

Complex social structure of southern flying squirrels is related to spatial proximity but not kinship

Colin J. Garroway · Jeff Bowman · Paul J. Wilson

Received: 19 June 2012 / Revised: 3 October 2012 / Accepted: 3 October 2012 / Published online: 19 October 2012
© Springer-Verlag Berlin Heidelberg 2012

Abstract Social individuals have organized relationships that affect fitness and so a species' tendency to be social has important implications for its population ecology, gene flow, and its distribution in space and time. We quantitatively examined the social structure of southern flying squirrels (*Glaucomys volans*) and tested for a role of kinship and prior familiarity in predicting social structure. To quantify social structure, we monitored nest group composition of southern flying squirrels. All squirrels at the study site were marked with passive integrated transponder (PIT) tags and nest cavity entrances were monitored with automated PIT tag recorders for a period of 28 months. Squirrels were genotyped at eight microsatellite loci. Permutation tests of associations suggested that individuals nested with other specific individuals more often than expected by chance.

The lagged association rate indicated that relationships were stable and persisted across seasons and years. Multiple summer nest associates came together in winter to form larger nest groups which were likely important for social thermoregulation. A measure of prior familiarity, but not kinship, was related to the proportion of time individuals nested together during winter. We suggest that the evolution of sociality in southern flying squirrels is driven largely by mutually beneficial behaviors related to social thermoregulation although other, as of yet, unidentified mechanisms are needed to explain sociality in the warm season. We hypothesize that minimum group size requirements associated with social thermoregulation could explain the absence of this species in patchy landscapes and aspects of range boundary dynamics near their northern range boundary.

Communicated by G. S. Wilkinson

C. J. Garroway
Environmental and Life Sciences Graduate Program,
Trent University,
Trent University DNA Building, 2140 East Bank Drive,
Peterborough, Ontario K9J 7B8, Canada

J. Bowman
Ontario Ministry of Natural Resources,
Trent University DNA Building, 2140 East Bank Drive,
Peterborough, Ontario K9J 7B8, Canada
e-mail: jeff.bowman@ontario.ca

P. J. Wilson
Biology Department, Trent University,
Trent University DNA Building, 2140 East Bank Drive,
Peterborough, Ontario K9J 7B8, Canada
e-mail: pawilson@trentu.ca

C. J. Garroway (✉)
Edward Grey Institute, Department of Zoology,
University of Oxford,
South Parks Road,
Oxford OX1 3PS, UK
e-mail: colin.garroway@zoo.ox.ac.uk

Keywords Social thermoregulation · Cooperation · Kin selection · Lagged association rate · *Glaucomys volans* · Mutualism

Introduction

A society is a group of cooperating and competing individuals with organized relationships that affect fitness. Social individuals seek to interact with other specific individuals, and the pattern and nature of these interactions over time defines a social structure (Hinde 1976). Social interactions are context dependent, contingent on the fitness costs and benefits associated with kinship and ecological constraints (Hamilton 1964a, b; Trivers 1971; Clutton-Brock 2009). Social structures can have particularly important effects on mating patterns, cooperation, competition, and spatial and temporal distributions of individuals and alleles. The tendency to be social is a basic biological property of many species and elucidating the various avenues through which sociality can evolve is a long-standing and active focus of evolutionary ecology (Darwin 1859; Clutton-Brock et al. 2009).

Prominent models for the evolution of sociality include reciprocal altruism, inclusive fitness, mutualism, and manipulation (Hamilton 1964a, b; Trivers 1971; Clutton-Brock 2009). Trivers (1971) showed that in theory, cooperation among non-kin could evolve if an individual that shares resources at an initial cost receives a net benefit in future exchanges. However, unambiguous evidence for reciprocity that can explicitly exclude inclusive fitness, mutualism, and manipulation, which are often simpler explanations for sociality, is rare (Clutton-Brock 2009). Hamilton (1964a, b) proposed that the concept of gene-based selection should be extended to include the fitness of gene copies within other individuals as well as an individual's own genes. Within the inclusive fitness or kin selection paradigm, the apparent fitness costs to individuals associated with some social interactions (i.e., cooperative rearing of young) can be ameliorated if the beneficiary is kin and the result is that more copies of an individual's genes are passed to future generations. In cases where kin selection is important, it often explains asymmetries in the tendency to be social among individuals as well as the persistence of sociality despite perceived high fitness costs to some individuals. Although kinship can facilitate the evolution of sociality, it is not a necessary prerequisite (Clutton-Brock 2009). Individuals can derive mutual, collective benefits from sociality such as occur as a result of pack hunting in carnivores. Benefits from manipulations can occur when individuals coerce others to provide some sort of assistance that can sometimes result in shared, if disproportionate benefits to both individuals. In each of these last two cases, the benefits of interactions are immediate. This is important because with no delay between the incurring of costs and accruing of benefits associated with an interaction, cheating strategies that exploit time lags between cost and benefits seem unlikely to evolve (Clutton-Brock 2009).

Southern flying squirrels (*Glaucomys volans*) nest communally in tree cavities, remain active year-round, and are nocturnal. They are not known to hibernate but rather confront the energetic demands of winter by caching tree seeds in autumn and socially thermoregulating within tree cavities. The effects of latitude and seasonality on communal nesting have been studied throughout their range and suggest that sociality is likely an important aspect of this species' biology (Muul 1968, 1973; Goertz et al. 1975; Heidt 1977; Sonenshine et al. 1979; Gilmore and Gates 1985; Sawyer and Rose 1985; Layne and Raymond 1994; Reynolds et al. 2009). These studies have found that nest groups can contain mixed sex and age individuals that persist throughout the year and that group sizes tend to be largest during winter, when social thermoregulation is particularly important (Stapp et al. 1991). Despite the importance of group nesting for social thermoregulation, there is no trend toward larger aggregations at higher latitudes as

might be predicted based upon exposure to increasingly cold temperatures. This suggests that there are likely benefits of communal nesting beyond shared thermoregulation in the species. Indeed, the largest reported mean and maximum group sizes reported for southern flying squirrels occurred in Florida, a locality with relatively warm winter temperatures (Layne and Raymond 1994). Further, Layne and Raymond (1994) monitored groups of marked individuals in nest boxes and noted that individuals that had scattered after disturbance were often later found together in a different nest box. Some pairs from their study groups remained associated across years (Layne and Raymond 1994). Taken together, these data are suggestive of long-term, nonrandom associations both in winter when social thermoregulation is important and in the summer breeding season when different benefits of sociality may maintain social behavior. Layne and Raymond (1994) speculated that additional benefits of sociality to flying squirrels could include reduced stress among individuals through increased familiarity of local residents, increased success finding mates, better predator detection, and increased foraging success. To date, however, there have been no field studies of southern flying squirrel social structure in the form of testing for nonrandom association between pairs of squirrels and the persistence of social relationships in time.

