

Intracolony social distance, signaling modality and association choice in the greater sac-winged bat (*Saccopteryx bilineata*)

Andrew Goldklank Fulmer · Mirjam Knörnschild

Received: 24 February 2011 / Accepted: 26 September 2011
© Japan Ethological Society and Springer 2011

Abstract Understanding patterns and motivations for social spacing greatly illuminates the structure and internal dynamics of given groups or social systems. The highly social, polygynous greater sac-winged bat, *Saccopteryx bilineata*, represents an excellent model for social spacing analysis, since the choice of individual roost-sites within a day-roost constitutes an enduring, often repeated decision about relative proximity to conspecifics. Day-roost colonies consist of one or multiple harem groups, each with several females and a single male. Additionally, non-harem males without females may be present. A social-distance–time-budget metric revealed that harem males, females, and non-harem males differed significantly in their respective spatial associations while roosting. Harem males and females were most closely associated, with harem males located at the center of harems instead of at the borders. Non-harem males associated significantly closer with one another than with harem females that they were trying to access. The signaling modality mediating social interactions depended on the respective social distances between communicating bats. Our results suggest a concentric social organization based around harem males, which may select roost sites in closest possible proximity to females to enhance courtship signal strength. This constitutes an interesting deviation from the normative form of harem maintenance, patrolling borders, in mammals.

Keywords Social spacing · Harem maintenance · Multimodal signals · Chiroptera

Introduction

In any given social system, patterns of affiliation and association have enormous influence on group composition and stability (Say and Pontier 2004; Prange et al. 2006). The distance between interacting individuals, i.e. the social distance, has been studied across several vertebrate taxa, including birds (Seibert and Crowell-Davis 2001), primates (Braune et al. 2005; Mitani and Amsler 2003; Arroyo-Rodríguez et al. 2006; Bezanson et al. 2008), ungulates (Ruckstuhl and Neuhaus 2009; McDonnell and Murray 1995; Weeks et al. 2000; Richardson and Weckerly 2007), pinnipeds (Mesnick and Le Boeuf 1991) and humans (Burgess 1983). Social distance studies have focused on signaling ecology (Braune et al. 2005), mother–offspring behavior (Arroyo-Rodríguez et al. 2006; Ruckstuhl and Neuhaus 2009), aggression (Weeks et al. 2000; Seibert and Crowell-Davis 2001) or mating systems (Mesnick and Le Boeuf 1991; McDonnell and Murray 1995; Mitani and Amsler 2003; Bezanson et al. 2008; Richardson and Weckerly 2007). While social organization has been studied in various bat species (reviewed in Bradbury 1977; McCracken and Wilkinson 2000), few studies have focused on the spatial association of individuals while roosting (Fleming et al. 1998; Kerth and König 1999; Ortega and Maldonado 2006). In this study, we examined the social spacing of the greater sac-winged bat, *Saccopteryx bilineata*, a highly social member of the family Emballonuridae. This species exhibits diverse social behaviors in the day-roost (Bradbury and Emmons 1974; Tannenbaum 1975), making observations of their social interactions especially

A. G. Fulmer
Hampshire College, Amherst, MA, USA

M. Knörnschild (✉)
Institute of Experimental Ecology, University of Ulm,
Albert-Einstein-Allee 11, 89081 Ulm, Germany
e-mail: mirjam.knoernschild@uni-ulm.de

viable. Individuals do not cluster together as in most bat species (Fenton 1985) but roost at a certain distance from one another (Bradbury and Emmons 1974). Since individual roost site selection is a relatively static indicator of affiliative choice, the system presents an excellent model for examining the relevance of individual social spacing to group organization.

Saccopteryx bilineata shows high roost fidelity (Bradbury and Emmons 1974; Tannenbaum 1975). Day-roosts are typically located on broad, rough surfaces with good shelter, for example in cavities formed by the buttresses of trees, or on walls of abandoned buildings. Day-roost colonies consist of 1–12 harems, and harems are composed of one reproductive male and up to eight females (Bradbury and Emmons 1974; Tannenbaum 1975). Within a colony, harem males defend roosting territories of 1–2 m² that are often adjacent to one another (Bradbury and Emmons 1974). Non-harem males queuing for harem access are often present as well (Voigt and Streich 2003). By definition, these males do not retain females, but may defend a territory and be reproductively active. In the *Saccopteryx* literature (reviewed in Voigt et al. 2008), the term non-harem male is synonymous with ‘satellite male’ and ‘peripheral male’. Males within a colony are sexually competitive, as females may be impregnated by males other than their own harem male (Heckel et al. 1999; Heckel and von Helversen 2002, 2003). Therefore, a harem male should be attentive to the positioning not just of his harem females but of the other males in his colony, no matter whether they are harem males or non-harem males. Young males may also occupy space within a harem male territory, roosting close to their mothers and exhibiting none of the male-specific courtship behaviors. These males are called cryptic males (sensu Tannenbaum 1975; Voigt et al. 2008). Both non-harem males and cryptic males may occupy vacant harem territories when the resident harem male disappears (Voigt and Streich 2003). In the day-roost, *S. bilineata* often changes location by crawling from one spot to another rather than flying. Disputes over territory borders are often settled by perching bats performing threat displays at the territory border (Tannenbaum 1975; Bradbury and Emmons 1974; Caspers and Voigt 2009). The air space within the territory borders is not defended as vigorously as the roosting space (own observations).

