debate.

Strictly adhering to the definition that behaviours must be arbitrary, in that they are non-functional behaviours because they do not directly improve survival or reproductive success (Galef 1992, de Waal and Bonnie 2009), may be too stringent given that seemingly arbitrary behaviours can in fact affect fitness and functional behaviours may also be social. For example, the grooming handclasp performed by chimpanzees is regarded as arbitrary because the posture itself does not serve a practical function, such as improved grooming, but instead strictly communicates the strength of social relationships (McGrew & Tutin 1978, McGrew et al. 2001, Nakamura 2002, Perry et al. 2003, Bonnie & de Waal 2006). However, failure to perform social behaviours can have significant fitness consequences, as failure to maintain social bonds may limit access to information on resources gathered by other group members (Perry et al. 2003, McNamara & Dall 2010), reduce attractiveness to mates (Danchin & Wagner 2010), and incite punishment (Hauser 1992). These actions, in turn, result in lost foraging opportunities (Hauser 1992), reduced reproductive success, limited social learning (van Schaik 2003) and pain (MacDonald & Leary 2005). While grooming in general is not considered arbitrary because it serves a functional, hygienic role that may improve survival, it also serves a significant social role for some species by strengthening social bonds and group cohesion (Koyama et al. 2006, Lehmann et al. 2007, Kutsukake et al. 2010) and therefore functional behaviours could be cultural. Similarly, groups may differ with respect to

which functional behaviours they use, which may be arbitrarily established within groups. For example, chimpanzees could use several options to remove honey from a log, such as a finger, stick or leaf; yet, which option they choose depends on socially acquired and reinforced preferences, and thus chimpanzee groups differ arbitrarily in tool preferences (Gruber et al. 2009). Thus, seemingly arbitrary and functional behaviours can both play important social roles and therefore they both have the potential to have cultural significance. Consequently, a definition of culture requiring that social behaviours be strictly "arbitrary" is overly stringent provided behaviours are normative and symbolic of group identity.

Normative and symbolic behaviours are central to culture because they maintain group differences, allowing group members to recognize one another, which can have significant fitness consequences. Normative behaviours are those that are repeated by the majority of group members to conform to group norms and are thought to strengthen social bonds (Perry et al. 2003, Whiten 2009). These behaviours can then become symbolic of group identity because individuals use them to identify group members and to discriminate against unfamiliar conspecifics (Laland et al. 2000, Whiten et al. 2005, Leca et al. 2007, Gruber et al. 2009, Thornton & Malapert 2009). Failure to conform to group norms can in turn result in significant costs. For example, failure to maintain social bonds may limit access to information on resources gathered by other group members (Perry et al. 2003, McNamara & Dall 2010), reduce attractiveness to mates (Danchin & Wagner 2010), and incite punishment (Hauser 1992). These actions, in turn, result in lost foraging opportunities (Hauser 1992), reduced reproductive success, limited social learning (van Schaik 2003) and pain (MacDonald & Leary 2005). Thus, group members continue to perform similar behaviours, thus maintaining differences between groups. Therefore, normative and symbolic behaviours are important to culture because they allow group members to recognize one another and maintain group differences.

In summary, while arbitrary behaviours, such as gestures, may not directly improve survival or reproduction, failure to perform behaviours according to group norms can have significant fitness costs. Moreover, seemingly functional behaviours that may

directly affect fitness, such as foraging practices, can also be normative and symbolic of group identity (deWaal 1998, 2001; Perry 2009; Pesendorfer et al. 2009; Whiten & van Schaik 2007; Whiten 2009). Therefore, I accept the second condition of culture that social behaviours are normative and symbolic. However, I relax the more specific requirement that these behaviours must be arbitrary because social behaviours do in fact affect fitness and because functional behaviours can also be normative and symbolic.

5.1.3 Behaviours are Learned Specifically through Teaching and Imitation

Though less common, some definitions of culture include a third condition that behaviours must not only be learned socially, but they must be learned specifically through teaching and imitation (Table 1), where experienced individuals correct the behaviour of naive individuals and naive individuals in turn imitate the "specific motor patterns" of the behaviour (Laland et al. 2009). The reason this mechanism is thought to be important is because, unlike other social learning mechanisms (e.g., social facilitation, local enhancement, and emulation), it is thought to promote the spread of normative and symbolic behaviours, which should be stereotyped (repeated faithfully) so individuals can more easily detect deviations from group norms (Mundinger 1980, Nishida 1987, Russell & Russell 1990, Heyes 1993; Tomasello 1994, 2009; Boesch 1996, Rendell & Whitehead 2001, Horner et al. 2006, Marino et al. 2007, Laland et al. 2009, Whiten et al. 2009, Claidière & Sperber 2010, Danchin & Wagner 2010). Other social learning processes may not produce stereotyped behaviours because, although naive individuals may observe the behaviour or behavioural products of experienced individuals, they may not faithfully repeat the precise mechanics of the behaviours without direct interaction with experienced group members (Whiten and Ham 1993, Heyes 1994). Thus, behaviours learned through mechanisms other than teaching and imitation may remain essentially idiosyncratic and therefore they are unlikely to be normative and symbolic.

Evidence suggests, however, that teaching and imitation may not be necessary for behaviours to spread and become stereotyped (Heyes 1993). For example, naive roof rats (*Rattus rattus*) that discover partially consumed pine cones learn to open the cones to obtain seeds in a very stereotyped manner without directly observing other group

members performing the behaviour (Terkel 1995). Similarly, naive wild orangutans (*Pongo pygmaeus wurmbii*) are capable of copying highly specialized tool-use that has persisted for generations without any evidence of teaching from experienced individuals (Jaeggi et al. 2010). Moreover, a review of experimental and theoretical studies (Claidière & Sperber 2010) illustrates that although imitated behaviours can spread readily among naive group members, they do not necessarily persist over longer periods of time as individuals eventually discover alternative behaviours and ultimately converge on the least costly behaviour. Thus, teaching and imitation are not necessary for the spread and persistence of stereotyped, normative behaviours.

In summary, while teaching and imitation may promote the spread and persistence of behaviours that in turn become normative and symbolic, other learning mechanisms can also lead to normative and symbolic behaviours. Therefore, I do not support the third condition of culture that behaviours must be learned specifically through teaching and imitation. I therefore relax more specific definitions of culture to allow that behaviours learned through other social mechanisms be considered.

5.1.4 Summary

Based on the above review, I suggest that culture should be defined as group differences in behaviours that are acquired through any social learning mechanism and that are normative and symbolic. However, it is important to acknowledge that culture should not be viewed as a dichotomy of presence/absence, but instead "its extent, variety and effects" should be examined (Rendell & Whitehead 2001; Whitehead 2009, p.129; Whiten 2009).

5.2 Is There Evidence for Culture in Bats?

Several attributes that bats share in common with primates and cetaceans, suggests that bats too should have culture (see reviews within Laland & Galef 2009). For example, like primates and cetaceans, bats have relatively long life-spans for their size (over 30 years) and relatively large brains, and they are typically gregarious, often living in socially distinct groups (Brunet-Rossini & Austad 2004, Ratcliffe et al. 2006, Kerth 2008,

Dechman & Safi 2009). Animals with long-life spans often encounter changing environments where social learning improves survival (e.g., Whitehead 2007) and those with large brains living in groups are more likely to learn from one another than are solitary animals (Reader 2004, Deaner et al. 2007, Sol et al. 2008, Gonzalez-Lagos et al. 2010). In addition, animals living in socially distinct groups are more likely to share information with group members than with neighbouring conspecifics, and are therefore more likely to use normative behaviours that act as symbols of group identity (Ehrlich & Levin 2005, Voelkl & Noë 2010). Thus, based on these attributes, bats should, in theory, have culture.

To explore whether bats do in fact have behaviours consistent with my definition of culture, below I review the bat literature for possible examples of behaviours that are acquired through any social learning mechanism and that are normative and symbolic. For reasons discussed above, I relax the more specific requirement of some definitions that cultural behaviours cannot be correlated with genetics and ecology, provided they are learned socially. Certainly there is evidence that some bat behaviours, such as vocalizations, may be heritable (Scherrer & Wilkinson 1993, Knörnschild et al. 2007) and that social groups are genetically distinct (e.g., Kerth et al. 2000, Yoshino et al. 2008). Nevertheless, in keeping with my arguments above, I will operate under the assumption that, although there is likely a genetic component to the traits reviewed below, the genetic influence may be small relative to social influences on trait variation (Cavalli-Sforza & Feldman 1973).

