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Original Article

Female northern myotis (*Myotis septentrionalis*) that roost together are related

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Selection for cooperation, including nepotism, acts on individuals and so quantifying the genetic relationships between individuals that interact often is fundamental to understanding the evolution of sociality. Compared with stable kin groups, relatively little is known about the genetic relationships within groups with fission–fusion dynamics, and in particular between pairs that form long-term relationships. We examined the genetic relationships among female northern myotis, *Myotis septentrionalis*, that roost in maternity colonies consisting of multiple social groups, within which pairs form long-term relationships (i.e., familiar pairs). Using microsatellites and mitochondrial DNA, we found that females within colonies were not more closely related to one another than they were to females in neighboring colonies at the nuclear level, but they were at the maternal level. Females within social groups were more closely related than expected by chance at the nuclear but not at the maternal level. Furthermore, a comparison of pairwise associations and pairwise relatedness revealed that familiar pairs were more closely related than expected by chance at both the nuclear and maternal level. Kin selection may, therefore, play a role in shaping relationships within groups with fission–fusion dynamics.

Key words: **bat, fission–fusion, *Myotis septentrionalis*, pairwise association, pairwise relatedness, sociality.** *[Behav Ecol]*

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).

Although considered generally rare among animals (Aureli et al. 2008), fission–fusion dynamics appears to be relatively widespread among the roughly 1100 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). Females and their offspring gain thermoregulatory and antipredatory benefits from living in these groups (Kunz and Lumsden 2003) and may also benefit from reciprocity or nepotism if they form nonrandom associations or interact with relatives (Hamilton 1964; Maynard Smith 1964; Trivers 1971). 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 et al. 2011). Opportunities for cooperation are, therefore, more likely between these relatively stable, familiar pairs that may interact regularly in an otherwise dynamic system (Trivers 1971). Moreover, if these pairs are also kin, there may be opportunities to also gain inclusive fitness benefits through nepotism (Hamilton 1964; Maynard Smith 1964). For instance, much like other social taxa, several bat species show evidence of cooperative behaviors, including food sharing, allogrooming, allonursing, pup guarding, as well as information sharing about suitable foraging sites and shelter (Kerth 2008).

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 maternally inherited mitochondrial DNA (mtDNA) markers indicates that colonies typically consist of only a few matrilines

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that differ from neighboring colonies (Kerth et al. 2000; Kerth, Safi, et al. 2002; Vonhof et al. 2008; Kerth and Van Schaik 2011). Evidence from biparentally inherited nuclear markers 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, et al. 2002; Rossiter et al. 2002; Metheny 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 3 studies to date have examined genetic relatedness between familiar pairs within bat fission–fusion groups. Two of these studies found that familiar pairs were not more closely related than random pairs of females (Kerth and König 1999; Metheny et al. 2008). However, the genetic relationships could be determined for relatively few pairs in each population because genetic samples were available for only 28% and 50% of adults for which detailed association data were also available. This may have limited the ability to detect an effect of relatedness on association patterns. However, the third study had genetic samples and association data for nearly all group members in 2 different colonies. Here, they found that familiar pairs were not more closely related than random in one of the colonies they investigated, whereas they were in fact more closely related in the other (Kerth et al. 2011). Thus the results of the few studies conducted to date have not been consistent, suggesting that additional studies are needed to better understand the factors influencing associations among female bats in dynamic fission–fusion groups. Only then can we compare patterns across species, and ultimately across taxonomic groups, to better understand the evolution of these dynamics more broadly.