Unlike many other species which exhibit harem-based polygyny (Altmann et al. 1977; Weckerly 1998), *S. bilineata* males are smaller than their female counterparts (total length 7.4 vs. 7.6 cm; after Yancey et al. 1998). They cannot physically control females (Bradbury and Emmons 1974) and must rely on alternative means to retain females in their harem and maintain their own reproductive opportunities and social status (Voigt et al. 2006, 2008). During courtship, *S. bilineata* males employ conspicuous

multimodal displays in which a strong musk is released from the eponymous wing sacs and propelled towards the female by hovering in mid-air or vigorously shaking one forearm, the latter being referred to as “salting” (Bradbury and Emmons 1974; Voigt and von Helversen 1999; Caspers et al. 2008). Females only possess rudimentary wing-sacs unsuitable for storing odor (Starck 1958; Voigt and von Helversen 1999). Males also use territorial counter-singing tactics to defend their harems from other males and elaborate courtship songs to woo females (Behr and von Helversen 2004; Davidson and Wilkinson 2004; Behr et al. 2006, 2009). All male *S. bilineata* displays incorporate visual, olfactory and/or acoustic modalities (for an overview, see Voigt et al. 2008). For each of these, signal quality will be enhanced by physical proximity between sender and recipient (Bradbury and Vehrencamp 1998). An individual’s roost sites are probably selected at least partially in response to the above-mentioned social constraints.

Our study focused on the distance maintained by individual members of a colony from one another, with attention to the effects of sex, social status and harem affiliation. We also examined the relationship between social distance and signaling modality employed in terms of increase/decrease of social distance during a given signaling bout. We tested social distance relationships to describe the male harem maintenance mechanism: are harems physically organized with males on the exterior in order to expel intruders, or are they organized with males at the center to retain females with proximity-enhanced courtship signals?

Materials and methods

Social distance was defined as the physical space between a given pair of individual bats. Social type was defined as the sex and harem affiliation of each bat. Social types included harem male, harem female, non-harem male and cryptic male. Harem males (HM) were defined as males noted in daily census to have one or more females consistently roosting within the borders of their territories. Borders were mapped based on daily behavioral observations of aggressive displays or territorial scent-marking (sensu Caspers and Voigt 2009). Harem females (HF) were defined as females noted in daily census to roost within the borders of a male’s territory. Harem males and females could either belong to the same harem (i.e. HM and HF) or to another harem, respectively (i.e. OHM and OHF). Non-harem males (NHM) were noted in the daily census to be without consistent female presence. In our study, all NHMs defended territories. A single cryptic male (CM; sensu Tannenbaum 1975) was observed in the course of the study, defined as a male roosting close to his mother in the

territory of a harem male and not exhibiting typical male display behaviors. When measuring social distance, all social types except the cryptic male were combined into eight different bat pair types (i.e. HM–HF, HF–HF, HM–NHM, HF–NHM, NHM–NHM, HM–OHM, HM–OHF, and HF–OHF).

Research was conducted over the course of 46 days in 2009 in two distinct habitats during the Costa Rican dry season: lowland Atlantic rainforest at La Selva Biological Station (10°25'N, 84°00'W), and Pacific dry forest in Santa Rosa National Park (10°50'N, 85°37'W). At La Selva, three bat colonies were observed daily in randomized sequence. Each colony occupied an abandoned wooden house. At the Santa Rosa site, two colonies were observed. The smaller colony was located in the wooden rafters of a museum, and the larger on the wooden side of an occupied human dwelling. In our study, all harem territories belonging to the same colony had a border adjacent to another harem territory. We monitored a total of 60 bats (8 harem males, 40 harem females, 11 non-harem males, 1 cryptic male) in five colonies. Each colony was observed during ten observation sessions (only one session per colony and day) which were allocated equally over the entire period the bats spent in the day-roost (0500–1800 hours). During an observation session, each colony was first observed as a group to assess intracolony social distance between individual bats via scan-sampling. Afterwards, we conducted two ad libitum focal animal observations (sensu Altmann 1974; one harem male and one harem female were observed per colony) to investigate the relationship between association distance and the chosen signaling modality. Though all bats were habituated to human presence, a 10-min habituation interval preceded each observation session.