Below, I begin my exploration of bat culture with group differences in vocalizations, where I first determine whether they are at least partially shaped by social learning and then whether they have the potential to be normative and symbolic of group identity. I then follow with a similar review of group differences in foraging and roosting behaviour. I place particular emphasis on vocalizations as they play an important role in the social lives of bats and are therefore more likely to meet my definition of culture. Because bats are nocturnal, their behaviour is often cryptic and difficult to document. As a result, the long-term, longitudinal data necessary to identify culture are generally not

available for bat populations. Therefore, it is not my intention to provide conclusive evidence of culture in particular groups of bats, per se, but instead to explore whether bats possess behaviours consistent with my definition of culture and should therefore be more closely examined in future studies of culture.

5.2.1 Groups differ in socially-learned vocalizations that may be normative and symbolic

Although it was once believed bat echolocation calls were used primarily for navigation and foraging (Neuweiler 1989, 1990; Schnitzler et al. 2003), a growing body of evidence suggests they, along with audible vocalizations, are also used for social communication (e.g., Bastian & Schmidt 2008, Janssen & Schmidt 2009, Jones & Siemers 2010, Voigt-Heucke et al. 2010). Although vocalizations vary considerably within and among individuals due to the presence of conspecifics, differences in body size, age, reproductive condition, sex, body condition and mood (Masters et al. 1995, Esser & Lud 1997, Guillen et al. 2000, Kazial & Masters 2004, Kazial et al. 2008, Carter et al. 2008, Yovel et al. 2009, Jones & Siemers 2010, Melendez & Feng 2010, Voigt-Heucke et al. 2010), there is growing evidence that some call parameters differ between groups. For example, at least 18 species, representing seven Families from various parts of the world, show evidence of geographic variation in echolocation calls where bats in one region produce different calls than conspecifics in other parts of their range (Table 5.2). This geographic variation cannot simply be explained as local adaptation of bat calls to differences in ecology, such as clutter, temperature, and humidity, that can affect call transmission (Griffin 1971, Norberg & Rayner 1987, Barclay 1999, Humes et al. 1999, Law et al. 1999, Guillen et al. 2000, Patriquin et al. 2003, Gillam & McCracken 2007, Chiu et al. 2009, Adams et al. 2010), because in 9 of the 18 species the social groups are sympatric and because differences in calls do not improve foraging success (Jones & Barlow 2004, Kingston et al. 2001, Thabah et al. 2006). Thus, group differences in vocalizations may have resulted through other mechanisms, such as social learning.

The available evidence suggests that at least some bat vocalizations are indeed learned. While individuals learn through individual trial-and-error to produce echolocation calls

that are optimal under varying conditions (e.g., Wund 2005), growing evidence suggests calls are also socially-learned. In fact, in a review of vocal learning, Scharff & White (2004) included bats among their list of animals that, like humans, must learn their "vocal repertoire by imitation" (p. 325). The calls produced by juveniles, for example, converge on adult calls in several species (e.g., lesser bulldog, *Noctilio albiventris*, greater horseshoe, *Rhinolophus ferrumequinum*, lesser spear-nosed, *R. monoceros*, and greater sac-winged bats, *Saccopteryx bilineata*), which is most likely a result of juveniles imitating adult calls, rather than individual trial-and-error or maturation towards species-specific call structure (Brown et al. 1983, Esser & Schmidt 1989, Jones & Ransome 1993, Esser 1994, Knörnschild et al. 2010). For instance, the calls of juvenile lesser spear-nosed bats raised in isolation do not come to resemble adult calls, suggesting they rely on conspecific cues (Esser & Schmidt 1989, Esser 1994). Also, as juvenile greater sac-winged bats begin to produce adult-like calls they repeat portions of the individually-specific calls of resident harem males, again suggesting juveniles are using adult cues to develop their own calls (Knörnschild et al. 2006 and references within). Thus, there appears to be evidence that vocalizations are socially-learned and therefore may explain group differences in vocalizations.

Group differences in vocalizations may also be normative as they appear to be driven by group conformity. For example, when the group composition of captive populations of female greater spear-nosed bats and Taiwanese leaf-nosed bats, *Hipposideros terasensis*, was modified by adding or removing individuals, all group members, including resident and transferred individuals, modified their calls to converge on a new group-distinctive call within days or a few months (Boughman 1998, Hiryu et al. 2006). This convergence is not likely due to maturation because individuals showed changes more similar to their new group members than to individuals of similar age from their original groups (Boughman 1998). Moreover, when isolated from the group, Taiwanese leaf-nosed bats produce calls that appear to be less costly (Hiryu et al. 2006), which suggests individuals actively modify calls, at a cost, to conform to group norms. Thus, it appears that, at least in these two cases, group conformity drives group differences in bat calls and thus they appear to be normative.

Group differences in calls may also be symbolic of group identity as group members appear to use calls to recognize group members. Although some suggest that whether bats can use calls for individual, or group recognition, is equivocal because results vary with species, parameters, and conditions under which measurements are taken (Siemers & Kerth 2005, Bartonicka et al. 2006, Jones & Siemers 2010) evidence suggests they can in fact be used for recognition of conspecifcs and group members. For example, antiphonal and behavioural responses to individually-specific calls produced by lesser bulldog, white-winged vampire, *Diaemus youngi*, little brown, *Myotis lucifugus*, greater sac-winged, and Spix's disc-winged bats, *Thyroptera tricolor*, suggests they use these calls for individual recognition (e.g., Brown et al. 1983, Carter et al. 2008, 2010, Kazial et al. 2008a, Knornschild & von Helversen 2008, Chaverri et al. 2010, Voigt-Heucke et al. 2010). These findings, together with several other examples of individual recognition based on vocalizations (Boughman & Wilkinson 1998, Bohn et al. 2007, Arnold & Wilkinson 2011), suggest it is also possible that bats could use group-specific calls as symbols of group identity. Several studies have demonstrated that the average differences in call structures between groups would not likely result in improved prey-detection, suggesting differences serve a social, rather than a functional role (e.g., & Barlow 2001, Kingston et al. 2001, Thabah et al. 2006). Indeed, female greater spear-nosed bats, *Phyllostomus hastatus,* and lesser bulldog bats show different acoustic and behavioural responses to playback calls of group and non-group members, but show no differential response to different individuals from within their groups, which suggests they use group-specific calls to recognize group members (Boughman 1997, Wilkinson & Boughman 1998, Voigt-Heucke et al. 2010). Recognition of these group specific calls may then allow female greater spear-nosed bats to exclude non-group members from feeding areas (Boughman 2006). Thus, group specific calls, such as those discussed above, may indeed act as symbols of group identity.

Perhaps the strongest evidence that bat vocalizations are normative and symbolic of group identity is the fact that some species have language. Language can be defined as "symbols for encoding and decoding information", that is syntactic (rules used to combine symbols to create a new symbol) and semantic (symbols have meaning)

(McGrew 2009). Because individuals must learn and conform to a set of symbols in order to accurately understand a language and be understood, it is implied that language is normative and symbolic. Several species, including moustached bats, *Pteronotus parnellii*, greater horseshoe bats and Mexican free-tailed bats, produce different syllables that are combined following syntactical rules to produce syllable trains, phrases, monologues and dialogues that are used in specific interactions, such as mating, parent-offspring, antagonistic, social, human, and in flight (Kanwal et al. 1994, Clement et al. 2006, Ma et al. 2006, Bohn et al. 2008, 2009). A review by Pfalzer & Kusch (2003), along with studies on moustached bats and false vampire bats, also demonstrates that at least 18 species produce specific call types depending on behavioural context (mating, maternity roosts, in flight, foraging, distress), or mood (aggression or appeasement), suggesting their calls are semantic (Clement et al. 2006, Bastian & Schmidt 2008, Janssen & Schmidt 2009). Further evidence that moustached bats respond behaviourally to aggressive calls (Ma et al. 2010), suggests that bats are able to recognize and respond to semantic differences. Thus, these examples suggest that at least some species possess syntactical and semantic language, and therefore, culture.

Therefore, evidence suggests that bat vocalizations are consistent with my definition of culture. Some bats show group differences in vocalizations, some vocalizations appear to be socially-learned and some vocalizations are normative and symbolic. However, more rigorous field and experimental studies that clearly link social learning to documented cases of group differences in vocalizations are needed as, with the exception of studies on lesser spear-nosed bats and sac-winged bats, these are currently lacking.