Our goal was to quantify southern flying squirrel social structure and begin to examine the pathways through which it may have evolved. To do this, we continuously monitored (for 28 months) flying squirrel nest group composition within a population of flying squirrels. We used passive integrated transponder (PIT) tags that were implanted subcutaneously into squirrels and automated PIT tag recorder antennas placed over nest cavity entrances. We first tested for nonrandom associations of pairs of individuals at nest trees. We then calculated the probability of pairs reassociating over time to characterize the temporal permanence of relationships within southern flying squirrel nest groups. Random association patterns are suggestive of passive, non-social benefits of group nesting as they are not contingent upon specific relationships. In the absence of physical or geographical barriers, we considered nonrandom association patterns and group stability to show that individuals actively associated (i.e., they had social preferences).

Because we could not monitor interactions among individuals within cavities, we could not directly observe cooperative behaviors and could not test for forms of reciprocal altruism. However, given the close proximity of individuals within cavities, it is likely that all individuals within a cavity interacted. To determine whether there was a potential role for inclusive fitness benefits in the evolution of sociality in flying squirrels, we tested whether the degree of association among pairs of individuals (the estimated proportion of time individuals nested together) was related to kinship. Genetic

evidence for kin-based nest groups is equivocal with support both for (Thorington et al. 2010) and against (Winterrowd et al. 2005) kin-based social nesting in this species. Finally, we tested for a role of prior familiarity of individuals in predicting social associations (e.g., Thorington and Weigl 2011a). Specifically, we tested whether the spatial proximity of individual summer home ranges predicted winter associations. Suitable cavities were not limiting at this site and squirrels moved among cavities often and so spatial proximity of home ranges should be an indicator of familiarity. Within the context of kin selection, prior familiarity is one mechanism for kin identification. In the absence of kin-based sociality, associating with familiar individuals can still provide fitness benefits (Griffiths et al. 2004) and is indicative of a role for mutualism or manipulation in the evolution of flying squirrel sociality.

Methods

Field work

Field work took place from November 2006 to April 2010 at Trent University's James McLean Oliver Ecological Centre, Ontario, Canada (44.57°N, 78.49 W°). The property consisted of approximately 38 ha of primarily mature hardwood (sugar maple, *Acer saccharum*; white birch, *Betula papyrifera*; trembling aspen, *Populus tremuloides*; red oak *Quercus rubra*; and American beech, *Fagus grandifolia*) interspersed with some softwood (eastern white cedar, *Thuja occidentalis* and white pine, *Pinus strobus*) (Coombs et al. 2010). Squirrels were trapped throughout the study area with Tomahawk model 102 live traps (Tomahawk Live Trap, Tomahawk, WI, USA) using sunflower hearts as bait. On trap nights, between 20 and 67 traps were set at sunset and checked between one and four times per evening to reduce the time squirrels spent in traps and to reset traps that had been tripped by other species attracted to the bait. We aimed to trap for three nights per week throughout the study. Additionally, we trapped daily for approximately 2.5 weeks following the reproductive season and again, following winter to mark juveniles and immigrants. All trapped individuals had individually identifiable PIT tags (model TX1411SST, 12.50 mm×2.07 mm, 134.2 kHz ISO, 0.1020 g, Biomark Inc. Boise, ID, USA) injected subcutaneously for identification and tissue samples (either an ear punch or a pinch of hair with follicles) taken for subsequent genetic analysis.

Subsets of individuals were followed throughout the study via radio telemetry (1.8 g BD-2C radio collars, Holohil Systems Inc., Carp, Ontario, Canada) to locate nest trees. We trapped continuously throughout the study to develop and remove radio collars and to ensure all individuals

in the study area were marked. We tried to have one collar active per group of squirrels; between one and nine were active at any time. Collar batteries lasted approximately 2.5 months. Collars needed to be manually removed and so we removed collars from recaptured individuals for which we had greater than 1 month's nesting data. Collars with remaining battery life were redeployed. Where nest cavities were accessible, we placed circular antennas, either by climbing trees or with extension poles, where trees were unsafe to climb, attached to automated PIT tag recorders (model LID 650, Sherwood Park, AB) over cavities to monitor nest group composition. Inaccessible nest trees were typically those where we could not find the cavity entrance either visually or by climbing the tree.

Social analyses

We used the social affinity index (SAI; Lazo 1994), calculated from PIT tag association data, to estimate the proportion of days individuals nested together in the same tree. The SAI was calculated as: $N_{A,B}/\min(N_A, N_B)$ where $N_{A,B}$ was the number of days individual *A* and *B* nested together, N_A was the number of days individual *A* was identified and N_B was the number of days individual *B* was identified. The SAI accounts for the introduction and loss of individuals from a study area and so was the most appropriate association index for our study as flying squirrels have a high mortality rate as an important prey species and our study encompassed reproductive periods where new individuals were introduced to the population (Whitehead 2008). Pairs were considered to have nonrandom associations if they associated at rates above the null association rate, calculated as $n_{\text{associate}}/(N-1)$ where N was the total marked population and $n_{\text{associate}}$ was the individual's average group size (Whitehead 1995; Lusseau et al. 2006).