Focal group observations constituted a social-distance-time-budget metric (Altmann, 1974). For these observations, we employed a scan-sampling procedure (at 1 min intervals for 60 min) and recorded the social distance associated with each possible pair of individual bats in the colony. *Saccopteryx bilineata* typically reaches a total body length of about 7.5 cm (Yancey et al. 1998). Voigt et al. (2008) reported that day-roosting *S. bilineata* maintain a minimum social distance of 5–8 cm (indicating that body length may be a biologically relevant measure; see also Fleming et al. 1998; Seibert and Crowell-Davis 2001; Richardson and Weckerly 2007), which informs the parameter used for measuring spatial difference in the present study. First, we measured social distance in body lengths between conspecifics in a colony using all possible combinations of individual bat pairs during scan-sampling. Second, we combined distance values of individual bat pairs into values of bat pair types (bats belonging to the same social type) and conducted statistical analysis with distance values of bat pair types.

We assigned individual bat pairs to one of eight categories of social distance at a given time (once every minute during each 60-min observation session), with increments based on average body length (BL), i.e. cat1: 1 and 2 BL; cat2: 3 and 4 BL; cat3: 5 and 6 BL; cat4: 7 and 8 BL; cat5: 9 and 10 BL; cat6: 11 and 12 BL; cat7: more than 12 BL; cat8: more than 12 BL on separate roosting structures. For each observation session, the frequencies obtained for all eight distance categories (which sum up to 60) were transformed into a single value per individual bat pair. We achieved this by multiplying each category frequency with the respective category number, then summarizing all values and dividing the sum by 60. For example, a harem male–harem female pair with category frequencies of 16 (cat1), 23 (cat2), 6 (cat3), 7 (cat4), 3 (cat5), 1 (cat6), 4 (cat7) and 0 (cat8) has a combined value of $[(16 \times 1) + (23 \times 2) + (6 \times 3) + (7 \times 4) + (3 \times 5) + (1 \times 6) + (4 \times 7) + (0 \times 8)]/60 = 2.61$. The combined value ranged between 1.0 and 8.0 (if all the time was spent in distance category 1 or 8, respectively). Low values indicate that a bat pair roosted most of the time in close proximity, whereas high values indicate that most of the time was spent roosting further apart. For each individual bat pair, the combined distance value was averaged over all ten observation sessions. Subsequently, we averaged the distance of individual bat pairs belonging to the same social type for each colony (e.g., distance between harem male and harem female 1, distance between harem male and harem female 2, etc. was averaged to 'distance between harem male and harem females', HM–HF) in order to avoid using repetitive individual pairs in the subsequent analyses. Thus, we obtained distance data for up to eight different bat pair types per colony (HM–HF, HF–HF, HM–NHM, HF–NHM, NHM–NHM, HM–OHM, HM–OHF, HF–OHF). Four bat pair types occurred in all five study colonies (HM–HF, HF–HF, HM–NHM, HF–NHM), whereas the remaining four bat pair types occurred in only three of the five study colonies (NHM–NHM, HM–OHM, HM–OHF, HF–OHF). In total, the average distance data of 32 bat pair types belonging to five colonies were used for statistical analyses. For each colony, every bat pair type was used only once in the analyses. Linear models (normal probability distribution, identity link function) with 'distance' as dependent variable and 'bat pair types' as well as 'colony(studysite)' ('colony' nested within 'study site') as fixed factors were performed. We used Kolmogorov–Smirnov tests to check the normal distribution of the residuals of the fitted models.

Focal animal observations with ad libitum sampling (sensu Altmann 1974) succeeded the scan-sampling of the whole social group. During focal animal observations, one harem male and one harem female of each colony were observed on ten different days for 10 min each. This resulted in a total of ten focal animals. A continuous recording procedure was used to record all behaviors, any

change in social distance (expanding or closing the distance between the focal bat and any conspecific in the colony), the modal nature of any signaling behavior (tactile, visual, olfactory, acoustic, or a mixture of the former) which might be occurring at the time of observation, as well as information relevant to the social type of the interacting bats (sex, harem affiliation). When both focal bats in a colony were not visible together, a digital video camera (Panasonic VDR-M30) was used to supplement human observation. The resulting cumulative count data were analyzed with Fisher's exact tests. Bonferroni corrections were applied following Holm (1979). Mean \pm SD are given unless stated otherwise. All statistical tests were two-tailed ($\alpha = 0.05$) and conducted using SPSS version 17.0 (SPSS, Chicago, IL, USA).