5.2.2 Groups differ in socially-learned foraging behaviours that may be normative and symbolic

Some bat species also show group differences in foraging behaviour, such as diet preferences and feeding grounds. Perhaps the most striking example is that of a population of pallid bats, *Antrozous pallidus*, in the Baja California peninsula, Mexico, that feed on the nectar of cardon cacti, *Pachycereus pringlei*, where the typical diet elsewhere consists of insects and terrestrial arthropods (Frick et al. 2009). Although this

group difference in diet could be the result of differences in available resources, their typical prey are also readily available in the Baja California peninsula as they are included their diet there. In addition, cacti are also available and regularly used by other bat species in neighbouring Sonora, Mexico, yet there is no evidence of pallid bats in this region feeding on nectar (Fleming, pers. comm. as cited in Frick et al. 2009). Thus, ecology does not adequately account for differences in diet, and instead these preferences may have spread within groups through social learning. Some bats also show group differences in preferred foraging grounds. For example, social groups of greater bulldog bats, greater spear-nosed bats, lesser bulldog bats, and the molossid *Molossus molossus*, can be found foraging together in areas that they defend against neighbouring social groups (Brooke 1997, Boughman 2006, Dechmann et al. 2009, 2010). In at least two cases (greater bulldog bats and greater spear-nosed bats), observed differences in foraging areas between groups cannot be explained by differences in ecology as social groups in these studies are sympatric, sometimes living in the same roost, and are thus exposed to similar food availability and diets (Brooke 1997, Boughman 2006, Dechmann et al. 2009). Thus, it appears groups of bats have different diet preferences and feeding grounds that are not explained entirely by differences in ecology, which suggests these differences may be a result of socially-learned behaviours spreading within groups.

Indeed, bats appear to learn foraging behaviour from conspecifics. For example, experimental studies suggest that at least three species of bats learn novel feeding tasks more quickly by observing conspecifics than through individual trial-and-error (Gaudet & Fenton 1996, Page & Ryan 2006, Wright et al. 2011), suggesting they readily learn from one another. Also under experimental conditions, several bat species develop taste-aversions to food items (Ratcliffe et al. 2003), suggesting they are capable of learning to discriminate between foods, and therefore may be equally-likely to also learn preferences for particular food items. In the wild, bats may learn about food items through food sharing at roosts, as some species consume food in their roosts rather than on the wing (Wilkinson & Boughman 1999). Field studies suggest that at least five species may learn which feeding sites to visit by attracting one another through vocalizations or by following more successful group members from roosts (Wilkinson 1992, Gopukumar et

al. 2003, Rhodes 2007, Fortuna et al. 2009, reviewed in Wilkinson & Boughman 1999). Once bats are recruited to feeding territories, they may then learn to revisit these sites. Thus, bats appear capable of learning foraging behaviours from conspecifics.

Foraging behaviours could also be normative. For example, the food preferences of short-tailed fruit bats, *Carollia perspicillata*, can be reversed when exposed to group members trained to eat new foods, which suggests they may conform to the behaviour of other group members (Ratcliffe & ter Hofstede 2005). However, whether foraging behaviour could be symbolic of group identity is unclear. Xenophobia provides convincing evidence of an ability to recognize group members and discriminate against unfamiliar conspecifics and would therefore suggest bats use normative and symbolic behaviours (McGrew 2009). While several species appear to exclude unfamiliar conspecifics from feeding grounds (reviewed in Wilkinson & Boughman 1999), it is likely that vocalizations, rather than the feeding territories themselves, are used to identify group members (Pfalzer & Kusch 2003). Thus, current evidence of normative and symbolic foraging behaviours is limited.

In summary, group differences in foraging behaviours are partially consistent with my definition of culture. Evidence suggests that some bats show group differences in foraging behaviours and that these behaviours can be learned from conspecifics. However, as with vocalizations, evidence directly linking documented group differences with social learning is lacking. Also, evidence that these behaviours are normative is limited and whether they are symbolic remains to be tested. Thus, considerably more research is necessary to determine whether food preferences and feeding territories are in fact normative and symbolic to provide more convincing support for culture in bats.

5.2.3 Groups differ in socially-learned roosting behaviours that may be normative and symbolic

There is evidence of group differences in roosting behaviour. For example, across their range, groups of female little brown bats can be found roosting in different structures, such as trees and buildings (discussed in Broders & Forbes 2004), as can groups of

female big brown bats, *Eptesicus fuscus*, which can also be found in rock crevices (Agosta 2002, Lausen & Barclay 2003, 2006). Similarly, at a finer scale, female long-legged bats, *Myotis volans*, in the Pacific Northwest tend to use snags, but specific site and roost characteristics show geographic variation (Lacki et al. 2010). Because of their significant influence on thermoregulation, and thus survival and reproductive success, suitable roosts, rather than foraging habitat, are believed to be a limiting resource for bats (Kunz & Lumsden 2003). Differences in ecology are therefore likely a stronger influence on group differences in roost use than on vocalizations and foraging behaviour. Thus, a large part of the variation in roost-use can be attributed to differences in availability of preferred structures or roost characteristics that may offer higher reproductive success through improved thermoregulation or closer proximity to foraging sites (Lewis 1996, Kerth et al. 2001, Chruszcz & Barclay 2002, Lausen & Barclay 2003, Dietz & Kalko 2006, Lausen & Barclay 2006, Willis et al. 2006, Lacki et al. 2010, Ruczynski et al. 2010, Poissant et al. In press). More detailed studies similar to that of Campbell et al. (2006), who compare differences in roost use with roost availability across sympatric groups of conspecifics, are therefore necessary to establish the role of ecology in group differences in roost use.

Nevertheless, there is at least one example where ecology does not adequately explain group differences in roosting behaviour. Female tricoloured bats (*Perimyotis subflavus;* formerly known as the eastern pipistrelle, *Pipistrellus subflavus*) roost almost exclusively in lichen, *Usnea trichodea*, in Kejimkujik National Park, Nova Scotia, Canada (Quinn & Broders 2007) whereas they roost generally in buildings, caves and tree foliage throughout the rest of their range (Veilleux et al. 2003, Perry & Thill 2007). Populations in Indiana regularly roost in oak leaves; yet, despite availability of oak in Kejimkujik National Park, extensive studies have yet to document use of oak leaves there (Veilleux et al. 2003, Poissant et al. In press), suggesting ecology does not entirely explain group differences in roost use and instead they may be socially-learned.

Limited evidence suggests that roost use may be socially-learned. For example, inexperienced female Bechstein's bats, *M. bechsteinii*, as well as evening bats, *Nycticeius*

humeralis, appear to learn about available roosts from more experienced, or more exploratory, group members who actively recruit group members to roosts (Wilkinson 1992, Kerth et al. 2001, Kerth & Reckardt 2003, Chaverri et al. 2010). Thus, it is possible group differences in roost use may emerge as members of one group learn about different roosts than those learned by females in neighbouring groups. Clearly more direct evidence that roosting behaviours are socially-learned is needed to offer convincing support that they are examples of culture in bats.

Group differences in roost use among bats could also potentially be normative and symbolic; however, the social significance of these group differences has not been explored and therefore much of what follows is largely speculative. For example, white-striped free-tailed bats, *Tadarida australis*, live in a fission-fusion society where group members are spread among a network of roosts, resulting in labile group composition (Rhodes 2007). However, all members regularly use one central communal night roost, which may serve a functional role as shelter from predators or weather while bats digest between foraging bouts (Bradbury 1977, Kunz 1982, Kunz & Lumsden 2003). Here, individuals can interact with members of a larger social network that are separated across multiple day-roosts (Barclay 1982, Rhodes 2007). Therefore, I propose that night-roosts may also allow group members that roost apart in different day-roosts to maintain group-specific markers, such as odours (McCracken & Bradbury 1981, Kerth et al. 2003, Safi & Kerth 2003). By extension, these communal night-roosts could then become symbolic of a particular social network of bats, similar to places of worship that are symbolic of different religious groups in humans. Bechstein's bats behave aggressively toward unfamiliar conspecifics from neighbouring social groups when experimentally placed in their roosts, which suggests they recognize and discriminate against unfamiliar group members and therefore recognize group identity (Kerth et al. 2002). However, what cues are used to recognize group members remains unclear.

In summary, group differences in roosting behaviours are partially consistent with my definition of culture. Evidence suggests that some bats show group differences in roosting behaviour, however a large part of this variation can be explained by differences

in ecology and only limited evidence that it is socially-learned is currently available. In addition, as with vocalizations and foraging behaviour, evidence directly linking documented group differences with social learning is lacking. Though speculative, night roosts in particular may indeed be symbolic as group members may use them to identify other group members that are otherwise separated in different day-roosts. Thus, considerably more research is necessary to determine whether group differences in roosting behaviour are socially-learned, normative and symbolic to provide more convincing support that they are examples of culture in bats.

