

Do social networks of female northern long-eared bats vary with reproductive period and age?

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Abstract Social structure, which is a function of the patterns of interactions among individuals, is particularly variable in fission–fusion societies. The underlying factors that drive this variation are poorly understood. Female northern long-eared bats (*Myotis septentrionalis*) live in fission–fusion societies where females form preferred associations within groups that vary daily in size and composition as individuals switch roosts. The goal of our study was to test the predictions that preferred associations and social networks of female northern long-eared bats vary with reproductive period and age. We also tested the prediction that preferred relationships persist across years despite movements from summer roosts to winter hibernacula. Network analyses revealed that during gestation, females roosted in smaller groups where they roosted more regularly with fewer individuals than during lactation. This variation may reflect different social strategies to mediate higher energetic costs during lactation. Females of all ages roosted more often with younger individuals, which in turn had more direct and indirect associations than all other age classes. Younger individuals may play a role in maintaining connections between individuals, perhaps as a result of

younger individuals being more exploratory. Temporal analyses suggested that relationships can persist for years as some pairs roosted together for multiple summers. We suggest that the dynamic nature of fission–fusion societies is associated with individual strategies to increase fitness relative to individual characteristics, in this case reproductive condition and age.

Keywords Associations · Bat · Fission–fusion · *Myotis septentrionalis* · Social networks · Social structure

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

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(Vicente et al. 2007), and population genetics (Krause et al. 2007).

Sociality is taxonomically and geographically widespread among the roughly 1,200 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 bechsteini*) 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 (*Myotis 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 that 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; Podlutzky 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 disk-winged bats (*Thyroptera tricolor*), a tropical species that roosts in unfurling leaves, maintained preferred associations for at least 100 days, and up to 4 years (Vanhof 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 that 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.

Materials and methods

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) 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.

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 do 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, EIDAP Inc, Sherwood Park, Alberta, Canada), subcutaneously between the scapula of all new captures (56 and nine 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, FL, 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., CA, USA) and three-element yagi antenna (AF Antronics Inc., Urbana, IL, 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.

Analyses

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 3 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 $S^2 \times H > 5$ (Whitehead 2008c).

To graphically illustrate pairwise associations and groups, we used average linkage clustering analyses to create dendrograms 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 dendrogram was considered a good representation of the data if the cophenetic correlation coefficient (the correlation between pairwise HWI and the dendrogram linkages between pairs) was 0.8 or greater (Whitehead 2008b).

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 3 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, and 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; and (4) two levels of casual acquaintances, where pairs disassociate over time, but at two different rates (Table 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 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	$g(T) = a_2 + a_3 \exp(-a_1 T)$	16.16	0	2	3
2 levels of CA	$g(T) = a_3 \exp(-a_1 T) + a_4 \exp(-a_2 T)$	0	0.79	3	1

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

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 yield 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).

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 ($\pm 95\%$

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 ($\pm 95\%$ CI) HWI and weighted networks statistics, including strength, reach, and betweenness (see above), for young, intermediate, and old age classes (described above).

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 \pm 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 \pm 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 \pm SE = 7.20 ± 0.14 g), which is considerably lower than the accepted “5% rule” (Aldridge and

Brigham 1988). Average transmitter mass (mean \pm 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 \pm SD residency time = 1.20 ± 0.33 days) and those with PIT 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- 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 \pm SD residency time = 1.40 ± 0.64 days) and roosted in groups of variable sizes (range 1–67, mean=20, $n=59$ emergence counts).

Associations

The 83 females located on two or more occasions (mean \pm 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 ($S^2 \times H = 1.03^2 \times 47.23 = 49.805$), and our estimates of association indices were a good representation of the true pattern ($r=0.62$).