To further test whether pairs associated more or less frequently (preferred and avoided association) than random expectation, we compared the standard deviation from the observed association matrix to those of randomly permuted association matrices (Manly 1995; Bejder et al. 1998; Whitehead 1999; Miklos and Podani 2004; Whitehead et al. 2005; Whitehead 2008). When there are preferred associations, avoided associations, or both, the standard deviation of association indices will be higher than that expected if associations are random (Bejder et al. 1998). Data were permuted such that group size and the number of times an individual was identified were kept constant, thus retaining important features of the real data during permutations. As this method permutes association matrices sequentially and begins with the original data set, permutations are not independent of each other. Thus, the number of permutations needed to generate accurate *p* values is higher than that needed using standard Monte Carlo methods (Bejder et al. 1998).

The number of permutations required is determined by increasing the number of permutations until p values stabilize (Bejder et al. 1998). The SAI was calculated for each permutation and individuals were considered to associate significantly if the standard deviation of the SAI was greater than 95 % of permuted standard deviation values (one-tailed; Bejder et al. 1998). An advantage of comparing pairwise associations to null association rates is that the comparison relies directly on observed association values. However, because the SAI is a proportion, it is affected by the number of times an individual is observed. The permutation test takes this uncertainty into account; however, it relies on an arbitrary cutoff point for significance and can be affected by spatial structure and so it is valuable to compare the SAI to the null association rate as well as to perform permutation tests.

We calculated the temporal permanence of pairwise relationships using the lagged association rate (Whitehead 1995). The lagged association rate is an estimate of the probability that a random associate of an individual on a day will be identified with that individual subsequently at a given time lag. We also calculated the lagged identification rate to aid in the interpretation of the lagged association rate. The lagged identification rate is an estimate of the probability that an animal in the study area at a time will be the same as a randomly chosen individual at a later time (the probability of remaining in the study area divided by the population size) and thus is not a social measure. A decline in the lagged identification rate indicates animals are leaving the study area either through immigration or mortality. Thus, coincidental drops in both the lagged identification and association rates suggest that changes in social association are demographic (dispersal or mortality), whereas changes in the lagged association rate without changes in the lagged identification rate suggest social dissociation.

Roles of familiarity and relatedness

Each individual was genotyped at eight microsatellite loci: SFS3, SFS15 (Fokidis et al. 2003), GS4, GS8, GS10 (Zittlau et al. 2000), Pvol41, Pvol74, and PvolE6 (Painter et al. 2004). For genotyping details, see Garroway et al. (2010, 2011). We calculated pairwise relatedness among individuals following Queller and Goodnight (1989), where the relatedness estimator is based upon allele frequency differences from the population mean. We tested for a relationship between the estimated proportion of time a pair nested together (the SAI) and relatedness with Mantel tests. To test for a role of familiarity, we calculated the pairwise distance between the centroids of summer nest tree ranges and compared these distances to the SAI for the subsequent winter with a Mantel test. Nest tree ranges were created by drawing 100 % minimum convex polygons around each individual's

nest trees in summer and winter. We divided years into summer and winter nesting seasons based upon an assessment of when group sizes began to increase prior to winter and decrease following winter. Winter was defined in each year as 17 November–28 February and summer, 1 March–16 November.

It was not possible to sample and mark juveniles while they were still in their nest cavities nursing. Thus, juveniles were not trapped until they were full grown and foraging on their own. There is undoubtedly a period of time when young of the year are dependent upon their mothers and nesting will, at least partially, be kin-based. Because we did not monitor associations between mothers and their nursing offspring, all of our inferences regarding the potential kin basis of associations are for free-ranging individuals.

The SAI, lagged association rate, and lagged identification rate were calculated using the software SOCPROG (Whitehead 2009). We used the adegenet package (Jombart 2008) for the R statistical language (R Core Development Team 2008) to calculate molecular statistics. All other statistics were calculated using R.

Results

Fieldwork

We captured and marked 123 southern flying squirrels. We radio-collared a subset of 43 squirrels and tracked them to 74 nest tree cavities from which we could obtain PIT tag recordings (55 trees in summer and 19 in winter). During the summer, radio-collared squirrels used a mean [SD] of 6 [4] nest trees within a mean 2.8 ha [3.9] nest tree home range. During the winter, squirrels used 2.7 [1.1] nest trees within a 2.1 ha [1.2] nest tree home range. Squirrels reused nest trees extensively within seasons but not across seasons. Thus, nest trees could be monitored continuously throughout particular seasons by monitoring nests with and without radio-collared squirrels. Indeed between ten and 15 PIT tag recorders were active throughout the entire 28 months of the study with between zero and five collecting nesting association data on any given day. We recorded 88 marked individuals on between 7 and 238 days each (mean: 83 [45]; median: 73.5; about 7,300 squirrel days of recordings). The mean estimated proportion of days individuals nested together across the entire population, as estimated by the SAI, was 0.05 [0.16]. The mean proportion of time individuals nested together excluding pairs that never associated (mean of all nonzero association values) was 0.26 [0.21]. The null association rate was 0.06. We successfully amplified genotypes for 76 of the 88 marked individuals (Table 1). Some individuals could not be genotyped due to low amplification success of DNA from hairs.

Table 1 Summary of molecular data by locus (*Na* number of alleles, *Ho* observed heterozygosity, *He* expected heterozygosity)

Locus	Na	Ho	He	Reference
SFS14	10	0.66	0.74	Fokidis et al. (2003)
SFS15	8	0.76	0.81	Fokidis et al. (2003)
SF203	7	0.54	0.64	Fokidis et al. (2003)
Pvol41	19	0.85	0.88	Painter et al. (2004)
Pvol74	14	0.76	0.88	Painter et al. (2004)
PvolE6	18	0.70	0.72	Painter et al. (2004)
GS10	11	0.77	0.85	Zittlau et al. (2000)
GS8	9	0.79	0.80	Zittlau et al. (2000)

Social analyses

Permutation tests suggested that associations were highly nonrandom both within years and across the entire study period; the standard deviation of SAI was greater than 99 % of permuted association index standard deviation values (*p* values stabilized after 50,000 permutations). There were two tiers of association apparent: a summer tier with a mean group size of 2.41 [± 1.11 SD, range 1–10] and a winter tier with a mean group size of 6.21 [± 3.58 SD, range 1–22] (Fig. 1). Pairs with $SAI > \sim 0.5$ typically nested together throughout the year, whereas pairs with 0.06 (null) $< SAI < 0.5$ typically were only winter associates. The cophenetic correlation coefficients, a measure of the fit of the dendrogram representation to the underlying data, were 0.97 for year 1 (Fig. 1a) and 0.92 for year 2 (Fig. 1b). This suggests that the dendrograms were good representations of the data and that the two levels of association in the dendrograms were features of the data and not of dendrogram construction.