5.2.4 Summary

Although examples of bat vocalizations, along with foraging and roosting behaviour, appear to be partially consistent with my definition of culture, considerably more research is necessary to clearly link group differences with social learning and to determine whether behaviours are indeed normative and symbolic. In addition, I acknowledge that genetic variation may also play an important role in group differences in behaviour; however, as argued above this variation is less likely than learning to contribute to group differences in vocalizations or foraging and roosting behaviour. Nevertheless, a better understanding of population genetics of those groups with differences in behaviours would provide stronger support for culture in bats. Moreover, bats are an incredibly diverse group with over 1,100 species living in a wide array of environments and social structures that likely influence the potential for culture (Kunz & Fenton 2003, Wilson & Reeder 2005, Whitehead 2007, Kerth 2008, Sargeant & Mann 2009). Thus, the patterns documented in this review may not be observed across all species.

Thus, a closer examination of possible group differences within and across species, and a more complete understanding of population genetic structure and learning mechanisms in bats are necessary to provide convincing support for culture in bats. Ideally, more robust studies would involve experimental manipulations and translocations to establish how different behaviours are transmitted (Laland et al. 2009). Bats enjoy a panmictic

distribution, prosper in captivity with proper care and perform well in experimental studies, thus offering opportunities to execute carefully designed field and captive studies

5.3 POSSIBLE IMPLICATIONS OF BAT CULTURE

Once we gain a better understanding of the extent of culture in bats, we can then gain a better understanding of its influence on fitness and population persistence. For example, the ability to discriminate among familiar and unfamiliar individuals, as well as familiar individuals of varying social relationships, may help bats determine whether or not to engage in cooperative behaviours, such as sharing food, roosts, or foraging grounds, allogrooming, alloparenting, and roost switching (Wilkinson 1985, 1992, McCracken 1984, Boughman 1998, Wilkinson & Boughman 1998, Rossiter et al. 2002, Kerth et al. 2003, 2006, Bohn et al. 2009, Kerth 2010) and may minimize costs associated with agonistic interactions (Voigt-Heucke et al. 2010) and thus improve reproductive success.

In addition, because culture generally involves social learning, it can improve individual survival and population persistence under changing conditions. Populations containing social learners are more likely to persist in changing environments because social learners can copy the behaviours of others and therefore respond more quickly than asocial learners, who spend time and energy on trial-and-error learning, or individuals with genetically fixed behaviours (Boyd & Richerson 1995, Feldman & Laland 1996, Laland et al. 2000, 2001, Reader 2004, Whitehead et al. 2004, Aoki et al. 2005, Richerson & Boyd 2005, Borenstein et al. 2007, Whitehead 2007, Aoki & Nakahashi 2008, van der Post & Hogeweg 2009, Whitehead & Richerson 2009, Laland & Boogert 2010, McNamara & Dall 2010, Schmidt et al. 2010). Because bats are long-lived, environmental conditions vary across their lifetimes, especially in areas exposed to human-altered landscapes that remove roosting and foraging habitat. Nevertheless, bat populations have persisted under changing conditions, and some have even expanded their ranges, which may be a result of social learners copying asocial learners who have successfully occupied novel or marginal habitat (Beltman & Metz 2005, Sutter & Kawecki 2009, Schmidt et al. 2010), as demonstrated for a variety of birds and mammals (Sol et al. 2002; Sol et al 2008).

Culture may have also facilitated the radiation of bats. As group differences in learned behaviours become more pronounced, interactions between members in neighbouring conspecific groups may be limited, which could result in reproductive isolation, and, eventually, speciation (Cavalli-Sforza & Feldman 1973, Slabberkoorn & Smith 2002, Beltman & Metz 2005, Verzijden et al. 2005, Tramm & Servedio 2008, van der Post & Hogeweg 2009). For example, birds in different groups learn group-specific songs, or dialects, and females preferentially mate with males with similar dialects as their own, thus reinforcing group differentiation that over time may lead to speciation through learned sexual preferences (Slabberkoorn & Smith 2002). Similarly, different dialects may have ultimately led to speciation in bats. There are several groups of bats that appear morphologically similar but have distinct phonic types and are also genetically distinct, which has led to the designation, or proposed designation, of phonic groups as either distinct species or subspecies, as has been well documented in the European pipistrelles, *Pipistrellus pipistrellus* and *P. pygmaeus* (for more examples see review in Jones & Barlow 2004 and Chattopadhyay et al. 2010). In most instances, acoustic divergence does not appear to be related to differences in prey detection or habitat use, instead individuals may have initially used different frequencies to avoid interference or eavesdropping while foraging, or to recognize group members, which may have then lead to social and reproductive isolation (Kingston & Rossiter 2004, Chattopadhyay et al. 2010, reviewed in Jones & Barlow 2004). Barratt et al. (1997) argue that vocal divergence in bats likely happened after genetic divergence, rather than the inverse. They argued this is likely because echolocation calls are highly conserved to ensure optimal foraging. Yet, as discussed above, more recent evidence of high intra- and interindividual variation in echolocation calls with habitat and identity suggests calls are not so highly conserved. Thus, it remains possible that vocal divergence may have played a role in the radiation of bats.

Although culture can be beneficial, under some conditions it can also reduce fitness, lead to population declines and, ultimately, extirpation. Behaviours can become maladaptive if individuals fail to modify their behaviours in response to changed conditions.

Individuals may fail to modify their behaviours because of the pressure to conform to existing group norms ("standard or ideal behaviors 'typical' of groups"; Ehrlich & Levin 2005, p.0943) or because obligate social learners continue to copy inappropriate behaviours since asocial learners that may modify their behaviours in response to change are no longer present, or too few in number, to act as models (Whitehead et al. 2004, Richerson & Boyd 2005, Whitehead 2007, Laland et al. 2009, Nunn et al. 2009, Whitehead 2009, Whitehead & Richerson 2009, Rendell et al. 2009). Bats often use the same roosts year after year and may continue to do so despite human disturbance to roosts (e.g., Tuttle 1979). Thus, much like populations that continue to use traditional migration routes or foraging patches that become suboptimal due to environmental changes (Laland et al. 2009), bats may continue to use suboptimal roosts because deviating from the group could result in increased predation risk or thermoregulatory costs. Thus, culture may negatively affect bat populations.

A better understanding of whether bats have culture, and to what extent, will not only provide a better understanding of individual survival, population persistence, speciation and extinction in bats, but it will also provide an excellent opportunity to test predictions of cultural theory. For example, theory predicts that behaviours are more likely to spread quickly and become normative in fission-fusion groups of moderate size as the opportunities to learn, group conformity, and the importance of signalling group identity are more likely than in highly structured hierarchies, for example (Hinde 1976, Coussi-Korbel & Fragaszy 1995, van Schaik 2003, van Schaik et al. 2003, Ehrlich & Levin 2005, Whiten et al. 2005, Nunn et al 2009, Perry 2009, Sargeant & Mann 2009, Voelkl & Noe 2010). Behaviours are less likely to spread within highly structured groups, such as hierarchies, because the opportunity to learn is restricted between individuals of similar rank, for example, whereas information can spread more quickly in more dynamic, mixed groups (Sargeant & Mann 2009, Voelkl & Noe 2010). Moreover, behaviours are less likely to spread and become normative in large groups because it may be too difficult to reach a consensus on group behaviour (Ehrlich & Levin 2005). Finally, the need for normative behaviours that signal group identity (i.e., ethnic markers or badges) is less likely in stable groups as individuals may not regularly encounter unfamiliar

conspecifics, thus Perry (2009) "find[s] it more plausible that ethnic markers exist in cetaceans, birds or bats than in nonhuman primates" (p.267). Bats offer an excellent opportunity to empirically test these predictions, because, as mentioned above, there is considerable inter- and intraspecific variability in resource use and social structure among the roughly 1100 species of bats. Bats exploit food resources that range in predictability from fairly predictable patches of fruit to ephemeral patches of insects. Bats also use shelters that range in stability, from permanent caves to temporary roosts, such as unfurling banana leaves. Moreover, bats live in a wide array of social structures, ranging from stable, permanent groups to highly dynamic fission-fusion societies (Kerth 2008). Thus, bats offer the opportunity to test predictions about the influence of resource stability and social structure on learning and culture.