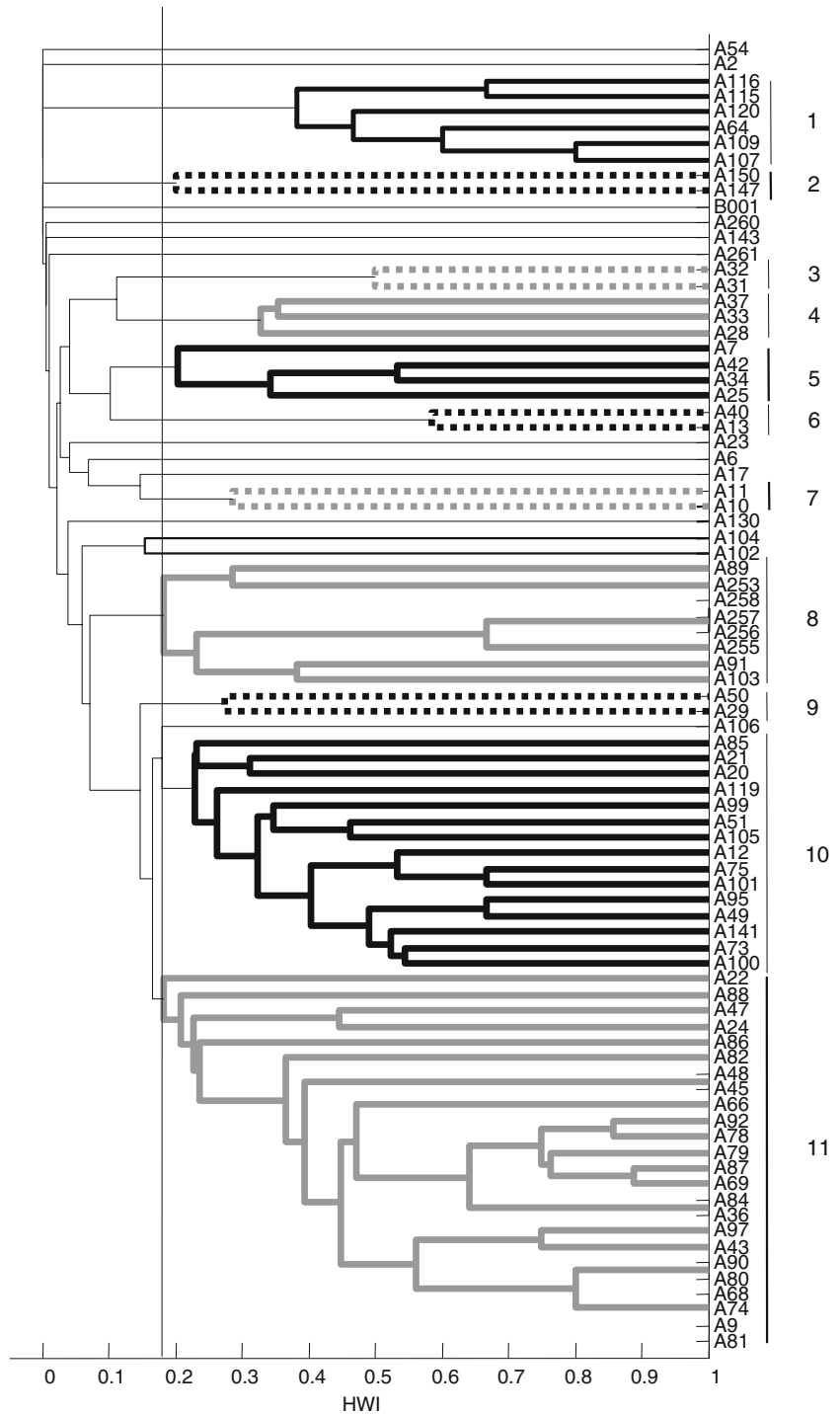
On average, pairs roosted together on 9% (range = 0 – 100%) of the total number of days they were located over the three summers (mean \pm SD observed HWI = 0.09 ± 0.16), though not necessarily on consecutive days. Although there were no significant differences between years (Mantel's $p > 0.50$ in all 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 (Fig. 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). Al-

though 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 (Fig. 1).

Fig. 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 (demarcated by *bold solid*, *hashed black*, and *gray lines*) were identified based on individuals with HWI values greater than twice the mean random HWI (>0.18; indicated by *vertical line*)



Temporal pattern

The SLAR dropped until day 10 at which point it reached an asymptote above the null association rate (Fig. 2). This pattern, together with the best fit decay model [$0.024245 \times \exp(-0.0014345 \times td) + 0.032077 \times \exp(-0.40395 \times td)$; Fig. 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 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.

Reproductive period

Females switched roosts almost daily during gestation (mean residency time \pm 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 \pm 95%CI = 12.91 ± 4.96 ; $n=24$) than lactation (16.42 ± 5.83 ; $n=17$; Fig. 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 \pm 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 \pm 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 \pm 95% CI = 12.09 ± 2.90 ; reach = 219.79 ± 124.56 ; Fig. 3) than lactation (strength = 6.30 ± 1.27 ; reach = 67.45 ± 33.50 ; Fig. 3).