Our main goal, then, was to determine whether female northern myotis preferentially associate with related individuals and, if so, whether this could help explain relationships within fission–fusion dynamics among bats. Like other bats and taxonomic groups with fission–fusion dynamics, female northern myotis appear to live in matrilineal, multitiered societies. In this case, females display natal philopatry to summer roosting areas where they live in at least 2 independent colonies, each composed of multiple groups of females that roost together during the day (Garroway and Broders 2007; Patriquin et al. 2010). Although the size and composition of female groups found in each roost (i.e., a roost group) change daily, some females are found roosting together more often than expected by chance over the long term. These so-called 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). Although several studies have considered relatedness within roost groups (Burland et al. 1999; Kerth and König 1999; Rossiter et al. 2002; Metheny et al. 2008), genetic relationships within social groups may provide a better understanding of longer-term social relationships (e.g., Wilkinson 1985; Kerth et al. 2011). Within social groups, some pairs form stable relationships that can last for months or years (hereafter referred to as familiar pairs; Garroway and Broders 2007; Patriquin et al. 2010). The role of relatedness in shaping social relationships at these different levels has yet to be tested for this species. Therefore, based on samples collected from most (85%) of the known females in the study area, we use nuclear and mtDNA markers to determine whether female northern myotis live in matrilineal groups and to determine the genetic relationships among females within colonies and social groups, and between pairs.

MATERIALS AND METHODS

Capture and marking

We conducted our study in Dollar Lake Provincial Park (DLPP), Nova Scotia, Canada (4455′N, 6319′W; see Garroway and Broders 2007 for site description) from June to August 2005–2007. We captured bats using mist nets (Avinet, Dryden, NY, 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 behavior (Kunz and Parsons 2009).

DNA extraction and genotyping

We successfully genotyped 71 of the 83 females from the known social groups described in Patriquin et al. (2010) at 7 autosomal microsatellite loci and sequenced the mtDNA sequence from the hypervariable II portion of the control region (HVII). 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 Supplementary Material.

Statistical analyses

To quantify biparental relatedness, we used a maximum likelihood estimate of relatedness to estimate the probability that 2 alleles are identical by descent based on allelic frequencies from nuclear loci of the 114 females sampled from our study area (ML-Relate; Kalinowski et al. 2006). Although most studies have typically used Queller and Goodnight's (1989) coefficient of kinship to investigate relatedness in bats (e.g., Wilkinson 1992; Burland and Worthington Wilmer 2001; Kerth, Safi, et al. 2002; Rossiter et al. 2002; Veith et al. 2004; Metheny et al. 2008; Bohn et al. 2009), we used a maximum likelihood estimate of relatedness as it is typically more accurate when samples consist of loci with potential null alleles (Wagner et al. 2006), indications of which were found in 3 of our 7 loci (see Supplementary Material for details). Ignoring null alleles or removing loci with null alleles from analyses can result in biased estimates of relatedness and population structure (Kalinowski and Taper 2006; Chapuis and Estoup 2007). Therefore, by using a maximum likelihood estimate of relatedness and reference allele frequencies from within our study area, we improved our power to detect structure in small samples and minimized the likelihood of artificially high estimates of relatedness without affecting the expectation that average relatedness would be zero in a randomly mating population (Kalinowski and Taper 2006; Chapuis and Estoup 2007; Lehmann and Rousset 2010). To confirm that we

had sufficient power to detect structure, we compared observed and expected estimates of relatedness based on simulations of different population structures, such as parent–offspring, cousins, unrelated, or some combination of these relationship types. For simulation details, see Supplementary Material.

To determine if females within colonies and social groups were more related at the nuclear level than expected by chance, Mantel's tests were performed where individuals were permuted (10 000 times) either among colonies or social groups (R Core Team 2012). For this and all subsequent permutation tests, observed values were significantly greater than random ($P < 0.05$, 1-tailed) if they were greater than the permuted values on 95% or more permutations. Nine of the 71 females were excluded from the permutations between colonies as they were not previously identified as belonging to either of the 2 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 5 groups with 3, 3, 6, 11, and 19 females, for analysis.

To determine if 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 (see Supplementary Material). We then compared the distribution of haplotypes within each colony or social group to that expected under a random distribution using exact tests, which perform better than chi-square tests when samples sizes are small and expected values are low (McDonald 2009), as in our data. In addition, we used Mantel's tests, as described above, where individuals were permuted among matrilines to determine whether females belonging to the same matriline were also closely related at nuclear loci.