5.4 CONCLUSIONS

Once we gain a better understanding of culture in bats, we can then make broader comparisons across taxa to further understand the evolution and implications of culture. For example, Whitehead (2003) proposed the idea of a "colossal convergence" in sociality among large mammals, such as sperm whales and elephants, due to similarities that appear to favour (or are a result of) sociality, including long life-spans, complex brains and low genetic diversity (mtDNA typically) via cultural hitchhiking. As discussed above, bats share a number attributes with these larger mammals, as they too are long-lived, have disproportionally large brains, high investment in offspring, and low mtDNA diversity within populations and, as I have demonstrated they also have some behaviours consistent with culture. With more direct studies of culture in bats, it will be interesting to see how bats "size up" in comparison to these larger mammals commonly regarded as cultural.

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Table 5.1 Definitions of culture (cultural traits/traditions) quoted directly from sources reviewed in this chapter, with a summary of conditions discussed in this chapter that are specified in each definition

Definition	Group differences[a]	Social learning[b]	Social behaviour[c]	Teaching & imitation[d]	Ratchet effect[e]	Source
That complex whole which includes knowledge, belief, art, law, morals, custom and any other capabilities and habits acquired by man as a member of society.	no	implied	yes	no	no	Tyler 1871 (cited in McGrew 1998, p.303)
If one ape devised or learnt a new dance step, or a particular posture, or an attitude toward the object about which the dance revolved; and if these new acts were taken up by other chimpanzees, and became more or less standardized; especially if they survived beyond the influence of the inventor, were taken up by other communities, or passed on to generations after him. In that case, we would legitimately feel that we were on solid ground of an ape culture.	no	yes	yes	no	no	Kroeber 1928 (cited in McGrew 1998, p. 331)
Socially transmitted adjustable behavior.	no	yes	no	no	yes	Imanishi 1952 (cited in deWaal & Seres 1997, p. 339)
The behaviour between two groups with the same gene pool and the same type of habitat can differ only by culture.	yes	implied	no	no	no	Kummer 1971 (cited in van Schaik 2009, p. 74)
One community can be readily distinguished from another on the basis of socially transmitted behaviour.	yes	yes	no	no	no	Menzel 1973a, Bonner 1980
Social learning.	no	yes	no	no	no	Mundinger 1980
Any extragenetic form of acquired information transmission.	no	yes	no	no	no	Lumsden et al. 1981 (cited in Laland & Galef 2009, p. 5)
The activities, values, and behavior of an individual that are acquired through instruction or imitation.	no	yes	yes	yes	no	Cavalli-Sforza et al. 1982, p.19
At the very least culture would seem to require some form of social learning.	no	yes	no	no	no	Tomasello 1990 (cited in Aoki 2001, p. 253)
Shared ideational phenomena (ideas, beliefs, values, knowledge) that are learned and socially transmitted between individuals.	yes	yes	yes	no	no	Feldman & Laland 1996, p. 453
Group-specific behavior that is acquired, at least in part, from social influences.	yes	yes	no	no	no	McGrew 1998, p.305

Definition	Group differences[a]	Social learning[b]	Social behaviour[c]	Teaching & imitation[d]	Ratchet effect[e]	Source
Information that may cause variation in behavior and that is acquired from conspecifics by imitation or learning.	yes	yes	no	yes	no	Whitehead 1998, p. 1710
Animals that learn their life's lessons, habits, and songs from one another.	no	yes	no	no	no	deWaal 2001 (cited in van Schaik 2009, p. 363)
All socially learned information.	no	yes	no	no	no	Galef & Giraldeau 2001 (cited in van Schaik 2009, p.70)
Information or behaviour – shared by a group of animals – which is acquired from conspecifics through some form of social learning.	yes	yes	no	no	no	Rendell & Whitehead 2001, p. 310
Presence of language-based, locally specific meanings of symbols and institutions.	yes	no	yes	no	no	Tuttle 2001 (cited in van Schaik 2009, p70)
First, culture is learned from group members; it is not transmitted genetically nor does it represent simply an adaptation to particular ecological conditions. Second, culture is a distinctive collective practice. Third, anthropologists tend to speak of a symbolic system to express the fact that culture is based on shared meanings between members of the same group or society.	yes	yes	yes	no	no	Boesch 2003, p.83
The information acquired by individuals via social learning; cultural learning/transmission/acquisition is the subset of social learning capacities that allow for cumulative cultural evolution.	no	yes	no	no	yes	Henrich & McElreath 2003, p.124
Group-typical behavior patterns shared by members of a community that rely on socially learned and transmitted information.	yes	yes	no	no	no	Laland & Hoppitt 2003, p. 151
A practice that is relatively long-lasting and shared among members of a group, each new practitioner relying to some extent upon social influence to learn to perform it.	yes	yes	no	no	no	Perry et al. 2003, p. 243
The phenomenon whereby features of behaviour pass by learning from one individual to another.	no	yes	no	no	no	Whiten et al. 2003, p. 92

Definition	Group differences[a]	Social learning[b]	Social behaviour[c]	Teaching & imitation[d]	Ratchet effect[e]	Source
The sum of traditions and information that vary among groups; the transmission of these differences across generations rests on social interactions (imprinting, imitation, learning, or teaching) that change phenotype lastingly.	yes	yes	no	no	no	Danchin et al. 2004, p.489
A behavioral trait is considered to vary culturally if it is acquired through social learning from conspecifics and transmitted repeatedly within or between generations.	yes	yes	no	no	no	Krutzen et al. 2005, p. 8939
Behavioral variation that owes its existence at least in part to social learning processes.	yes	yes	no	no	no	Perry 2006 (cited in McGrew 2009, p.67)
A behavior or skill acquired through horizontal transmission: social learning.	no	yes	no	no	no	Ryan 2006, p. 1321
Any variation acquired and maintained by social learning.	yes	yes	no	no	no	Laiolo & Tella 2007, p.68
A package of multiple related traditions, and 'cultures' as distinctive arrays of clustered traditions. We define 'tradition' as a local behavioural variant, showing different frequencies of occurrence across the study sites, i.e., being customary or habitual in at least one site, but absent elsewhere.	yes	no	no	no	no	Leca et al. 2007, p. 253
The transmission of learned behaviour.	no	yes	no	no	no	Marino et al. 2007, p. 0970
Presence in multiple domains of socially transmitted innovations.	no	yes	no	no	yes	Whiten & van Schaik 2007 (cited in van Schaik 2009, p.70)
A socially transmitted heritage peculiar to a particular society.	yes	yes	no	no	no	Caldwell & Millen 2008, p. 3529
Determinants of cultural behavior, including innovation, transmission, acquisition, developmental constraints thereof, long-term maintenance, and intergroup variation.	yes	yes	no	no	yes	Huffman et al. 2008, p. 410
A population-typical behaviour that is at least partly acquired and transmitted through mechanisms of social learning.	yes	yes	no	no	no	Mobius et al. 2008, p.37

Definition	Group differences[a]	Social learning[b]	Social behaviour[c]	Teaching & imitation[d]	Ratchet effect[e]	Source
A behavioural trait repeatedly transmitted through social learning among conspecifics (as opposed to environmentally determined, individual trial-and-error learning or genetic transmission).	no	yes	no	no	no	Schöning et al. 2008, p. 48
Regional variations in behaviour, attributable to social learning. Where there is evidence that such variations are sustained (e.g. across generations) they are typically referred to as traditions or cultural variations.	yes	yes	no	no	no	Whiten & Mesoudi 2008, p.3477
Transmission of social positions, preferences, habits and attitudes... and a capacity to observationally learn the significance of arbitrary actions (latter half was made specifically in reference to human culture).	no	yes	yes	no	no	deWaal & Bonnie 2009, p.29
Behavioral variation resulting from imitation and tuition.	yes	yes	no	yes	no	Galef 2009, p. 223
A community-specific set of behaviors that an individual is exposed to and can socially learn from.	yes	yes	no	no	no	Gruber et al. 2009, p. 1809
Any instance of social transmission of behaviour, regardless of the underlying social learning process.	no	yes	no	no	no	Kendal et al. 2009, p.1
Phenotypic difference between individuals, observed within or between populations, that are to some degree attributable to differences in what they learned socially.	yes	yes	no	no	no	Laland et al. 2009 p.178
Behaviour patterns shared by members of a population that are to some degree reliant on socially learned and transmitted information.	yes	yes	no	no	no	Laland et al. 2009 p.178
Acts performed normatively by appropriate subsets within a group (e.g., cooks cook, elders advise) + vertical transmission of information across generations, from old to young.	yes	yes	yes	no	no	McGrew 2009, pp.48 & 50
Preservation of multiple traditions...defined as a distinctive behaviour pattern shared by two or more individuals in a social unit that persists over time and that new practitioners may acquire in part through socially aided learning.	yes	yes	no	no	no	Pesendorfer et al. 2009, p.1 (e4472)
Behaviour is inherited from one generation to the next through socially influenced learning; behavioural variation between groups that is independent of ecological and genetic variation.	yes	yes	no	no	no	van der Post & Hogeweg 2009, p. 155
Process by which social learning homogenizes behaviour within sections of a population.	yes	yes	no	no	no	Whitehead 2009, p.126