Age

We assigned age class scores to 58 adult females (14 young, 31 intermediate, and 13 old) observed on two or more occasions (mean \pm CI observations— 6.93 ± 2.86 young, 7.23 ± 2.26 intermediate, and 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 ($S^2 \times H = 1.05^2 \times 46.81 = 51.45$) and that our estimates of association indices were a good representation of the true pattern ($r=0.62$). A

Fig. 2 Standardized lagged association rate, 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 (two 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

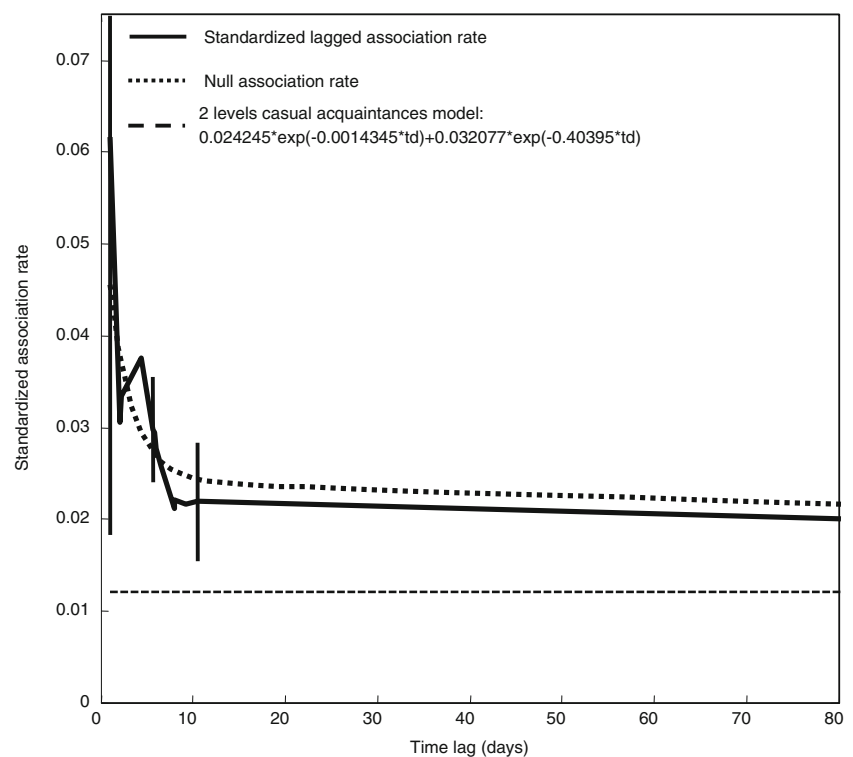
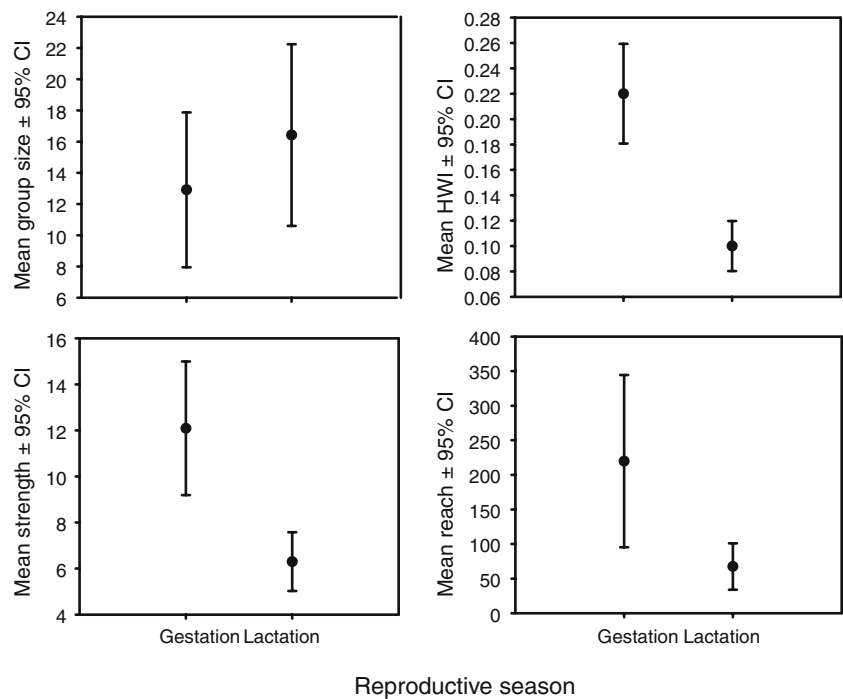