Results

Association choice between social types

A linear model revealed significant differences in social distance among different bat pair types (likelihood ratio $\chi^2 = 34.537$, $df = 7$, $P < 0.0001$; Fig. 1). Harem males and harem females (HM–HF) roosted closest together, maintaining less social distance than most other associative pairings, either from the same harem (HM–HF vs. HF–HF, $P = 0.002$; HM–HF vs. HM–NHM and vs. HF–NHM, both $P < 0.0001$; HM–HF vs. NHM–NHM, $P = 0.999$) or from different harems (HM–HF vs. HM–OHM and vs. HM–OHF and vs. HF–OHF, all $P < 0.0001$). Non-harem males (NHM–NHM) maintained the second closest social distance to one another (on average 6–7 body lengths),

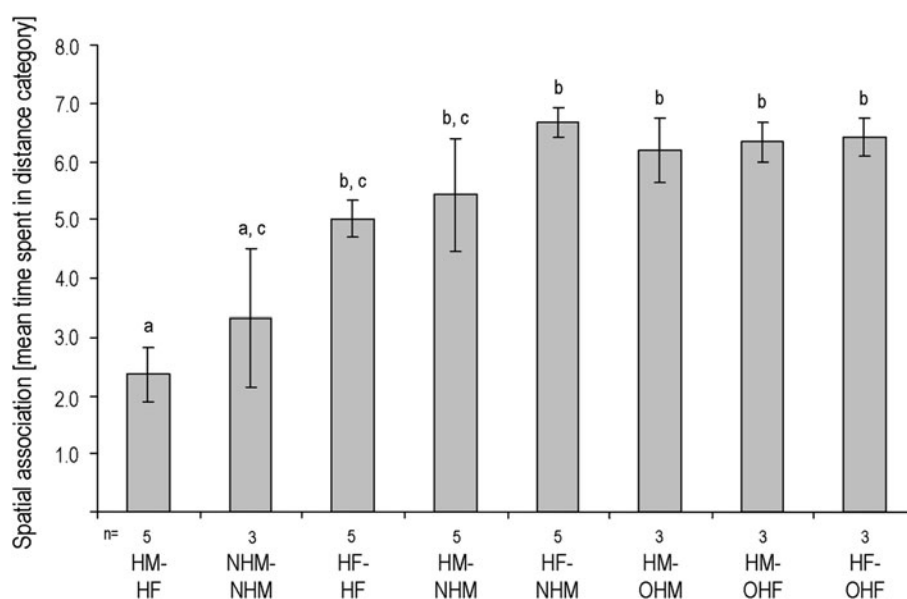
which was significantly closer than the distance to the harem females they were queuing to get access to (on average >12 body lengths; NHM–NHM vs. HF–NHM, $P = 0.001$). Colony or study site did not have a significant effect on social distance between different bat pair types (likelihood ratio $\chi^2 = 1.299$, $df = 4$, $P = 0.862$).

Hence, harem males did not roost in close physical association with other harem or non-harem males (as they would during frequent border patrols between two adjacent territories), but instead in close proximity to the females of their respective harems. In theory, the close proximity of harem males and harem females could be caused either by males spending most time in the center of their territory or at the border that is furthest away from an adjacent territory. However, the latter roosting position was only rarely observed throughout the study ($<1\%$ of all observations), suggesting a concentric harem organization around the harem male (Fig. 2a). We obtained data for one cryptic male in one colony but did not include it in the analysis. Nevertheless, we report the social distance for all bat pair types involving the cryptic male for comparative reasons (CM–HM 4.71; CM–HF 4.41; CM–NHM, CM–OHM, and CM–OHF 7.0).

Signaling modality and social distance

We observed five different signaling modalities (olfactory–visual–acoustic, visual, tactile, tactile–acoustic, acoustic) and seven associated behavior types (roosting, flying, locomoting, stretching, hovering, salting, and hitting) during behavioral interactions of harem males and harem females with conspecifics ($n = 153$) and during non-interactive behavior ($n = 309$). Most signaling modalities

Fig. 1 Spatial association (mean time spent in distance categories 1–8) for different bat pair types of greater sac-winged bats, *Saccopteryx bilineata*. Distance categories are based on estimates of number of body lengths of *S. bilineata* (see “Materials and methods” for details). Low values indicate that most time was spent roosting in close proximity, whereas high values indicate that most time was spent roosting further apart. Mean \pm SD and sample sizes (i.e. number of colonies with respective bat pair types) are shown. Different superscript letters depict a significant difference ($P \leq 0.002$)



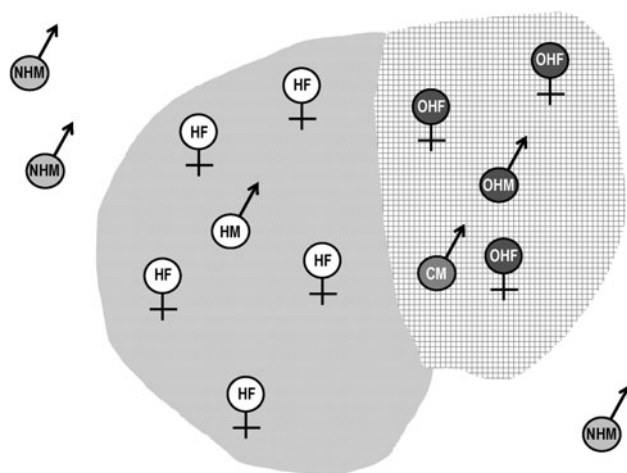


Fig. 2 Spatial distribution of colony members in the day-roost. Two adjacent harems are depicted. The harem on the *left* consists of one harem male (HM) with five harem females (HF); two non-harem males (NHM) are in the vicinity. The other harem on the *right* consists of one harem male (OHM) with three harem females (OHF) and one cryptic male (CM); one non-harem male (NHM) is roosting in close proximity. The respective territory defended by each harem male is marked in different shades of gray