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 pairwise association values (half-weight index, HWI; see Patriquin et al. 2010 for details) across all pairwise combinations for the 71 genotyped females and the matrix of pairwise relatedness coefficients for all 71 individuals. We determined correlation coefficients between matrices and compared these with 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 2-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 with the time they spent with females from different matrilines. We then compared the observed difference between the average of these 2 values with a permuted distribution (10 000 permutations).

RESULTS

Pairwise relatedness was highly variable as the matrix of all pairwise kinship coefficients for all 71 females showed values ranging from 0 to 0.905. Relatedness at the maternal level was less variable, as there were only 4 haplotypes distributed among the 71 females. Haplotypes A, B, and C were shared by 43%, 38%, and 17% of the females, respectively. Haplotype D was found in only 1 female, which was omitted from further analyses of maternal relationships (Figure 1; see Table S2 for consensus sequence and haplotypes).

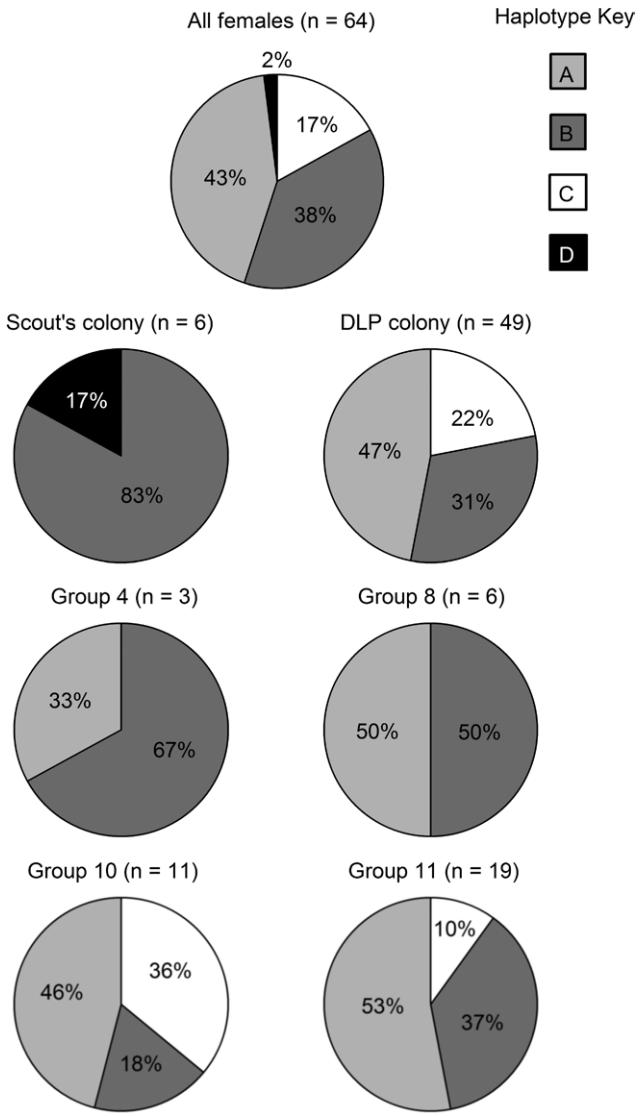

Figure 1
Haplotype distribution of female northern myotis, *Myotis septentrionalis*, within colonies and social groups in DLPP, Nova Scotia (2005–2007).

Average pairwise nuclear relatedness across all individuals in both colonies ($n = 62$ individuals) and across all 5 social groups ($n = 42$ individuals) was low (Table 1), indicating that the likelihood of shared alleles through common descent was low in all cases. Average nuclear relatedness within each colony was not significantly higher than between colonies ($P = 0.492$; Table 1), suggesting that females within each colony were not more closely related to one another than expected by chance. Simulation results indicate that failure to detect a difference in relatedness is not likely due to low power (see Table S3). Average nuclear relatedness within each social group was significantly higher than among social groups ($P = 0.002$; Table 1), suggesting that females within social groups were more closely related to one another than expected by chance. At the maternal level, there was overlap in haplotype distribution between the 2 colonies, but each colony also had a unique haplotype and the proportion of haplotypes within each of the 2 colonies differed significantly (Fisher's Exact test $P = 0.002$, degrees