Both tiers were comprised of mixed sex groups with both reproductive and nonreproductive individuals. Beginning in November, summer nest groups began to associate with each other with group size peaking in January (Fig. 2). The lagged association rate declined with time but remained well above the null association rate until a time lag of 613 days had passed (Fig. 3). The lagged identification rate mirrored the lagged association rate suggesting that the decrease in the probability of reassociating in time was related to demographic processes such as mortality and emigration rather than a breakdown of social relationships (Fig. 3). This suggests that social relationships were typically stable, long-term (as many as 20 months) entities with turnover related to individuals entering and leaving the system.

Roles of familiarity and relatedness

To test for relationships between relatedness and association and prior familiarity and association, we broke the data

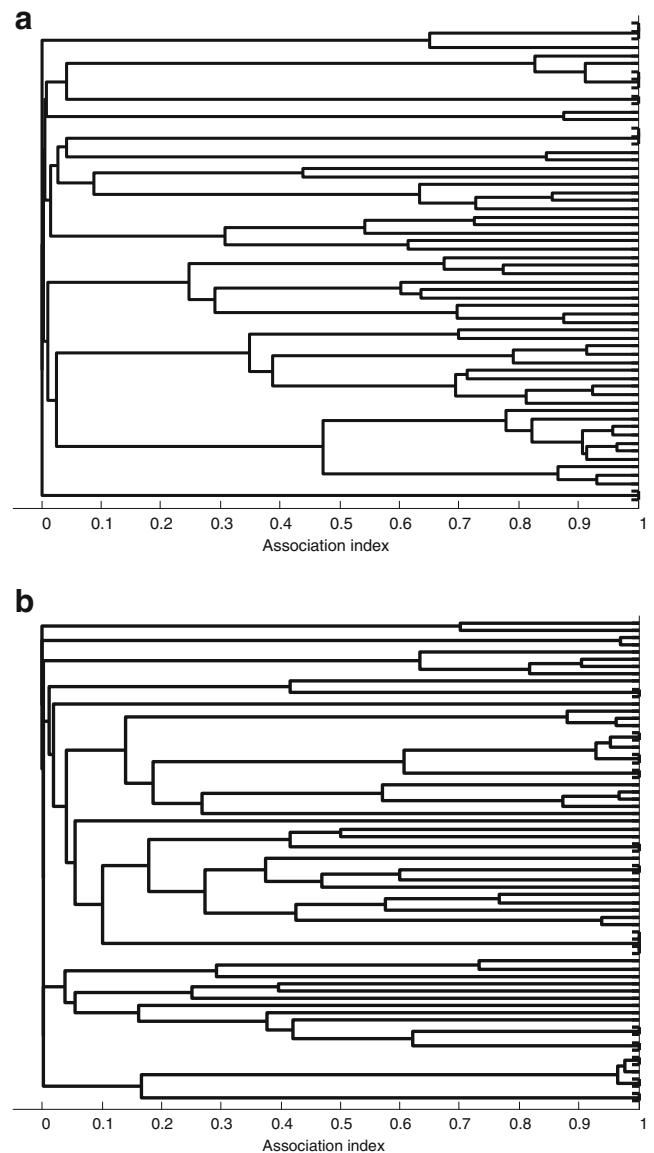


Fig. 1 Dendrogram representations of nesting associations among southern flying squirrels (*G. volans*) sampled in Ontario, Canada between the 17 November 2006 and 16 November 2007 (a) and 17 November 2007 and 16 November 2008 (b). Association data were collected via automated PIT tag recorder antennas placed over nest cavities. The proportion of time individuals nested together was estimated with the social affinity index (SAI) and the dendrograms were constructed using average linkage clustering. Pairs with $SAI > \sim 0.5$ typically nested together throughout the year, whereas pairs with 0.06 (null) $< SAI < 0.5$ typically were only winter associates

down into two full summer and three full winter seasons (overall length of the time series was 28 months). Mean relatedness was 0.02 [0.19] among summer groups and -0.03 [0.21] among winter groups. The mean relatedness among all individuals was -0.012 [0.19]. Relatedness between pairs of individuals was not a good predictor of the estimated proportion of time those individuals nested together (Mantel tests: summer 1, $n_{\text{individuals}}=51$, $r=0.03$,

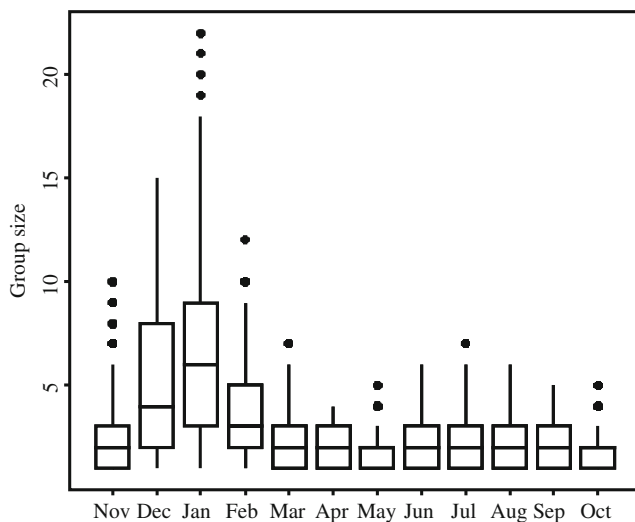


Fig. 2 Boxplot of mean monthly nest group sizes of southern flying squirrels (*G. volans*) in Ontario, Canada during November 2006 to April 2010. Data were pooled across years

