Evidence of social preferences in big brown bats (Eptesicus fuscus)

R.J. Kilgour, P.A. Faure, and R.M. Brigham

Abstract: Among social species, iterative interactions may lead to social preferences among group-mates and often are associated with increased mating opportunities or improved indirect fitness benefits. Although preferential associations have been documented in multiple species, this phenomenon has never been empirically studied in bats—the second largest order of mammals, where many of the 1200+ species live in groups of tens to hundreds of individuals. Given the current understanding of the social behavior exhibited in this species, we explored the possibility that adult female big brown bats (Eptesicus fuscus (Beauvois, 1796)) show preferential association between group-mates using a pairwise choice design with individuals from a captive colony. Focal individuals were placed in a Y-maze and were given free choice of two familiar conspecifics. We measured the time focal individuals spent in close proximity to each conspecific. Our results indicate that some bats exhibit preferential association between group-mates, as multiple individuals spent significantly more time in close proximity to one conspecific versus another, despite randomizing the position of stimulus bats between trials. Given the frequent and long-term associations between group members of this species, social preferences could play a significant role in the outcomes of their long-term fitness.

Key words: social associations, Eptesicus fuscus, social bias, Y-maze.

Introduction

As an adapted response to counter the costs of predation, mate finding, and resource limitation, many animals congregate in groups ranging in size from tens to hundreds to millions of individuals (Wilson 2000). Such aggregations increase interaction rates among group members and can lead to asymmetries in associations between individuals (Kutsukake 2009). Asymmetrical social relationships between group-mates can be caused by iterative interactions between individuals with similar interests or resource requirements. These relationships may then generate a positive feedback loop, creating biases in interaction rates and resource requirements. These relationships may then generate a dynamic pattern of preferences among group-mates and often are associated with increased mating opportunities or improved indirect fitness benefits. Although preferential associations have been documented in multiple species, this phenomenon has never been empirically studied in bats—the second largest order of mammals, where many of the 1200+ species live in groups of tens to hundreds of individuals. Given the current understanding of the social behavior exhibited in this species, we explored the possibility that adult female big brown bats (Eptesicus fuscus (Beauvois, 1796)) show preferential association between group-mates using a pairwise choice design with individuals from a captive colony. Focal individuals were placed in a Y-maze and were given free choice of two familiar conspecifics. We measured the time focal individuals spent in close proximity to each conspecific. Our results indicate that some bats exhibit preferential association between group-mates, as multiple individuals spent significantly more time in close proximity to one conspecific versus another, despite randomizing the position of stimulus bats between trials. Given the frequent and long-term associations between group members of this species, social preferences could play a significant role in the outcomes of their long-term fitness.

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Introduction

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The majority of studies exploring social behavior and interactions in bats (order Chiroptera) have focused on the diversity of social organization and types of mating systems employed (for a review see McCracken and Wilkinson 2000). For example, several tropical species form harem organizations, often with stable female group membership across years, and research on these systems tend to emphasize group dynamics and mating success (Voigt et al. 2001; Heckel and von Helversen 2002). Fulmer and Knörnschild (2012) examined social interactions between sac-winged bats (Saccopteryx bilineata (Temminck, 1838)) and found...
preferential roosting in proximity to harem-mates, although only across sexes. Although mating behaviour and social organization is well documented in many bat species, few studies have focused on intrasexual interactions among mainly single-sex colonies, such as maternity colonies. Like many temperate bat species, female big brown bats (Eptesicus fuscus (Beauvois, 1796)) live in maternity colonies, and during the reproductive season, group size varies from tens to hundreds of individuals (Kurta and Baker 1990). Like several other species, groups of big brown bats follow a fission–fusion conformation (Kerth and Konig 1999; Rhodes 2007; Willis and Brigham 2004). Fission–fusion is a means of minimizing the ecological costs of social groups (Lehmann et al. 2007) and can result in the periodic formation and reformation of subgroups. A fission–fusion society leads to short-term interactions between specific individuals that may be unequal across all group-mates. Indeed, analyses of association patterns within fission–fusion species suggest that subgroup membership is driven by relatedness, spatial overlap, and individual preference (Carter et al. 2013). Social network analyses show differential associations between conspecifics, where some individuals show biased interaction with specific group-mates, while others show more even interactions across a wider range of individuals (Patriquin et al. 2010).