Fig. 3 Mean ($\pm 95\%$ confidence intervals) group size, half-weight index (*HWI*), strength, and reach during the gestation and lactation periods for female northern long-eared bats (*Myotis septentrionalis*) observed from June to August, 2005–2007, in Dollar Lake Provincial Park, Nova Scotia, Canada



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. 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 (Fig. 4).

interconnected, as evidenced by the spring-embedded network (Fig. 5). Although not significant based on overlapping CIs, young females had higher strength, reach, and betweenness (mean strength $\pm 95\%$ CI = 8.43 ± 2.78 , reach = 85.94 ± 55.66 , and betweenness = 23.04 ± 23.55 ; Fig. 6) than did intermediate (strength = 6.67 ± 2.16 , reach = 63.70 ± 41.44 , and betweenness = 10.75 ± 8.04 ; Fig. 6) and old females (strength = 5.97 ± 1.86 , reach = 61.72 ± 38.18 , and betweenness = 9.32 ± 8.33).

Fig. 4 Mean ($\pm 95\%$ 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

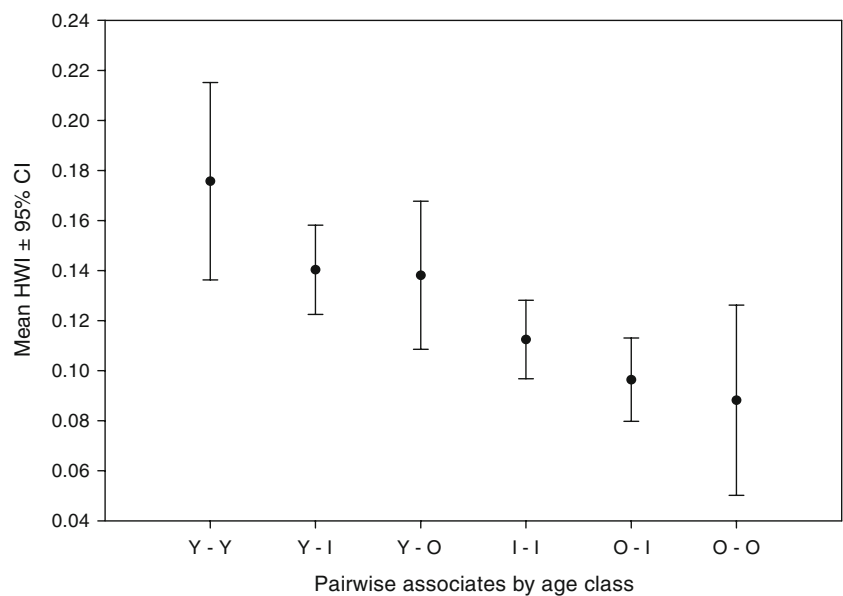
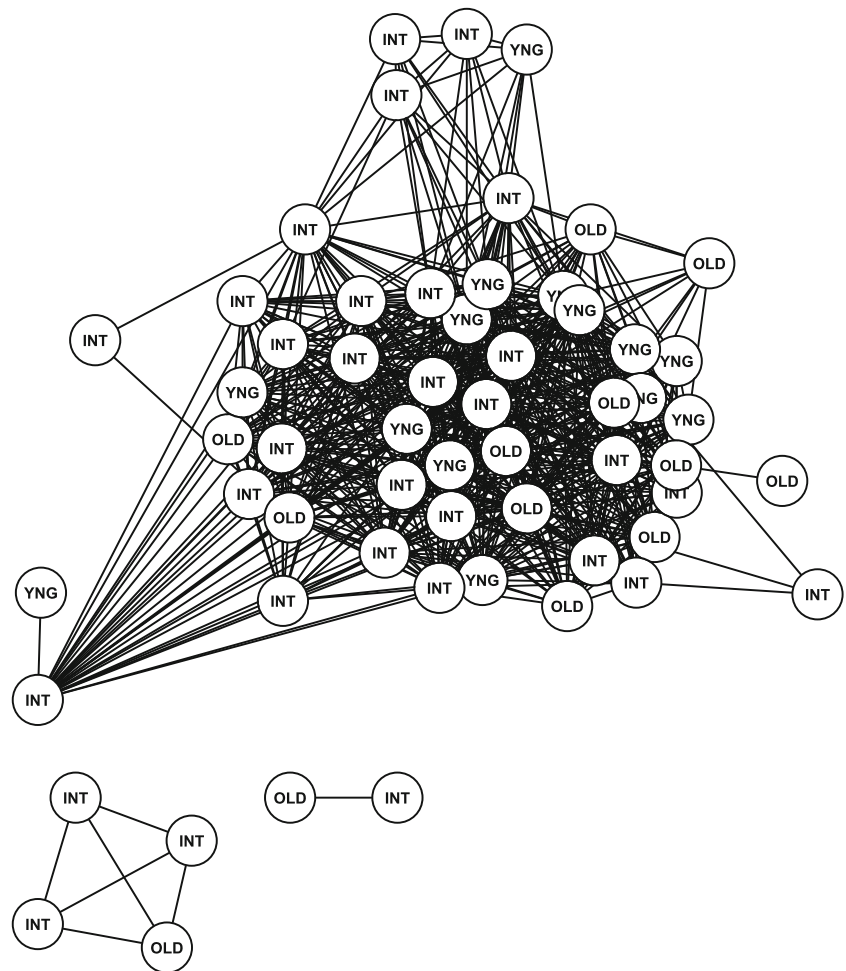