$p=0.20$, summer 2, $n_{\text{individuals}}=42$, $r=0.02$, $p=0.41$, winter 1, $n_{\text{individuals}}=31$, $r=0.05$, $p=0.14$, winter 2, $n_{\text{individuals}}=45$, $r=0.03$, $p=0.16$, winter 3, $n_{\text{individuals}}=33$, $r=0.09$, $p=0.45$; Fig. 4). Instead the distance between the centroid of summer nest home ranges of individuals was negatively related to the proportion of time individuals spent together during winter

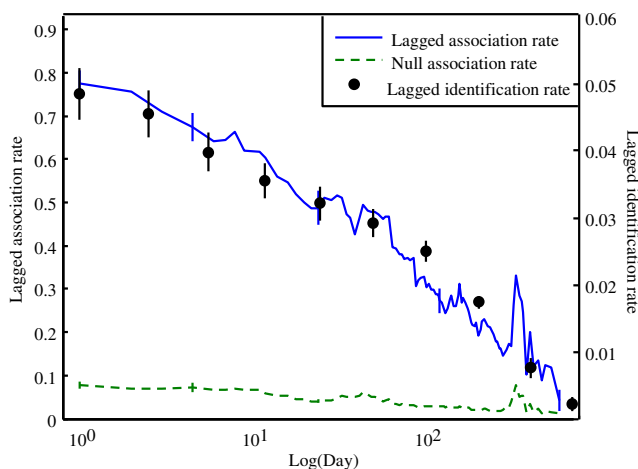


Fig. 3 A plot of the probability that pairs of southern flying squirrels (*G. volans*) nesting together on a particular day would be found together at a later time (lagged association rate), the expected association rate if associations were random (null association rate), and the probability that squirrel in the study area at a particular time will be the same as a randomly chosen individual at a later time (lagged identification rate). The precision of the estimated association rates was determined by jackknifing and the error in the lagged identification rate was determined by bootstrapping. The lagged association rate falls throughout the study until it reaches the null association rate after just over 600 days. The lagged identification rate mirrors the lagged association rate closely. This suggests that the drop in the probability of pairs reassociating in time is likely related to individuals leaving the study system either through mortality or immigration

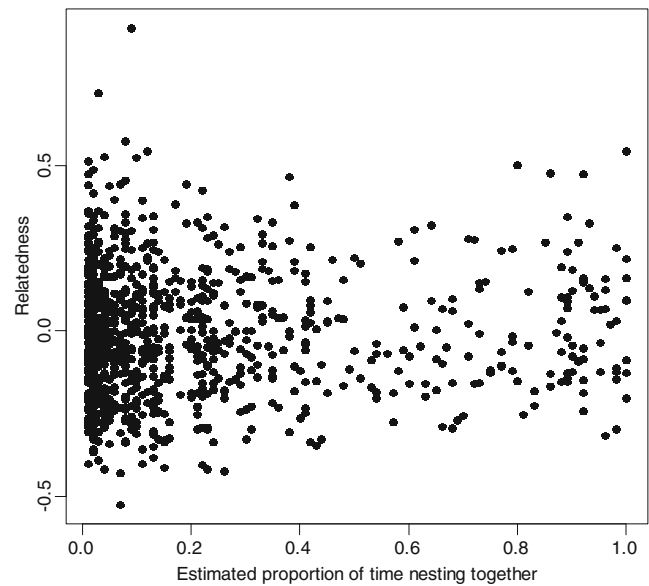


Fig. 4 A plot of pairwise relatedness and the estimated proportion of time southern flying squirrels (*G. volans*) nested together across the study period. Mantel tests suggested that there is no relationship between social association and relatedness. Both related and unrelated individuals nested together at a rate expected if associations were at random. (Queller and Goodnight 1989)

(summer 1 range – winter 2 SAI, $n_{\text{individuals}}=45$, $r=0.19$, $p=0.03$; summer 2 range – winter 3 SAI, $n_{\text{individuals}}=33$, $r=0.23$, $p=0.02$). Multiple, spatially close summer groups came together to form winter nest groups.

Discussion

We found that southern flying squirrels had a stable, non-random social structure. Individuals nested predominantly with other specific long-term associates. There seemed to be two tiers of social organization; a summer tier characterized by mixed sex groups followed by a winter tier comprised of multiple summer groups. Although there were preferred and avoided associations, individuals and groups interacted with one another throughout the study. Genetic analyses suggested neither tier of organization that we detected was kin-based. However, the spatial proximity of individuals on their summer nesting home ranges was a significant predictor of winter associations. Allowing for mortality, emigration, and the introduction of new individuals, relationships remained stable throughout the entire study.

Long-term monitoring of individually marked animals has found similar social structures to those described here across a wide range of taxonomic groups such as bats (e.g., Garroway and Broders 2007; Metheny et al. 2008; Patriquin et al. 2010), cetaceans (e.g., Christal and Whitehead 2001; Gero et al. 2008), African elephants (*Loxodonta africana*; e.g., Wittemyer et al. 2005; Archie et al. 2006), and hyenas

(*Crocota crocuta*; e.g., Van Horn et al. 2004). Big brown bats (*Eptesicus fuscus*) have a similar social structure to that of southern flying squirrels in that roosting relationships are long-term, nonrandom, and not kin-based (Willis and Brigham 2004; Metheny et al. 2008). African elephants also have long-term nonrandom associations with multiple smaller groups that come together seasonally in larger groups (Wittemyer et al. 2005); however, for elephants, associations are kin-based (Archie et al. 2006).