used during behavioral interactions were consistently associated with the closing of social distance between signaler and receiver (94 vs. 6%; Fisher's exact test $P < 0.0001$, Bonferroni corrected $\alpha = 0.0125$). Olfactory–visual–acoustic, tactile and tactile–acoustic modalities were employed exclusively when the social distance between signaler and receiver was reduced. The behavior types mainly associated with these modalities, hovering, salting, and hitting, demonstrated corresponding results (94 vs. 6%; Fisher's exact test $P < 0.0001$, Bonferroni corrected $\alpha = 0.0125$) by being observed mainly while social distance was decreasing. Visual and acoustic modalities were also employed when the social distance between signaler and receiver expanded. There were significant differences in the association of signaling modalities with behavior types (Fisher's exact test $P < 0.0001$, Bonferroni corrected $\alpha = 0.0125$; see Table 1). Males used various signaling modalities significantly more often than females (82 vs. 18%; Fisher's exact test $P < 0.0001$, Bonferroni corrected $\alpha = 0.0125$). Females were never observed using olfactory–visual–acoustic signals, whereas males used them readily when hovering or salting.

Discussion

Social distance and association choice

Social spacing, though important to an understanding of any social organism's patterns of association, has primarily

Table 1 Cumulative occurrence of different signaling modalities used by focal greater sac-winged bats, *Saccopteryx bilineata*

| Behaviors | Signaling modalities used by harem males/harem females | |
|------------|--|--|
| | No modality | Modalities (OVA, V, T, TA, A) ^a |
| Flying | 33/49 | 1/6 (A) |
| Hitting | 0/0 | 4/0 (T) and 0/12 (TA) |
| Hovering | 0/0 | 7/0 (OVA) and 0/2 (V) |
| Locomoting | 85/52 | 4/3 (A) |
| Roosting | 56/34 | 0/0 |
| Salting | 0/0 | 112/0 (OVA) |
| Stretching | 0/0 | 2/0 (V) |

Cumulative occurrences of behaviors ($n = 462$) were derived from a total of 1,000 min of focal animal sampling (10 min each per harem male and harem female for each of ten observation sessions per colony)

^a Abbreviations represent different signaling modalities: OVA olfactory–visual–acoustic, V visual, T tactile, TA tactile–acoustic, A acoustic

been studied in the context of highly mobile animals under dispersed social conditions (e.g., Brown and Orians 1970; Weeks et al. 2000; Braune et al. 2005; Ruckstuhl and Neuhaus 2009). Such a description fits *S. bilineata* well during the night, when individuals forage separately from their colony members (Hoffmann et al. 2007), but not in the comparatively static structure of the day-roost. Foraging patches themselves are believed to be plastic, as food supply fluctuates with the season (in turn influencing population size) and may be exhausted by foraging bats on a regular basis; necessitating a new patch every 5–10 weeks (Bradbury and Vehrencamp 1976b). The relatively consistent location of the day-roost, along with the high level of diurnal activity in *S. bilineata*, makes it an important forum for reinforcing social structure.

The present study found that harem males were spaced at the concentric focal point of the harem, roosting most proximately to harem females. This result is in contrast to the existing information on social spacing in other harem defending species, for example, the northern elephant seal (*Mirounga angustirostris*) where males may pursue departing females to the borders of the harem-occupied territory and attempt to restrain them by physical force or aggression (Mesnick and Le Boeuf 1991). When harem male seals are not successful, the females are likely to copulate with subordinate males on the territorial border (Mesnick and Le Boeuf 1991)—a position analogous to the non-harem male role in *S. bilineata* colonies. Among domestic horses (*Equus ferus caballus*), harem stallions are known to patrol the borders of a harem range (McDonnell and Murray 1995), ostensibly as a mate-guarding behavior.