Our knowledge of fission–fusion in bat societies suggests that preferential relationships are complex and may be explained by motivations other than simple kinship (Gillam et al. 2011; Metheny et al. 2008; Patriquin et al. 2010; Kilgour and Brigham 2013). For example, females big brown bats are highly philopatric and live in colonies with overlapping matriline (Vonhof et al. 2008). With their long lifespan, individual big brown bats have the potential to interact with the same group or colony-mates for many years. Given the frequency and intensity of these social interactions and the possible fitness benefits that result, as observed in a wide range of mammals (baboons, Papio cynocephalus ursinus (= Papio hamadryas (L., 1758)); Silk et al. 2009; meerkats, Suricata suricatta (Schreber, 1776); Russell et al. 2007; bottlenose dolphins, Tursiops truncatus (Montagu, 1821); Perelberg and Schuster 2008), we sought to document the potential for female big brown bats to exhibit social biases (i.e., preferential associations) with specific group-mates. Based on current understanding of fission–fusion organization and our knowledge that individual bats often distribute their social interactions unevenly across group-mates, we hypothesized that adult female big brown bats would show preferences in their social interactions and would therefore associate with certain individuals more often than others.

Materials and methods

We conducted a pairwise choice experiment using adult female big brown bats housed in a captive research colony at McMaster University in Hamilton, Ontario, Canada (Faure et al. 2009). Bats were housed in a free-flight husbandry room (2.5 m × 1.5 m × 2.3 m), where the colony temperature and lighting varied according to ambient conditions. Bats were given ad libitum access to water and mealworms (larvae of the genus Tenebrio) and to an outdoor flying area (2.5 m × 3.8 m × 3.1 m). At the time of the study, the colony consisted of 35 individuals (6 males, 29 females). During daylight hours, females typically roosted together in a cluster, with males roosting in a separate area of the enclosure. Based on previous observations and the fact that they were housed in the same enclosure, we assume all individuals had equal opportunity to interact with one another prior to the start of our trials.

Eight females were selected from the colony based on general health scores, availability relative to other concurrent experiments, and time spent habituated to captivity. The eight bats tested had been in captivity for at least 1 year, were in good physical health, and exhibited standard social and nonaggressive behaviour toward conspecifics. Prior to commencing our behavioural assays, bats were held in a 145 L Exo Terra flexarium (Rolf C. Hagen Inc., Montréal, Quebec, Canada) for 2 days, during which time habituation trials took place. Individuals received daily health and behaviour checks and were weighed to ensure they maintained their healthy status throughout the duration of the study (4 days).

A pairwise behavioural choice assay was used to assess individual social preferences. An individual “focal” bat was selected and permitted to move freely within a plexiglass Y-maze, with isolated (caged) “stimulus” bat conspecifics placed at either end of the Y (Fig. 1). Stimulus bats were held at the end of each arm of the Y-maze in stainless steel wire-mesh cages (24 cm × 21 cm × 19 cm). This arrangement permitted the focal bat to sense visual, olfactory, and acoustic cues from the stimulus bats. Prior to the start of test trials, focal bats were allowed to freely roam and habituate to the Y-maze for 90 min with the room lights on and no stimulus bats or observers present. Illumination of the maze was required for video recordings and we observed no evidence that behaviour of the bats was influenced by room light.

Each of the eight bats served as a focal individual, with the two choice bats selected at random from the remaining seven bats. Each focal individual was tested eight times with its stimulus partner, the position of the stimulus bat randomized between trials. All individuals were used as part of the stimulus pair at least once and two individuals served as stimulus bats to three focal bats. Despite this repetition, all trials (one focal and two stimulus bats) that we tested were composed of different individuals and hence analysed independently. Trials lasted 5 min and began when the focal bat initiated movement after placement in the Y-maze. Between trials, the mesh dividers and isolation cages were cleaned with a mild soap solution to remove odours from conspecifics. Trials were conducted between the hours of 2000 and 0400 over a 4 day period. Focal bats were tested twice per night and the order of testing was randomized with the exception that a focal individual was not used in two consecutive trials. Focal bats were individually housed and permitted to rest for at least 5 min between trials.