The apparent lack of kin selection during social nesting by flying squirrels suggests that this behavior is mutually beneficial. Social thermoregulation should provide mutual benefits to flying squirrels (Stapp et al. 1991) by conferring immediate and mutually shared energetic savings for much of the year. Laboratory analyses of the energy savings associated with group living in southern flying squirrels have shown that at temperatures of 9 °C, individuals nesting in groups of three to six may be able to reduce their energy budget by as much as 36 % relative to solitary individuals (Stapp et al. 1991). In our study area, mean daily temperatures were above 9 °C for only 5 months of the year (Canadian Climate Normals, Environment Canada) suggesting that squirrels may benefit from social thermoregulation throughout much of the year. For flying squirrels, the energetic costs associated with cold temperatures and the benefits gained by social thermoregulation will be synchronous, making it unlikely that a cheater strategy of foregoing social nesting that exploits time lags between costs and benefits would evolve.

The year-round nature of sociality found both in our study, near the southern flying squirrel northern range limit and in warmer climates such as Florida (Layne and Raymond 1994), suggests that there are benefits of sociality beyond social thermoregulation. Nonthermoregulatory benefits seem likely to be related to foraging and food caching; however, we know little about these behaviors in flying squirrels. There have been observations of group travel and foraging (Madden 1974) and we occasionally trapped two squirrels together in a single trap during this study (Garroway and Bowman, unpublished data), suggesting that, at least sometimes, squirrels forage together. Data from captive colonies suggest that southern flying squirrels from the same group cache individually and gain a retriever's advantage via spatial memory (Winterrowd and Weigl 2006; Winterrowd 2008); however, caches that overlapped were often pilfered by nest mates (Winterrowd 2001). It is not clear whether social groups cache together under natural conditions and we do not know the degree to which caches may be shared or pilfered. The dynamics of social foraging and caching could partially explain aspects of southern flying squirrel sociality at nests and remain to be investigated.

The maintenance of group composition across seasons and years suggests a benefit of prior familiarity. We provide

further evidence for the role of familiarity in the formation of winter groups as we found that winter group composition was best predicted by the proximity of summer group home ranges. Summer foraging home ranges overlapped extensively. This suggests that individuals likely have prior knowledge of their winter nest mates from summer foraging as well as from prior years of association. Prior familiarity within social groups has been shown to provide both immediate and long-term fitness benefits in some contexts (Griffiths et al. 2004). The benefits of associating with familiar individuals are often attributed to reduced aggression among social group members due to established dominance hierarchies, enhanced predator avoidance, and increased foraging efficiency (Höjesjö et al. 1998). For example, groups of familiar brown trout responded to predator attacks more quickly and foraged more efficiently than groups with unfamiliar individuals (Griffiths et al. 2004). Benefits may be accrued by reducing the need for divided attention (Griffiths et al. 2004). In this case, individual brown trout could focus more on predator avoidance and foraging as aggressive interactions were reduced among individuals with prior familiarity as a dominance hierarchy was already established. For flying squirrels, prior familiarity might be important for locating potential nest mates. There are many suitable cavities within this system (Coombs et al. 2010) and so familiarity among individuals and their habits likely reduces costs associated with searching out individuals to nest with and assuring the presence of others. Recent captive experiments testing nest mate choice in southern flying squirrels have shown that individuals preferentially nest with familiar individuals and may exclude unfamiliar squirrels from groups (Thorington and Weigl 2011a, b).

The best interests of an individual within a mixed sex and age social group may not always seem to coincide with the group, such that the individual may appear to act with the group and against its own selfish interests. Kin selection is often invoked to explain the evolution of social coordination of activities that sometimes seem to entail fitness costs to individuals. In flying squirrels, evidence for a role for kinship in nest group formation has been equivocal (Muul 1968; Layne and Raymond 1994; Winterrowd et al. 2005; Thorington et al. 2010; Thorington and Weigl 2011a). Muul (1968) suggested that females and their young are the core social unit of southern flying squirrel nest groups. In a 5-year study of marked individuals within nest boxes in Florida, USA, Layne and Raymond (1994) found that at least 16 % of nest boxes contained at least one pair of first-order relatives and suggested that this was likely an underestimate due to their small sample of marked litters. Recent empirical studies have found contradictory results, suggesting that nest groups either are (Thorington et al. 2010, Thorington and Weigl 2011a, b) or are not (Winterrowd et al. 2005)

kin-based. Study of a captive population has shown that both familiarity and kinship can be important predictors of nest group membership (Thorington and Weigl 2011a, b). These contradictory findings may be related to ecological pressures, such that in the presence of high population turnover (and therefore reduced kin availability), the relative importance of familiarity may be enhanced compared to relatedness when selecting nest mates (Thorington and Weigl 2011b). Both studies that have found an absence of kin selection in nesting flying squirrels have been field studies in relatively high turnover environments: either close to the species' range limit (our study) or in a landscape where the species was undergoing population control (Winterrowd et al. 2005). Conversely, the largest positive effect of kin on nest group membership in flying squirrels has been observed in a captive population (Thorington and Weigl 2011a, b), where the relative importance of kin selection may have been enhanced by the artificial conditions.

The ecological implications of sociality can be broad. Allee (1931) suggested that individuals of social species would likely suffer from reduced reproductive output and survival at low densities (i.e., Allee effects) due to decreased social interactions. We suggest that southern flying squirrels, at least near their northern range boundary, are obligately social requiring a minimum group size for social thermoregulation and over-winter survival. This implies strong Allee effects (negative population growth rate at low density) and may explain some of the broad-scale distributional patterns of this species. For example, in association with climate warming in the region, the southern flying squirrel range boundary has expanded north (Bowman et al. 2005; Myers et al. 2009). However, cold winters still occur and range contractions can be strikingly abrupt (>240 km in a single winter) (Bowman et al. 2005). Allee effects could explain this rapid range contraction if mortality reduces group size to below a critical threshold, leading to rapid local extinction. Further, a number of studies have found that there is a minimum habitat patch size required to support southern flying squirrels (Rosenblatt et al. 1999; Nupp and Swihart 2000; Walpole and Bowman 2011). It seems likely that southern flying squirrels must occupy habitat patches large enough to sustain a sufficient number of individuals to ensure their survival through winter and may explain their absence from patchy landscapes (Walpole and Bowman 2011).