In southern sea lions (*Otaria flavescens*), males guard harems both by rebuffing intruders and attempting to herd their own females, when they have been displaced or prompted to stampede (Campagna et al. 1988). Behavior of this kind, where females are herded by their harem male have been most frequently observed in species with strong sexual dimorphism, typically where males are the larger and more physically powerful sex, likely because they are better equipped for combat with conspecifics than are females (Mesnick and Le Boeuf 1991). Larger male, smaller female dimorphism is prevalent among mammalian species in which dimorphism has been observed, making this format and strategy commonly plausible (Weckerly 1998). However, this paradigm does not extend to *S. bilineata*, as the females are larger and more powerful than the males (Bradbury and Emmons 1974; Voigt et al. 2005). The kind of sexual dimorphism shown in *S. bilineata* may help explain the physical layout of colonies and harems as described by the present study. If harem males are unable to physically influence their females (Bradbury and Emmons 1974; Tannenbaum 1975), and if females have nothing to fear from non-harem males, proximity to as many females as possible at a given moment may best enhance male reproductive success. Males may attract or maintain female attention through conspicuous multimodal displays (for an overview, see Voigt et al. 2008) relying on scent, visual and acoustic cues, all of which might be degraded with increased distance to the recipients (Bradbury and Vehrencamp 1998). Extra-harem paternity in *S. bilineata* can be quite high, with males siring as few as 30% of offspring born within their harem (Heckel et al. 1999), suggesting that the mating system relies heavily on female choice (Voigt et al. 2008). If a male can increase his own signal quality through the energy-inexpensive mechanism of proximal roosting, it may improve his chances of retaining female attention. It has been suggested that roosting in tree cavities or buttresses, commonly practiced by *S. bilineata*, may enable males to use more conspicuous signals (Bradbury and Vehrencamp 1976a), so the theory of space-choice for optimal signaling (Bradbury and Vehrencamp 1998) is not without precedent in this system.

Aggregation can have multiple advantages for *S. bilineata* (Bradbury and Vehrencamp 1976a). Eavesdroppers may use information from displays to assess relative strength of nearby individuals, and a group of displayers may appear stronger than a single individual, and be less likely to incite costly physical competition. Additionally, vigilance and social camouflage become easier with greater numbers (Bradbury and Vehrencamp 1976a). These factors may explain the close spatial association between non-harem males found in this study. Since these males do not have harem females available to them, their best chance for social partnership comes from other non-harem males, who

will not have as strong a reason to rebuff them as would harem males defending mates. Also, non-harem males queue for harem access such that the longest tenured male is the first in line (Voigt and Streich 2003). Since the period of residence as non-harem male controls to a great degree which male is taking over a vacant territory, non-harem males have little reason to be aggressive to one another. Our findings appear to be consistent between different study sites and colonies. However, they are based on a relatively low sample size; follow-up studies are therefore needed to investigate whether differences in social spacing exist between different populations of *S. bilineata*.

Social distance and signaling modality

At least three signaling modalities are commonly employed by *S. bilineata* in territorial and courtship displays: visual, acoustic and olfactory (for an overview, see Voigt et al. 2008). In our study, the use of particular signaling modalities was associated with the expansion or reduction of social distance. In many cases, these associated social movements appeared to be correlated with signaling enhancement: olfactory–visual–acoustic, tactile and tactile–acoustic modalities (marked by behaviors like hover displays, salting or agonistic physical contact) were employed exclusively when the social distance between signaler and receiver was reduced; visual and acoustic modalities were also employed when the social distance between signaler and receiver expanded. Olfactory cues released from the wing-sacs, and, to a lesser degree, visual and acoustic cues are exaggerated by proximity (Bradbury and Vehrencamp 1998). When bats were not employing any form of signal conspicuous to human observation, they roosted further apart, suggesting a “normative” state of relatively expanded social distance. A combination of olfactory–acoustical–visual signals was never observed to be employed by females in this study. The associated behaviors, salting and hovering, have previously been noted to be largely the domain of males (Voigt and von Helversen 1999; Voigt et al. 2008; Knörnschild et al. 2010), even though females occasionally engage in hovering (Strauss et al. 2010) and salting as well, but without accompanying vocalizations (M.K., personal observation).

Harem maintenance

The results of the present study indicate that harem maintenance by male *S. bilineata* differs from the mammalian convention of exterior ‘patrol’ (Campagna et al. 1988; McDonnell and Murray 1995). Even though male *S. bilineata* scent mark their territory borders (Caspers and Voigt 2009) and may engage in violent disputes there

(Tannenbaum 1975, Bradbury and Emmons 1974), they do not spend much time at the periphery of their territories. However, one has to take into account that the roosting space covers only the first two dimensions of a territory. Since *S. bilineata* can fly, a territory extends into the third dimension. A three-dimensional territory has the shape of a hemisphere and the best position for exterior patrol would be the territory center because there the distance to both the two-dimensional borders and the airspace within would be smallest. However, we do not believe that a defense-related advantage of males roosting at the harem center can explain the observed social spacing in *S. bilineata*. Usurpers often enter a harem territory by crawling on the roost surface rather than flying and the air space over a territory is not defended as vigorously as the roosting space within (M.K., personal observation), making the territory of *S. bilineata* less three-dimensional than one would expect for a flying animals and border patrols of the two-dimensional roosting space vital. We can, of course, not rule out that the central spacing of harem males is somewhat beneficial for territorial defense, but we are certain that it is adjuvant for courtship. Male *S. bilineata* appear to maintain harems by positioning themselves closest to the harem constituents, where signal strength is highest, rather than attempting to herd constituent females. This strategy may be the result of the unusual size dimorphism of *S. bilineata*; smaller males are unequipped to physically influence the larger females, and likely stand a better chance of retaining them by virtue of conspicuous signaling, which, in turn, is enhanced by roosting in close proximity to females.