Table 1

Observed and permuted average pairwise maximum likelihood estimate of relatedness (Kalinowski and Taper 2006) for female northern myotis, *Myotis septentrionalis*, in DLPP, Nova Scotia (2005–2007), within colonies, social groups, and matrilines

		Relationship coefficient		
Comparison	*n*	Observed (SE)	Permuted	*P*
Among colonies	62	0.046 (2.85×10^{-5})	0.045	0.492
Within colony 1	56	0.044 (0.002)	n/a	n/a
Within colony 2	6	0.045 (0.003)	n/a	n/a
Among social groups	42	0.08 (0.0001)	0.052	0.002
Within group 4[a]	3	0.224 (0.010)	n/a	n/a
Within group 5[a]	3	0.090 (0.11)	n/a	n/a
Within group 8[a]	6	0.048 (0.001)	n/a	n/a
Within group 10[a]	11	0.036 (0.0005)	n/a	n/a
Within group 11[a]	19	0.055 (0.0002)	n/a	n/a
Among matrilines	71	0.067 (1.63×10^{-5})	0.061	0.011
Within matriline A	13	0.054 (0.019)	n/a	n/a
Within matriline B	29	0.021 (0.008)	n/a	n/a
Within matriline C	29	0.008 (0.014)	n/a	n/a

n/a = permutation tests of significance are irrelevant at this level as we are not interested in differences between specific groups.
[a]Group labels refer to those used in Patriquin et al. (2010).

of freedom [df] = 3; Figure 1). There was, however, no significant difference in the proportion of haplotypes shared by the females within each social group (Fisher's Exact test $P = 0.575$, df = 6). Average nuclear relatedness across matrilines was low, indicating a low likelihood that females across matrilines shared alleles through common descent. Average nuclear relatedness also differed for each matriline and was significantly higher within than among matrilines ($P = 0.011$; Table 1), indicating that females within the same matriline were more likely to share alleles.

Based on the maximum likelihood estimate of relatedness, there was a small but significant positive correlation between pairwise association and pairwise nuclear relatedness (Dietz matrix correlation coefficient = 0.055; $P = 0.003$). Pairs of females from the same matriline spent significantly (18 permutations greater than observed mean difference in HWI, $P = 0.0018$) more time together ($\bar{X}\text{HWI} \pm \text{SD} = 0.14 \pm 0.26$) than did pairs of females from different matrilines ($\bar{X}\text{HWI} \pm \text{SD} = 0.10 \pm 0.18$).

DISCUSSION

Females within each of our 2 colonies were no more closely related to one another at the nuclear level than to females in the neighboring colony, but they were in fact more closely related at the maternal level. These results are consistent with the contention that colonies are founded by females that share a matriline and are therefore more likely to be genetically distinct at the maternal level (Metheny et al. 2008), supporting the behavioral observation that there are at least 2 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 et al. 2001; Kerth, Safi, et al. 2002; Metheny et al. 2008; Flanders et al. 2009; Kerth and Van Schaik 2011). Thus, failure to detect genetic structure within colonies is not likely a result of limited power, as we had a comparable number of loci (7) as many of these other studies that also did not detect structure within colonies (5–17 loci; mean = 10), and allelic richness was higher (16–30 alleles/locus) for all 7 loci than observed in most of these studies (4–19 alleles/locus). Instead, low relatedness within colonies has been attributed to a high level of mixing during mating at hibernacula and strong female natal philopatry to summer areas following hibernation (Kerth et al. 2000; Burland and Worthington Wilmer 2001; Kerth, Mayer, et al. 2002; Kerth and Morf 2004; Veith et al. 2004; Metheny 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).