Definition	Group differences[a]	Social learning[b]	Social behaviour[c]	Teaching & imitation[d]	Ratchet effect[e]	Source
Behaviour acquired from conspecifics by means other than genetic transmission.	no	yes	no	no	no	Bryson 2010, p.50
Community specific behaviour...that cannot be readily attributed to genetic or environmental induction, thus suggesting a cultural character. For acquired behaviour to clearly count as cultural, two conditions must be met: it must propagate in a social group, and it must remain self-similar or stable across generations in the process of propagation.	yes	yes	no	no	no	Claidiere & Sperber 2010, p.651
The part of phenotypic variance that is transmitted through social learning.	yes	yes	no	no	no	Danchin & Wagner 2010, p. 213
Behavioral practices that are inherited over generations through social learning.	no	yes	no	no	no	Jaeggi et al. 2010, p.62
Enduring behavioral practices that are shared by several individuals of a species and transmitted through social learning.	yes	yes	no	no	no	Muller & Cant 2010, p.1

[a] Behaviour must differ between groups, or be group-specific. Note that in my review I combine group-differences and socially-learned behaviour as a single conditions because evidence of group differences would not be sufficient for culture and instead they must be a result of behaviours spreading through social learning.

[b] Behaviour must be learned socially and not a result of genetics or local adaptation to ecology.

[c] Behaviour must be normative (performed by most group members) and symbolic of group identity (used to recognize group members and discriminate against unfamiliar conspecifics).

[d] Behaviour must be learned specifically through teaching and imitation rather than other possible social learning mechanisms.

[e] Behaviour must change over time to become increasingly complex and changes are passed on to subsequent generations.

Table 5.2 Summary of species that show group differences in vocalizations.

Species	Family	Region of study	Sources
greater sac-winged bat, *Saccopteryx bilineata*	Emballonuridae	Trinidad & Costa Rica	Davidson & Wilkinson 2002, Knornschild et al. 2010
golden horseshoe bat, *Rhinonycteris aurantia*	Hipposideridae	western & northern Australia	Armstrong and Coles 2007
intermediate leaf-nosed bat, *Hipposideros larvatus*	Hipposideridae	mainland China	Jiang et al. 2010
Mexican free-tailed bat, *Tadarida brasiliensis*	Molossidae	United States	Gillam & McCracken 2007
African molossid, *Otomops martiensseni*	Molossidae	South Africa	Fenton et al. 2004
lesser bulldog bat, *Noctilio albiventris*	Noctilionidae	Panama	Voigt-Heucke et al. 2010
greater spear-nosed bat, *Phyllostomus hastatus*	Phyllostomidae	Trinidad	Boughman 1997, Wilkinson & Boughman 1998
lesser spear-nosed bat, *Phyllostomus discolor*	Phyllostomidae	Costa Rica & Colombia	Esser & Schubert 1998
Okinawan least horseshoe bat, *Rhinolophus pumilus*	Rhinolophidae	Ryukyu Archipelago (south of Japan)	Yoshino et al. 2006, 2008
Formosan lesser horseshoe bat, *Rhinolophus monocerus*	Rhinolophidae	Taiwan	Chen et al. 2009
little brown bat, *Myotis lucifugus*	Vespertilionidae	United States	Pearl & Fenton 1996
little forest bat, *Vespadelus vulturnus*	Vespertilionidae	eastern Australia	Law et al. 2002
southern forest bat, *Vespadelus regulus*	Vespertilionidae	eastern Australia	Law et al. 2002

Species	Family	Region of study	Sources
large forest bat, *Vespadelus darlingtoni*	Vespertilionidae	eastern Australia	Law et al. 2002
eastern cave bat, *Vespadelus troughtoni*	Vespertilionidae	eastern Australia	Law et al. 2002
eastern forest bat, *Vespadelus pumilus*	Vespertilionidae	eastern Australia	Law et al. 2002
evening bat, *Nycticeius cubanus*	Vespertilionidae	western Cuba	Mora et al. 2005

CHAPTER 6
CONCLUSIONS

6.1 CAUSES AND CONSEQUENCES OF FISSION-FUSION DYNAMICS

The primary objective of my research was to examine the causes and consequences of fission-fusion dynamics in female northern long-eared bats, *Myotis septentrionalis*. In Chapter 2, I examined roost-use and roost-switching behaviour of females to first understand why frequent roost-switching, which results in fission-fusion dynamics, has evolved. Females used roosts with different characteristics under different ambient conditions. For example, on cold, wet, windy days, females tended to use large, healthy trees where they typically roosted below the canopy. On warmer, drier, and calmer days, females also tended to roost in large trees, but instead they roosted near or above the canopy. Females were likely selecting roosts that offered more suitable microclimates for varying thermoregulatory needs under varying ambient conditions. The characteristics of the roosts used by females differed between years, which can likely be attributed to differences in ambient conditions between years. In addition, the characteristics of the roosts used by females differed between reproductive periods, which may reflect different thermoregulatory strategies used by females in different reproductive periods. I demonstrated that females moved from small trees in higher decay stages to taller trees in lower decay stages when conditions became unfavourable (i.e., temperature and pressure decreased). Therefore, frequent roost-switching by female bats can likely be explained as a response to changes in ambient conditions in order to locate roosts with more suitable microclimates.

In Chapter 3, I then examined the consequences of frequent roost-switching by quantifying the associations among female northern long-eared bats. Generally, there were at least two distinct social colonies in my study area as individuals from each colony were never observed roosting together. Within the larger colony, there were several interconnected social groups within which females formed preferred social

relationships that could persist for years. Therefore, despite seasonal movements from summer areas to hibernacula in the fall, females maintained social relationships across years, which suggests the opportunity exists for cooperation among group members. Social relationships varied with reproductive period, as females formed stronger relationships during the gestation period by spending more time with fewer individuals than during the lactation period. These differences may be due in part to different thermoregulatory strategies during different reproductive periods. Using network analyses, I found that younger females tended to have more direct and indirect connections with other group members than did other age classes. Younger females may therefore play an important role in maintaining social connections among group members spread among a network of roosts. Females of all age classes appeared to roost more often with younger individuals than with other age classes, suggesting that roost groups were made up of many younger individuals and fewer older individuals. This age structure is consistent with matrilineal societies consisting of older females and their descendant young.

In Chapter 4, I examined whether the social relationships observed in Chapter 3 could be explained by genetic relatedness. Females within each of the colonies were more closely related to one another than they were to females in adjacent colonies at the maternal level, but not at the nuclear level. This appears to support the argument made in Chapter 3 that fission-fusion groups may be matrilineal. Females within the different social groups that made up the colonies were not more closely related to one another at either the maternal or nuclear level. However, familiar pairs within these groups were in fact closely related at both the nuclear and maternal level. Kin selection may therefore play a role in shaping relationships within groups with fission-fusion dynamics. However, this has generally been overlooked in previous studies that considered only average group relatedness.

In Chapter 5, as part of exploring the consequences of bat sociality, I examined whether there is evidence of culture in bat populations. Based on a review of the literature, I defined culture as group differences in behaviours that are acquired through any social

learning mechanism and that are normative and symbolic. However, I also acknowledged that when examining groups for culture, "its extent, variety and effects" should be examined rather than assessing presence/absence. Based on a review of the literature, I demonstrated that there are examples of group differences in vocalizations, foraging behaviour, and roosting behaviour in bat populations. While some of these differences may be due to genetic differences between groups, social learning likely played a stronger role in shaping the group differences in behaviours. However, it remains unclear whether these behaviours are normative and symbolic. Therefore, some bat populations appear to possess features suggesting that culture may exist. Carefully designed studies that examine group differences, learning mechanisms, and population genetics are needed, however, to better determine whether culture exists in bat populations.