Acknowledgments We are indebted to M. Metz and M. Nagy for providing helpful comments on the manuscript. The suggestions of two anonymous reviewers substantially improved the manuscript. The Organization for Tropical Studies (OTS) and the National System of Conservation Areas (SINAC) granted permission to conduct research at the Biological Station La Selva and the National Park Santa Rosa. We thank the Costa Rican authorities, especially Javier Guevara, for support and research permissions. Funding was provided by the National Geographic Society. The study complied with the current laws of Costa Rica.

References

- Altmann J (1974) Observational study of behaviour: sampling methods. *Behaviour* 49:227–267
- Altmann SA, Wagner SS, Lenington S (1977) Two models for the evolution of polygyny. *Behav Ecol Sociobiol* 2:397–410
- Arroyo-Rodríguez V, Serio-Silva JC, Alamo-García J, Ordano M (2006) Exploring immature-to-mother social distance in Mexican mantled howler monkeys at Los Tuxtlas, Mexico. *Am J Primatol* 69:173–181
- Behr O, von Helversen O (2004) Bat serenades—complex courtship songs of the sac-winged bat (*Saccopteryx bilineata*). *Behav Ecol Sociobiol* 56:106–115
- Behr O, von Helversen O, Heckel G, Nagy M, Voigt CC, Mayer F (2006) Territorial songs indicate male quality in the sac-winged bat *Saccopteryx bilineata* (Chiroptera, Emballonuridae). *Behav Ecol* 17:810–817
- Behr O, Knörnschild M, von Helversen O (2009) Territorial counter-singing in male sac-winged bats (*Saccopteryx bilineata*): low-frequency songs trigger a stronger response. *Behav Ecol Sociobiol* 63:442–443
- Bezanson M, Garber PA, Murphy JT, Premo LS (2008) Patterns of subgrouping and spatial affiliation in a community of mantled howling monkeys (*Alouatta palliata*). *Am J Primatol* 70:282–293
- Bradbury JW (1977) Social organization and communication. In: Wimsatt WA (ed) *Biology of bats*. Academic, New York, pp 1–72
- Bradbury JW, Emmons LH (1974) Social organization of some Trinidad bats I. Emballonuridae. *Z Tierpsychol* 36:137–183
- Bradbury JW, Vehrencamp SL (1976a) Social organization and foraging in Emballonurid bats. I: field studies. *Behav Ecol Sociobiol* 1:337–381
- Bradbury JW, Vehrencamp S (1976b) Social organization and foraging in Emballonurid bats. II: a model for the determination of group size. *Behav Ecol Sociobiol* 1:383–404
- Bradbury JW, Vehrencamp SL (1998) Principles of animal communication. Sinauer, Sunderland
- Braune P, Schmidt S, Zimmermann E (2005) Spacing and group coordination in a nocturnal primate, the golden brown mouse lemur (*Microcebus ravelobensis*): the role of olfactory and acoustic signals. *Behav Ecol Sociobiol* 58:587–596
- Brown JL, Orians GH (1970) Spacing patterns in mobile animals. *Annu Rev Ecol Syst* 1:239–262
- Burgess JW (1983) Interpersonal spacing behavior between surrounding nearest neighbors reflects both familiarity and environmental density. *Ethol Sociobiol* 4:11–17
- Campagna C, Le Boeuf BJ, Cappelozzo HL (1988) Group raids: a mating strategy of male southern sea lions. *Behaviour* 105:233–261
- Caspers B, Franke S, Voigt CC (2008) The wing-sac odour of male greater sac-winged bats *Saccopteryx bilineata* (Emballonuridae) as a composite trait: seasonal and individual differences. In: Hurst J, Beynon RJ, Roberts SC, Wyatt TD (eds) *Chemical signals in vertebrates XI*. Springer, Berlin, pp 151–160
- Caspers B, Voigt CC (2009) Temporal and spatial distribution of male scent marks in the polygynous greater sac-winged bat. *Ethology* 115:713–720
- Davidson SM, Wilkinson GS (2004) Function of male song in the greater white-lined bat, *Saccopteryx bilineata*. *Anim Behav* 67:883–891
- Fenton MB (1985) *Communication in the Chiroptera*. Indiana University Press, Bloomington
- Fleming TH, Nelson AA, Dalton VM (1998) Roosting behavior of the lesser-long-nosed bat, *Leptonycteris curasoae*. *J Mammal* 79:147–155
- Heckel G, Voigt CC, Mayer F, von Helversen O (1999) Extra-harem paternity in the white-lined bat *Saccopteryx bilineata*. *Behaviour* 136:1173–1185
- Heckel G, von Helversen O (2002) Male tactics and reproductive success in the harem polygynous bat *Saccopteryx bilineata*. *Behav Ecol* 12:219–227
- Heckel G, von Helversen O (2003) Genetic mating system and the significance of harem associations in the bat *Saccopteryx bilineata*. *Mol Ecol* 12:219–227
- Hoffmann FF, Hejuk J, Caspers B, Siemers BM, Voigt CC (2007) In the mating system of the bat *Saccopteryx bilineata*, bioacoustic constraints impede male eavesdropping on female echolocation calls for their surveillance. *Can J Zool* 85:863–872
- Holm S (1979) A simple sequentially rejective multiple test procedure. *Scand J Stat* 6:65–70
- Kerth G, König B (1999) Fission, fusion and nonrandom associations in female Bechstein's bats (*Myotis bechsteinii*). *Behaviour* 136:1187–1202