Consistent with findings for female vampire bats, *Desmodus rotundus* (Wilkinson 1985), we found that females were indeed more closely related within social groups than across social groups at the nuclear level, but not at the maternal level. A recent study (Kerth et al. 2011) investigated relatedness among female Bechstein's bats within communities, which are qualitatively similar to social groups as they represent subgroups within colonies that associate more regularly over time despite frequent roost switching. Female Bechstein's bats within communities are not more related at the nuclear level but they are at the maternal level (Kerth et al. 2011). Although communities are qualitatively similar to social groups defined here and for vampire bats, they are quantitatively different, thus limiting our ability to interpret the differences between the studies. Nevertheless, we cautiously speculate that the differences may be due in part to differences in the stability of group composition and the number of different matrilines. Female Bechstein's bat communities are highly stable across years, whereas female northern myotis move among social groups regularly within and between years. Familiarity may therefore be a reliable predictor of the potential for cooperation in Bechstein's bat communities, whereas relatedness may be a more reliable predictor in less stable female northern myotis social groups. Moreover, given that the entire colony of northern myotis consisted of considerably fewer matrilines than Bechstein's bat communities, it is perhaps not surprising that maternal relatedness is not a strong predictor of associations at the social group level.

Thus, although maternal relatedness among female northern myotis may play a role in shaping social relationships at the colony level, likely owing to strong female natal philopatry, it does not appear to play a strong role at the social group level. Because we could not observe interactions among group members, it is not clear why female northern myotis 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 et al. 2008). Alternatively, social groups may reflect shared preferences for roosts that provide optimal conditions for gestation, nursing, and pup development (Metheny et al. 2008).

Perhaps most importantly, by looking at relatedness between all genotyped pairs, we were able to demonstrate that, although 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. These findings contrast those of the few studies that have investigated similar relationships in female bats but found that familiar pairs were not more closely related (Kerth and König 1999; Metheny et al. 2008; Kerth et al. 2011). Interestingly, familiar pairs were in fact more closely related in the larger of 2 female Bechstein's bat colonies (Kerth et al. 2011).

Therefore, it is possible that females may shape relationships based on familiarity in smaller groups, whereas they may rely on cues about similarity, such as relatedness, in larger groups (Couzin and Laidre 2009).

Our results also suggest that the potential exists for cooperation between related female pairs in this dynamic system (Hamilton 1964).

A combination of kin selection and reciprocity may therefore play an important role in shaping social relationships, and ultimately cooperative behaviors, among group members living in dynamic fission–fusion groups. For instance, female northern myotis, among other species discussed above, live in matrilineal colonies comprised of social groups made up of relatives within which at least some pairs of females spend more time roosting with relatives (Hamilton 1964). However, as observed for other taxa, estimates of relatedness varied widely among female northern myotis and on average were generally low. Thus, although at least some females appear to form associations based on relatedness, females also regularly associated with unrelated individuals, which suggests cooperative behaviors may also evolve through reciprocity (Trivers 1971). Although 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 address 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, overall relatedness will not be high and may then obscure the strength of relatedness of specific pairs. As a result, the potential for kin selection may not be detected. In addition, relationships at the pairwise 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 pairwise relationships and to perform relevant tests to determine appropriate estimators for their populations.

In conclusion, our results further support the suggestion that female bats with fission–fusion dynamics live in systems analogous to those of other taxa (Kerth et al. 2011), such as African elephants, *Loxodonta africana*, and sperm whales, *Physeter macrocephalus*, that also live in multitiered groups with fission–fusion dynamics. For instance, female African elephants and sperm whales live in matrilineal groups (analogous to colonies) comprised of multiple smaller subgroups (analogous to social groups) that are also closely related at the nuclear level (Archie et al. 2006, 2008; Pinela et al. 2009). In addition, familiar pairs of female elephants are also closely related (Archie et al. 2006, 2008). However, in contrast to our findings, African elephant subgroups are also related at the maternal level (Archie et al. 2008). Thus, although there appear to be some consistent patterns of relatedness and social structure across species of bats, and other taxonomic groups, with fission–fusion dynamics, there is also considerable variation. This variation may be due to a combination of differences in constraints on group size, cognitive abilities, and the extent of fission–fusion dynamics, which may influence the degree to which individuals may rely on relatedness or familiarity to shape social relationships (Dunbar and Shultz 2007; Couzin and Laidre 2009). Each of these factors therefore requires further examination to better understand the evolution of these dynamic systems.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/

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