Our approach has made a number of assumptions. We could only monitor a subset of trees that groups used and so it is possible that we missed some important patterns. We did not measure tree characteristics for all nest trees and so cannot compare differences between monitored and unmonitored nests. Further, our detection method could not always identify whether an individual squirrel was entering or exiting the cavity (although squirrels generally exited cavities

at dusk). We assumed that individuals identified at the same cavity on the same day interacted. We suggest that our considerable sample size lessens the impact of these potential biases and assume that our measures of association are accurate and our subsample of the population is representative of the whole.

We have found that southern flying squirrels confront both winter and summer seasons within a nonrandom social structure composed of stable social groups of largely unrelated individuals. The evolution of sociality in this species seems driven by a combination of ecologically adapted, mutually beneficial relationships. The importance of nest-based sociality likely contributes to the range boundary dynamics in the species and can explain their absence in patchy landscapes through Allee effects. We still know very little about social interactions during foraging and these aspects of flying squirrel social structure will likely be important if we are to explain sociality outside of the cold seasons. Experimental manipulations of the degree of familiarity, perhaps testing the responses of groups of familiar and unfamiliar individuals to simulated predator attack and examining for differences in search times for social group formation will be important for further understanding of the benefits of familiarity.

Acknowledgments This project was funded by the Natural Science and Engineering Research Council (NSERC) Discovery Grants to JB and PJW; an NSERC Canada Graduate and Ontario Graduate Scholarships to CJG; Applied Research and Development Branch (OMNR) granted support to JB. We would also like to thank the numerous laboratory and field assistants that worked on the project and Gary Burness and Meghan Murrant for helpful discussion and comments on earlier drafts.

Ethical standards This study was conducted according to the standards of the Trent University Animal Care Committee, the Canadian Council on Animal Care, and the Ontario Ministry of Natural Resources.

Conflict of interest None.

References

- Allee WC (1931) Animal aggregations. A study in general sociology. University of Chicago Press, Chicago
- Archie EA, Moss CJ, Alberts SC (2006) The ties that bind: genetic relatedness predicts the fission and fusion of social groups in wild African elephants. *Proc R Soc Lond B* 273:513–522
- Bejder L, Fletcher D, Brager S (1998) A method for testing association patterns of social animals. *Anim Behav* 56:719–725
- Bowman J, Holloway GL, Malcolm JR, Middel KR, Wilson PJ (2005) Northern range boundary dynamics of southern flying squirrels: evidence of an energetic bottleneck. *Can J Zool* 83:1486–1494
- Christal J, Whitehead H (2001) Social affiliations within sperm whale (*Physeter macrocephalus*) groups. *Ethology* 107:323–340
- Clutton-Brock T (2009) Cooperation between non-kin in animal societies. *Nature* 462:51–57