Fig. 5 Network diagram illustrating associations among individuals of young (*YNG*), intermediate (*INT*), and old (*OLD*) age classes for female northern long-eared bats (*Myotis septentrionalis*) observed from June to August, 2005–2007, in Dollar Lake Provincial Park, Nova Scotia, Canada



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 that 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

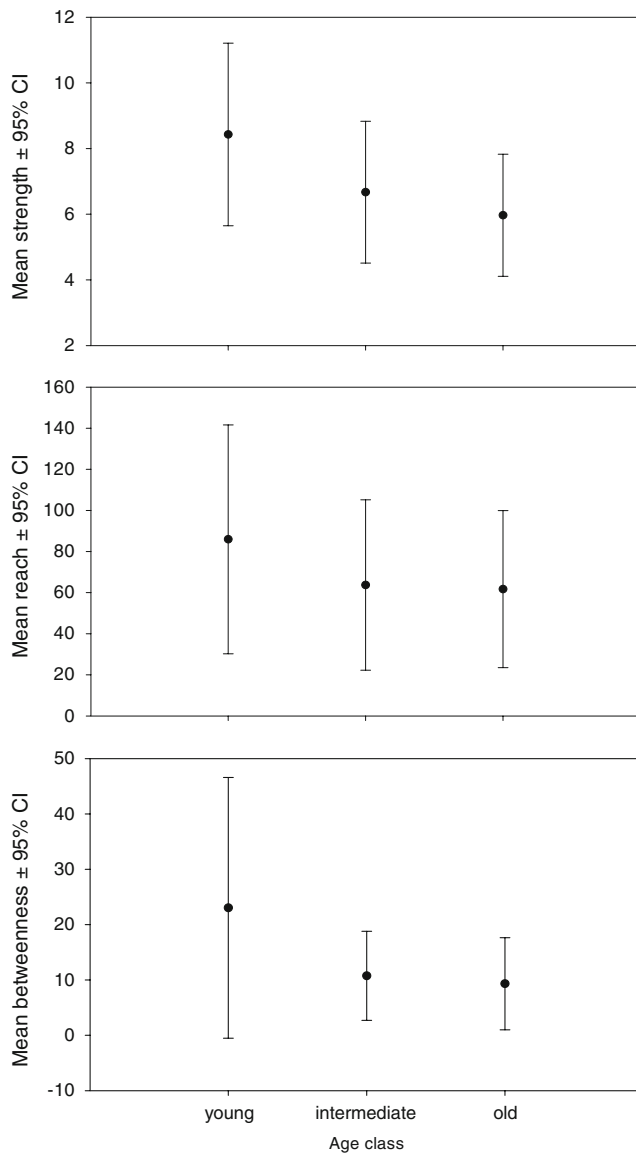


Fig. 6 Mean ($\pm 95\%$ confidence intervals) strength, reach, and betweenness for young, intermediate, and old age classes for female northern long-eared bats (*Myotis septentrionalis*) observed from June to August, 2005–2007, in Dollar Lake Provincial Park, Nova Scotia, Canada

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 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 matrilineal societies 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 that 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 (Bourjade 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, b). 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 Garroay 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. Garroay 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 König 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, and 0.46 across 3 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, and 18 across 3 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 (Garroay 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 USA, 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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Statement of integrity of research and reporting This study was conducted according to the standards of the Dalhousie University Committee on Laboratory Animals, the Canadian Council on Animal Care, and the Nova Scotia Department of Natural Resources Wildlife Act. The authors declare that they have no conflict of interest.

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