In summary, the goal of my thesis was to examine possible causes and consequence of fission-fusion dynamics in bats. My work answered a number of questions that had not been previously addressed by demonstrating that: fission-fusion dynamics may be explained by changes in ambient conditions that prompt frequent roost-switching; despite the highly dynamic nature of these groups, females form long-term social relationships; these relationships are based in part on age and genetic relatedness. However, my work raises additional questions that must be addressed if we are to fully understand the evolution of fission-fusion dynamics. For example, the question remains whether species with different thermoregulatory requirements, and thus different degrees of roost-switching, show the same social structure. Similarly, it remains to be tested whether sympatric groups of conspecifics that use roosts with different thermal properties, and therefore also show different degrees of roost-switching, show the same social structure. After identifying the causes and consequences of fission-fusion dynamics across species of bats, we can then look for parallels with other taxa to better understand the evolution of these dynamic systems.

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APPENDIX A

PUBLICATIONS

The work presented in Chapter 3 also appears in:
Patriquin, KJ, ML Leonard, HG Broders and CJ Garroway. 2010. Do social networks of female northern long-eared bats vary with reproductive period and age? Behavioral Ecology and Sociobiology 64: 899-913. doi 10.1007/s00265-010-0905-4

The work presented in Chapter 4 has also been submitted:
Patriquin, KJ, Palstra, F, Leonard, ML, and Broders, HG. Submitted March 28, 2012. Female northern long-eared (*Myotis septentrionalis*) that roost together are related. Behavioral Ecology.

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Introduction

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APPENDIX B

DNA EXTRACTION AND GENOTYPING

Because it can be difficult to obtain high DNA yields from pigmented bat tissue, we applied a DNA extraction method developed specifically for obtaining high yields from degraded DNA in archived fish scales (Palstra et al. 2009). This procedure involved a phenol/chloroform protocol adapted from (Taggart et al. 1992) combined with micro-concentrator tubes (Amicon) that kept DNA in solution during the entire extraction procedure (see Nielsen et al. 1999). With this procedure we successfully extracted DNA from tissue samples from 71 of the 83 females from the known social groups described in Patriquin et al. (2010). Samples for genetic analyses were not available for the remaining 12 individuals. DNA was extracted from an additional 43 individuals sampled from the same study area for which insufficient social data were available to establish pair-wise associations (see Patriquin et al. 2010) but instead were used to establish baseline allele frequencies.

We genotyped individuals at eight microsatellite loci using polymerase chain reactions (PCR). These microsatellite loci were previously used for other *Myotis* species (Table B1; Kerth et al. 2002), including *M. septentrionalis* in other regions (Arnold 2007) and were also tested for use in another study with *M. septentrionalis* in our region (L Burns, personal communication). Primers for the loci were fluorescently labelled to enable visualization on LiCor gel imaging systems. PCR amplifications were performed in a reaction volume of 15 uL containing 1X ThermoPol PCR Reaction Buffer (10mM KCl, 10mM (NH4)2S04, 20 mM Tris-HCl, 2 mM MgSo4, 0.1% Triton-X-100, pH 8.8 @25°C; New England Biolabs), 0.2 mM dNTP's, 0.016 uM of each forward tailed bat primer, 0.16 uM of each reverse bat primer and M13 primer, 0.05 units of Taq DNA polymerase, and 1 uL of DNA template. PCR conditions included an initial heating step (5 minutes at 95°C), followed by 35 cycles of amplification (30s denaturing at 95°C; 30s annealing of primers at specific temperatures outlined in Table 1; 1 minute of extension at 72°C), concluded by a final extension step (10 minutes at 72°C). We visually scored allele sizes

for individuals based on a standard pUC ladder, as well as allelic size ladders constructed from individual samples.

To verify reliability of our genetic data, the amplification quality of each microsatellite marker was evaluated as follows. The occurrence of genotyping errors (technological artefacts, such as null alleles) was assessed using Microchecker (Van Oosterhout et al. 2004). We used FSTAT 2.09 (Goudet 1995) to estimate genetic diversity (observed and expected heterozygosity, and allelic richness) and to test for possible deviations from Hardy-Weinberg equilibrium (HWE). One of the microsatellite markers (*Efu-21*) could not be amplified successfully and three others (*Efu-4, Efu-6*, and *Mmy-D15*) deviated from HWE as indicated by their inbreeding coefficients (F_{is}; Table 1). Upon closer inspection, these loci had higher than expected levels of homozygosity and relatively low amplification success, suggesting the likely presence of null alleles, which was confirmed by Microchecker analyses. Subsequent analyses were therefore based on the four markers (*Mmy-E24, Mmy-F19, Mmy-G9*, and *Mybe-15*) that were in HWE, showed relatively high amplification success, and displayed no indications of null alleles. Moreover, these four loci had a relatively high genetic diversity with an average of 22.5 alleles per locus (range: 16-27; Table B1). Seven of the 71 genotyped females were excluded from statistical analyses as we were unable to obtain complete genotypes at all four loci. Thus, of the females with previously described social relationships, we had 64 females with complete genotypes available for subsequent analyses.

To test for maternal relationships, we amplified sequences from the hypervariable II portion of the control region (HVII) of mitochondrial DNA using forward primer L16517 (Fumagalli et al. 1996) and reverse primer sH651 (Castella et al. 2001). PCR amplifications were performed in a reaction volume of 25 µl that contained 12.5 ng DNA, 1.0 µM of each primer, 1.5 mM MgCl2, 0.2 mM dNTPS, and 1 unit of Taq (Promega). PCR conditions included an initial heating step (3 minutes at 94°C), followed by 30 cycles of amplification (1 minute denaturing at 94°C; 1minute annealing of primers at 54°C; 1.5 minutes of extension at 72°C), concluded by a final extension step (5 minutes at 72°C). We sequenced 290bp segments using forward primer L16517 and a reverse

primer from Metheny et al. (2008). Consensus sequence was obtained and sequences were aligned in ClustalX 2.1 (Tables B2 and B3, Thompson et al. 1997).

SIMULATIONS

Ritland's coefficient of kinship is more conservative than the various relatedness coefficients used in other studies of bat population genetics (e.g., Kerth and König 1999; Rossiter et al. 2002; Furmankiewicz and Altringham 2006; Metheny et al. 2008), which instead calculate the proportion of alleles shared by two individuals. These other estimators therefore offer no information about identity-by-decent as individuals could share alleles that were not necessarily inherited from recent common ancestors (Stevens et al. 2011). Because each estimator has its own inherent bias, its ability to detect structure varies with the structure of a particular social system (Van de Casteele et al. 2001; Csilléry et al. 2006). Thus, to ensure that Ritland's estimator was the most appropriate for detecting relationships in our study, we performed post-hoc comparisons of estimates based on our data using several different estimators in Coancestry 1.0.0.1 (Wang 2011). Although our relatedness analyses were performed using SPAGeDi, we used Coancestry to run power simulations. Although these software packages estimate relatedness in slightly different ways, we preferred SPAGeDi for empirical data as it allows permutation tests that provide more robust tests of significance than bootstrapping in Coancestry. We also conducted post-hoc simulations using our data to compare observed and expected values for different relationship types (e.g., parent-offspring, full-siblings, etc) to test the reliability of our empirical estimates of relatedness.

In Coancestry, the allelic frequencies from our study population were bootstrapped 100 times to then simulate genotypes for a population that contains individuals with user-specified relationships. We performed simulations for each of the following relationship types: twins, parent-offspring, full siblings, half siblings/grandparent-grandchild, double first cousins, first cousins, second cousins, and unrelated. We also performed simulations for different proportions of relationship types as follows: Combination 1: 0.25 twins + 0.25 parent-offspring + 0.25 full siblings + 0.25 half siblings; Combination 2: 0.25

parent-offspring + 0.25 full siblings + 0.25 half siblings + 0.25 unrelated; Combination 3: 0.187 parent-offspring + 0.156 full siblings + 0.156 half siblings + 0.156 first cousins + 0.156 second cousins + 0.187 unrelated. We chose these combinations based on our knowledge of the biology of other bat species in temperate regions that are believed to be matrilineal but with a high degree of mixing during breeding, resulting in close relatives at the maternal level, but large variation in relatedness at the nuclear level. From these different simulated genotypes, we then estimated average pair-wise relatedness among all individuals.