- Clutton-Brock T, West S, Ratnieks F, Foley R (2009) The evolution of society. *Philos T Roy Soc B* 364:3127–3133
- Coombs AB, Bowman J, Garroway CJ (2010) Thermal properties of tree cavities during winter in a northern hardwood forest. *J Wildlife Manage* 74:1875–1881
- Darwin C (1859) *The origin of species*. The Modern Library, New York
- Fokidis HB, Schable NA, Hagen C, Glenn TC, Risch TS (2003) Characterization of microsatellite DNA loci for the southern flying squirrel (*Glaucomys volans*). *Mol Ecol Notes* 3:616–618
- Garroway CJ, Broders HG (2007) Nonrandom association patterns at northern long-eared bat maternity roosts. *Can J Zool* 85:956–964
- Garroway CJ, Bowman J, Cascaden TJ, Holloway GL, Mahan CG, Malcolm JR, Steele MA, Turner G, Wilson PJ (2010) Climate change induced hybridization in flying squirrels. *Glob Change Biol* 16:113–121
- Garroway CJ, Bowman J, Holloway GL, Malcolm JR, Wilson PJ (2011) The genetic signature of rapid range expansion by flying squirrels in response to contemporary climate warming. *Glob Change Biol* 17:1760–1769
- Gero S, Engelhaupt D, Whitehead H (2008) Heterogeneous social associations within a sperm whale, *Physeter macrocephalus*, unit reflect pairwise relatedness. *Behav Ecol Sociobiol* 63:143–151
- Gilmore RM, Gates JE (1985) Habitat use by the southern flying squirrel at a hemlock-northern hardwood ecotone. *J Wildlife Manage* 49:703–710
- Goertz JW, Dawson RM, Mowbray EE (1975) Response to nest boxes and reproduction by *Glaucomys volans* in northern Louisiana. *J Mammal* 56:933–939
- Griffiths SW, Brockmark S, Höjesjö J, Johnsson JI (2004) Coping with divided attention: the advantage of familiarity. *Proc R Soc Lond B* 271:695–699
- Hamilton W (1964a) The genetical evolution of social behaviour I. *J Theor Biol* 7:1–16
- Hamilton W (1964b) The genetical evolution of social behaviour II. *J Theor Biol* 7:17–52
- Heidt GA (1977) Utilization of nest boxes by the southern flying squirrel *Glaucomys volans* in central Arkansas. *Proc Arkansas Acad Sci* 31:55–57
- Hinde R (1976) Interactions, relationships and social structure. *Man* 11:1–17
- Höjesjö J, Johnsson JI, Petersson E, Järvi T (1998) The importance of being familiar: individual recognition and social behavior in sea trout (*Salmo trutta*). *Behav Ecol* 9:445–451
- Jombart T (2008) adegenet: a R package for the multivariate analysis of genetic markers. *Bioinformatics* 24:1403–1405
- Layne JN, Raymond MAV (1994) Communal nesting of southern flying squirrels in Florida. *J Mammal* 75:110–120
- Lazo A (1994) Social segregation and the maintenance of social stability in a feral cattle population. *Anim Behav* 48:1133–1141
- Lusseau D, Wilson BEN, Hammond PS, Grellier K, Durban JW, Parsons KM, Barton TR, Thompson PM (2006) Quantifying the influence of sociality on population structure in bottlenose dolphins. *J Anim Ecol* 75:14–24
- Madden JR (1974) Female territoriality in a Suffolk County, Long Island, population of *Glaucomys volans*. *J Mammal* 55:647–652
- Manly BFJ (1995) A note on the analysis of species cooccurrences. *Ecology* 76:1109–1115
- Metheny JD, Kalcounis-Rueppell MC, Willis CKR, Ka K, Brigham RM (2008) Genetic relationships between roost-mates in a fission–fusion society of tree-roosting big brown bats (*Eptesicus fuscus*). *Behav Ecol Sociobiol* 62:1043–1051
- Miklos I, Podani J (2004) Randomization of presence–absence matrices: comments and new algorithms. *Ecology* 85:86–92
- Muul I (1968) Behavioral and physiological influences on the distribution. *Miscellaneous Publications of the Museum of Zoology, University of Michigan*
- Muul I (1973) Geographic variation in the nesting habits of *Glaucomys volans*. *J Mammal* 55:840–844
- Myers P, Lundrigan BL, Hoffman SMG, Haraminac AP, Seto SH (2009) Climate-induced changes in the small mammal communities of the Northern Great Lakes Region. *Glob Change Biol* 15:1434–1454
- Nupp TE, Swihart RK (2000) Landscape-level correlates of small-mammal assemblages in forest fragments of farmland. *J Mammal* 81:512–526
- Painter JN, Selonen V, Hanski IK (2004) Microsatellite loci for the Siberian flying squirrel, *Pteromys volans*. *Mol Ecol Notes* 4:119–121
- Patriquin KJ, Leonard ML, Broders HG, Garroway CJ (2010) Do social networks of female northern long-eared bats vary with reproductive period and age? *Behav Ecol Sociobiol* 64:899–913
- Queller DC, Goodnight KF (1989) Estimating relatedness using genetic markers. *Evolution* 43:258–275
- R Development Core Team (2008) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, ISBN 3-900051-07-0, URL <http://www.R-project.org>
- Reynolds RJ, Fies ML, Pagels JF (2009) Communal nesting and reproduction of the southern flying squirrel in Montane Virginia. *Northeast Nat* 16:563–576
- Rosenblatt DL, Heske EJ, Nelson SL, Barber DH, Miller MA, MacAllister B (1999) Forest fragments in east-central Illinois: islands or habitat patches for mammals? *Am Midl Nat* 141:115–123
- Sawyer SL, Rose RK (1985) Homing in and ecology of the southern flying squirrel *Glaucomys volans* in southeastern Virginia. *Am Midl Nat* 113:238–244
- Sonenshine DE, Laur DM, Walker TC, Elisberg BL (1979) The ecology of *Glaucomys volans* (Linnaeus, 1758) in Virginia. *Acta Theriol* 24:363–377
- Stapp P, Pekins PJ, Mautz WW (1991) Winter energy-expenditure and the distribution of southern flying squirrels. *Can J Zool* 69:2548–2555
- Thorington KK, Weigl PD (2011a) Role of kinship in the formation of southern flying squirrel winter aggregations. *J Mammal* 92:179–189
- Thorington KK, Weigl PD (2011b) Persistence of southern flying squirrel winter aggregations: roles of kinship, familiarity, and intruder squirrels. *J Mammal* 92:1005–1012
- Thorington KK, Metheny JD, Kalcounis-Rueppell MC, Weigl PD (2010) Genetic relatedness in winter populations of seasonally gregarious southern flying squirrels, *Glaucomys volans*. *J Mammal* 91:897–904
- Trivers R (1971) The evolution of reciprocal altruism. *Quart Rev Biol* 46:35–57
- Van Horn RC, Engh AL, Scribner KT, Funk SM, Holekamp KE (2004) Behavioural structuring of relatedness in the spotted hyena (*Crocuta crocuta*) suggests direct fitness benefits of clan level cooperation. *Mol Ecol* 13:449–458
- Walpole AA, Bowman J (2011) Patch occupancy by squirrels in fragmented deciduous forest: effects of behaviour. *Acta Theriol* 56:63–72
- Whitehead H (1995) Investigating structure and temporal scale in social organizations using identified individuals. *Behav Ecol* 6:199–208
- Whitehead H (1999) Testing association patterns of social animals. *Anim Behav* 57:F26–F29
- Whitehead H (2008) Analyzing animal societies: Quantitative methods for vertebrate social analysis. The University of Chicago Press, Chicago
- Whitehead H (2009) SOCPROG programs: analysing animal social structures. *Behav Ecol Sociobiol* 63:765–778
- Whitehead H, Bejder L, Ottensmeyer C (2005) Testing association patterns: issues arising and extensions. *Anim Behav* 69:e1–e6
- Willis CKR, Brigham RM (2004) Roost switching, roost sharing, and social cohesion: forest-dwelling big brown bats, *Eptesicus fuscus*, conform to fission–fusion model. *Anim Behav* 68:495–505

- Winterrowd MF (2001) Food hoarding and group nesting in the southern flying squirrel, *Glaucomys volans*. PhD dissertation, Wake Forest University, Winston-Salem, NC
- Winterrowd MF (2008) The group-nesting and food-hoarding behaviour of the southern flying squirrel. *Curr Sc India* 95:10–14
- Winterrowd MF, Weigl PD (2006) Mechanisms of cache retrieval in the group nesting southern flying squirrel (*Glaucomys volans*). *Ethology* 112:1136–1144
- Winterrowd MF, Gergits WF, Laves KS, Weigl PD (2005) Relatedness within nest groups of the southern flying squirrel using microsatellite and discriminant function analyses. *J Mammal* 86:841–846
- Wittmyer G, Douglas-Hamilton I, Getz W (2005) The socioecology of elephants: analysis of the processes creating multitiered social structures. *Anim Behav* 69:1357–1371
- Zittlau KA, Davis CS, Strobeck C (2000) Characterization of microsatellite loci in northern flying squirrels (*Glaucomys sabrinus*). *Mol Ecol* 9:826–827