Social preference data were recorded using a Sony Handycam (HDR-XR200V; Sony, Tokyo, Japan) mounted on a tripod, positioned directly above the Y-maze. Videos were analysed by R.J.K.
We measured the time focal bats spent in each arm of the Y-maze along with the time spent within 15 cm (approximately one body length) of the stimulus bats. Pairwise t tests were used to determine if focal bats spent significantly more time with one stimulus bat relative to the other. Post hoc Bonferroni corrections were used to control for type I error. Research protocols were in accordance with the Canadian Council on Animal Care and were approved by the University of Regina President’s Committee on Animal Care (AUP No. 08-01) and the McMaster University Animal Research Ethics Board (AUP No. 08-07-34).

Results

Each focal bat was active during the experimental trial and displayed interest in the stimulus bats by moving about the Y-maze. None of the focal bats displayed nonresponsive behaviour, such as remaining at their start position or being mostly inactive during a trial. Indeed, at the start of the trial, each focal bat moved away from their start position and began exploring both arms of the Y-maze and thus were exposed to both stimulus bats. Periodically, bats would move through the arena and thus spent time in the no-choice area of the maze. Focal bats exhibited a diversity of time allocations between the stimulus bats, ranging from equal time spent near each conspecific to more than fivefold difference in time allocation at one stimulus bat (Fig. 2). Of the three individuals that were used as the stimulus bat in more than one trial, we did not observe any repeated preferences for that individual by the focal individuals. In other words, none of the three individuals were preferentially selected by multiple focal bats.

Of eight focal individuals tested, four spent substantially more time in the presence of one conspecific over the other (Table 1). Each of the four focal individuals displayed significant preference for a stimulus bat at the α = 0.05 level; however, only one bat was found to have a significant preference after Bonferroni corrections were applied. The remaining four focal individuals showed no preference in the amount of time spent with stimulus bats.

Discussion

We assessed preferential relationships in a small sample of adult female big brown bats living in a captive research colony. Based on data from a pairwise choice, we found that some bats show a preference for certain group-mates over others. Half of the bats in our experiment displayed selective associations for one stimulus bat, despite randomizing the location of the stimulus bats between repeated trials within the same trial.

Social preferences for specific group-mates are common among gregarious species and may be driven by processes like kin selection or reciprocal altruism. Asymmetric social relationships in bats may be predicted by cooperative behaviour as in reciprocal altruism, demonstrated by food sharing in the common vampire bat (Desmodus rotundus (E. Geoffroy, 1810)) (Wilkinson 1984; Carter and Wilkinson 2013). The majority of affiliative relationships observed in bats have been explored in relation to kin-based preferences. Kin-based association biases are predicted when there are direct and indirect fitness benefits to individuals (Wilson 2000) and when individuals are able to identify kin from nonkin in the social group (Toth et al. 2009). Kin-based association preferences are common in birds and mammals (Mitani et al. 2000; Parker et al. 1995; Toth et al. 2009) and may lead to selection for cooperative behaviours, although isolating exact fitness benefits can be difficult (Hatchwell 2010). Studies of Bechstein’s bat (Myotis bechsteinii Kuhl, 1817), a species with a similar social structure to big brown bats, supports affiliative associations between mothers and daughters during day roosting and also while foraging (Kerth et al. 2001). Similar relationships have been reported among

Table 1. Summary of paired t statistics and p values for each focal big brown bat (Eptesicus fuscus).

<table>
<thead>
<tr>
<th>Focal individual</th>
<th>Paired t</th>
<th>df</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.13634</td>
<td>7</td>
<td>0.895387</td>
</tr>
<tr>
<td>2</td>
<td>−0.68547</td>
<td>7</td>
<td>0.515098</td>
</tr>
<tr>
<td>3</td>
<td>3.970673</td>
<td>7</td>
<td>0.005388*</td>
</tr>
<tr>
<td>4</td>
<td>−2.50735</td>
<td>7</td>
<td>0.040554*</td>
</tr>
<tr>
<td>5</td>
<td>−0.37755</td>
<td>7</td>
<td>0.716954</td>
</tr>
<tr>
<td>6</td>
<td>−0.08505</td>
<td>7</td>
<td>0.9346</td>
</tr>
<tr>
<td>7</td>
<td>2.38436</td>
<td>7</td>
<td>0.048586*</td>
</tr>
<tr>
<td>8</td>
<td>2.42439</td>
<td>7</td>
<td>0.045796*</td>
</tr>
</tbody>
</table>