To determine if Ritland's coefficient of kinship was appropriate for our study, we compared the correlation of several different estimators of relatedness to the true value expected for the different simulated relationship types described above. The estimator with the highest correlation was deemed to be the best estimator for a given population structure (Table B4). To determine if we had sufficient power to detect a given population structure with our loci, we assessed whether the true value of the Ritland's estimator fell within the 95% confidence intervals (CIs) of the estimated value of a given simulated relationship type. If the true value fell within the 95% CIs, the estimated and true values were from the same distribution, indicating we had sufficient power to detect a given structure (Table B5).

In all cases, values were calculated across all possible pairs, as was the case for our empirical analyses of relatedness. As such, average values will naturally be lower than if they were calculated for only those pairs with the specified relatedness type. For example, in the simulated parent-offspring structure, there are also parent-parent and offspring-offspring pairs, which would likely be less related than parent-offspring. Thus, average relatedness across all pairs will be lower than an average across parent-offspring pairs only. In all cases, 100 reference individuals were used and 100 bootstraps were performed. Because large variances were observed for each of our estimates, we repeated simulations with 1000 and 10,000 bootstraps for the twin relationship type; however, they did not reduce the variance. We therefore used 100 bootstraps for all tests because they required less computational time and yielded essentially the same results as with 1000 or

10,000 bootstraps. Because we used SPAGeDi to obtain our empirical estimates of relatedness, we repeated our empirical tests in Coancestry. While the values we obtained differed slightly between the two programs, the trends were the same. Therefore, because SPAGeDi allowed us to perform permutation tests, which are more robust tests of significance than bootstrapping in Coancestry, we chose to present results obtained in SPAGeDi for the empirical data.

Based on these simulations we found that Ritland's estimator performed as well, or better, than other estimators for most relationship types (Table B4). Simulation tests with empirical data also demonstrated that observed estimates of relatedness using Ritland's estimator did not differ from expected simulated true values for all relationship types and combinations (Table B5). We therefore conclude that Ritland's kinship coefficient was appropriate for our study.

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Table B 1 PCR amplification conditions and genetic diversity measures for eight microsatellite loci from female northern long-eared, *Myotis septentrionalis*, in Dollar Lake Provincial Park, Nova Scotia (2005-2007).

Locus	Ta(^{o}C)	%OK	Allele size range (bp)	He	Ho	A	F_{is}	Null alleles?	Source species	Source of primers
Mmy-E24	**51.3**	**96.5**	**200-250**	**0.994**	**0.882**	**25**	**0.045**	**No**	*Myotis myotis*	Castella and Ruedi 2000
Mmy-G9	**55.0**	**96.5**	**130-180**	**0.898**	**0.872**	**18**	**0.029**	**No**	*M. myotis*	Castella and Ruedi 2000
Mmy-F19	**55.0**	**97.4**	**180-230**	**0.889**	**0.838**	**18**	**0.058**	**No**	*M. myotis*	Castella and Ruedi 2000
Mybe-15	**50.0**	**98.2**	**110-180**	**0.95**	**0.917**	**30**	**0.032**	**No**	*M. bechsteinii*	Kerth et al. 2002
Mmy-D15	51.3	63.2	70-140	0.939	0.792	27	0.158*	Yes	*M. myotis*	Castella and Ruedi 2000
Efu-4	45.0	77.2	200-260	0.907	0.591	17	0.349*	Yes	*Eptesicus fuscus*	Vonhof et al. 2002
Efu-6	47.4	82.5	180-240	0.867	0.745	16	0.142*	Yes	*E. fuscus*	Vonhof et al. 2002
Efu-21	47.4	-	-	-	-	-	-	-	*E. fuscus*	Vonhof et al. 2002

Bold indicates loci that were used in statistical analyses.
Efu-21 failed to amplify and therefore no results were obtained

Table B 2 Consensus sequence of the HVII region of mtDNA sequenced for female northern long-eared bats, *Myotis septentrionalis*, in Dollar Lake Provincial Park, Nova Scotia (2005-2007). Only the first 129 bp of the 290 bp sequence showed any variability.

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
G	A	A	T	A	C	T	C	A	A	T	C	A	A	C	C	A	T	T	A	A	C
23	24	25	26	27	28	29	30	31	32	33	I	35	36	37	38	39	40	41	42	43	44
A	T	T	G	T	A	A	G	A	T	T		A	C	C	T	T	A	A	T	A	T
45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66
G	T	C	C	T	T	A	G	A	T	C	A	T	T	A	A	C	C	T	A	C	A
67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88
G	T	C	C	T	G	C	T	C	C	C	T	C	A	T	T	A	T	G	T	G	G
89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110
G	T	T	T	A	G	G	G	T	G	T	A	C	A	T	T	C	T	A	G	G	T
111	112	113	114	115	116	117	118	119	120	121	122	123	124	125	126	127	128	129			
C	C	G	G	C	T	G	G	A	C	T	T	A	T	G	A	T	G	T			

Table B 3 Haplotypes based on 12 variable sites within HVII region of mtDNA sequenced for female northern long-eared bats, *Myotis septentrionalis*, in Dollar Lake Provincial Park, Nova Scotia (2005-2007). Only the first 129 bp of the 290 bp sequence showed any variability.

Site	20	21	22	24	33	34	62	64	106	124	125	129
CONSENSUS	A	A	C	T	T	T	C	A	T	T	G	C
Haplotype A	•	•	•	•	•	•	•	•	•	•	•	•
Haplotype B	•	G	T	•	•	•	•	G	C	C	A	•
Haplotype C	G	•	•	C	•	•	T	•	•	•	•	T
Haplotype D	•	•	T	C	C	C	T	•	•	•	•	T

Table B 4 Correlation coefficients of each relatedness estimator compared to the true value for each simulated structure.

Simulated structure	TrioML	Wang	LynchLi	LynchRd	Ritland	QuellerGt	DyadML
Twins	0.787	0.618	0.589	0.740	0.694	0.615	0.743
Parent-offspring	0.535	0.395	0.381	0.470	0.458	0.385	0.499
Full-siblings	0.492	0.381	0.395	0.460	0.468	0.403	0.477
Half-siblings, grandparent-grandchild	0.272	0.221	0.212	0.315	0.337	0.224	0.270
Double-first cousins	0.228	0.171	0.178	0.207	0.199	0.179	0.224
First cousins	0.116	0.090	0.078	0.113	0.099	0.082	0.113
Second cousins	-0.004	-0.015	-0.009	-0.016	-0.008	-0.003	-0.007
Unrelated	0.626	0.474	0.458	0.581	0.564	0.478	0.581
Combination 1*	0.626	0.474	0.458	0.581	0.564	0.478	0.581
Combination 2**	0.426	0.318	0.294	0.371	0.327	0.303	0.401
Combination 3***	0.342	0.259	0.235	0.337	0.321	0.238	0.327

Simulations with the highest correlation coefficient are the best estimators for that structure.

* 0.25 twins + 0.25 parent-offspring + 0.25 full siblings + 0.25 half siblings

** 0.25 parent-offspring + 0.25 full siblings + 0.25 half siblings + 0.25 unrelated

***0.187 parent-offspring + 0.156 full siblings + 0.156 half siblings + 0.156 first cousins + 0.156 second cousins + 0.187 unrelated

Table B 5 Simulation results for Ritland's estimator of relatedness (Ritland 1996) for different genetic structures.

Simulated structure	Expected true value	Observed estimate	Lower 95% CI	Upper 95%CI	True & Observed Differ?§
Twins	0.016	0.018	-0.085	0.152	No
Parent-offspring	0.008	0.015	-0.094	0.153	No
Full-siblings	0.008	0.014	-0.097	0.155	No
Half-siblings, grandparent-grandchild	0.004	0.005	-0.100	0.142	No
Double-first cousins	0.004	0.006	-0.102	0.149	No
First cousins	0.002	-0.002	-0.097	0.118	No
Second cousins	0.001	0.004	-0.096	0.129	No
Unrelated	0.000	-0.004	-0.102	0.119	No
Combination 1*	0.009	0.012	-0.093	0.150	No
Combination 2**	0.005	0.005	-0.098	0.141	No
Combination 3***	0.004	0.001	-0.097	0.129	No

Note: values are based on all pair-wise combinations and therefore true values are lower than would be expected for a given level of structure (see text for details).
§If true values fall within the 95% CI, then true and observed values are not different and we therefore had sufficient power to detect a particular level of structure.
*0.25 twins + 0.25 parent-offspring + 0.25 full siblings + 0.25 half siblings
**0.25 parent-offspring + 0.25 full siblings + 0.25 half siblings + 0.25 unrelated
***0.187 parent-offspring + 0.156 full siblings + 0.156 half siblings + 0.156 first cousins + 0.156 second cousins + 0.187 unrelated