*Focal bat showed a statistically significant preference (α ≤ 0.05) for one of two stimulus bats.
† Statistically significant preference after applying a Bonferroni correction (α = 0.00625).
greater horseshoe bats (Rhinolophus ferrumequinum (Schreber, 1774)) and such spatial associations can last several years (Rossiter et al. 2002); however, field studies on fission–fusion dynamics in big brown bats have shown that females do not select subgroup membership based on kin (Metheny et al. 2008). Other bat species have demonstrated asymmetrical association biases based on spatial proximity as juveniles; for example, associations between Kuhl’s pipistrelle (Pipistrellus kuhlii (Kuhl, 1817)) pups can lead to preferential relationships that persist into adulthood (Aincillootto et al. 2012). The studies described above demonstrate the complexities observed in social affiliations across different bat species. Given the diversity of social relationships and social structure, more studies are needed to understand the motivations behind asymmetrical associations. Although we did not control for relatedness between individuals, our data clearly demonstrate that preferential associations do occur between individual big brown bats.

Affiliative relationships, as demonstrated by preferential associations, may be further promoted by the synchronous activity of similar aged and (or) sex classes of individuals (Conradt and Roper 2000). Maintaining group synchrony can be costly when members differ in body size or activity levels (Aivaz and Ruckstuhl 2011) and this may lead to the temporary formation of subgroups as found in fission–fusion dynamics. If wild bats exhibit preferential associations, this suggests that individual interactions occur primarily during day-roost periods when females are often tightly congregated into clusters as observed in our captive colony. It is possible that preferential associations, either driven by relatedness, body size, reproductive status, or other factors, are important in balancing the costs of reproduction and metabolism. Maintaining thermoregulatory balance while roosting represents a substantial cost, particularly for pregnant females and their developing embryos (Kunz and Lumsden 2003). Female big brown bats give birth to one or two offspring per year and population growth is limited by juvenile overwinter survival (O’Shea et al. 2010). To limit costs associated with a reduced basal metabolic rate for the developing foetus, many bat species limit their use of torpor during pregnancy (Grinevitch et al. 1995; Pretzflacht et al. 2010). Therefore, social thermoregulation is likely to be a significant driving force behind the establishment of social relationships and preferences among females in many temperate bat species (Willis and Brigham 2007). Huddling behaviour is usually beneficial, particularly among homeotherms during the reproductive period, and the heat that is generated is a resource to exploit (Haig 2008). Social relationships and affiliated bonds produced during huddling may be so essential to bat development, ontogeny, and fitness that preferences cannot simply be reduced to kin-based affiliations. Among clusters of females, competition for the warmest position within the cluster may result in asymmetrical associations among group-mates, potentially driven by dominance rank. Dominance-based thermoregulatory interactions have been observed in other species (Calf et al. 2002; McGowan et al. 2006) but have yet to be confirmed in bats. Association preferences in bats can last for years (Patrquin et al. 2010). For example, specific affiliations among Bechstein’s bats last as long as 5 years and occur regardless of age, size, reproductive status, or relatedness (Kerth et al. 2011). Together with these studies, our data further emphasize the critical importance of bat social relationships.

To our knowledge, this is the first study to empirically examine social preferences in adult female big brown bats. Although we were unable to assess the influence of genetic relatedness on social preferences between the individuals included in our sample, our data in combination with previous studies suggest that preferential associations may be an important factor influencing social dynamics of big brown bats. Sample size was a considerable limitation to our study, as subjects came from a captive population containing only 35 individuals and most were participating in concurrent studies. Time constraints prevented us from running more replicates for each focal individual. Based on our results, it is clear that further study is necessary to better understand the nature of preferential relationships in our bats. Our study supports the growing body of evidence suggesting that social relationships created and maintained by temperate bat species may be crucial for survival and reproduction. Additional studies are needed to further our knowledge on how social relationships are created and maintained and to understand the benefits accrued to individuals who engage in asymmetrical affiliations.

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References