- Knörnschild M, Fulmer AG, von Helversen O (2010) Duration of courtship displays corresponds to social status in male greater sac-winged bats (*Saccopteryx bilineata*). *Can J Zool* 88:589–594
- McCracken GF, Wilkinson GS (2000) Bat mating systems. In: Crichton EG, Krutzsch PH (eds) *Reproductive biology of bats*. Academic, New York, pp 321–362
- McDonnell SM, Murray SC (1995) Bachelor and harem stallion behavior and endocrinology. *Biol Reprod* 1:577–590
- Mesnick SL, Le Boeuf BJ (1991) Sexual behavior of male northern elephant seals: II. Female response to potentially injurious encounters. *Behaviour* 117:262–280
- Mitani JC, Amsler SJ (2003) Social and spatial aspects of male subgrouping in a community of wild chimpanzees. *Behaviour* 140:869–884
- Ortega J, Maldonado JE (2006) Female interactions in harem groups of the Jamaican fruit-eating bat, *Artibeus jamaicensis* (Chiroptera: Phyllostomidae). *Acta Chiropterol* 8:485–495
- Prange S, Jordan T, Hunter C, Gehrt SD (2006) New radiocollars for the detection of proximity among individuals. *Wildl Soc Bull* 34:1333–1344
- Richardson KE, Weckerly FW (2007) Intersexual social behavior of urban white-tailed deer and its evolutionary implications. *Can J Zool* 85:759–766
- Ruckstuhl KE, Neuhaus P (2009) Activity budgets and sociality in a monomorphic ungulate: the African oryx (*Oryx gazelle*). *Can J Zool* 87:165–174
- Say LS, Pontier D (2004) Spacing pattern in a social group of stray cats: effects on male reproductive success. *Anim Behav* 68:175–180
- Seibert LM, Crowell-Davis SL (2001) Gender effects on aggression, dominance rank, and affiliative behaviors in a flock of captive adult cockatiels (*Nymphicus hollandicus*). *Appl Anim Behav Sci* 71:155–170
- Starck D (1958) Beitrag zur Kenntnis der Armtaschen und anderer Hautdrüsenorgane von *Saccopteryx bilineata*. *Gegenbaur Morphol Jahrb* 99:3–25
- Strauss M, von Helversen O, Knörnschild M (2010) The ontogeny of courtship behaviours in bat pups (*Saccopteryx bilineata*). *Behaviour* 147:661–676
- Tannenbaum R (1975) Reproductive strategies in the white-lined bat. PhD dissertation, Cornell University
- Voigt CC, von Helversen O (1999) Storage and display of odor by male *Saccopteryx bilineata* (Chiroptera; Emballonuridae). *Behav Ecol Sociobiol* 47:29–40
- Voigt CC, Streich WJ (2003) Queuing for harem access in colonies of the sac-winged bat. *Anim Behav* 65:149–156
- Voigt CC, Heckel G, Mayer F (2005) Sexual selection favours small and symmetric males in the polygynous greater sac-winged bat *Saccopteryx bilineata* (Emballonuridae, Chiroptera). *Behav Ecol Sociobiol* 57:457–464
- Voigt CC, Heckel G, von Helversen O (2006) Conflicts and strategies in the harem-polygynous mating system of the sac-winged bat *Saccopteryx bilineata*. In: McCracken G, Zubaid A, Kunz TH (eds) *Functional and evolutionary ecology of bats*. Oxford University Press, Oxford, pp 269–278
- Voigt CC, Behr O, Caspers B, von Helversen O, Knörnschild M, Mayer F, Nagy M (2008) Songs, scents, and senses: Sexual selection in the greater sac-winged bat, *Saccopteryx bilineata*. *J Mammal* 89:1401–1410
- Weckerly FW (1998) Sexual-size dimorphism: Influence of mass and mating systems in the most dimorphic mammals. *J Mammal* 79:33–52
- Weeks JW, Crowell-Davis SL, Caudle AB, Heusner GL (2000) Aggression and social spacing in light horse (*Equus caballus*) mares and foals. *Appl Anim Behav Sci* 68:319–337
- Yancey F II, Goetze J, Jones C (1998) *Saccopteryx bilineata*. *Mammal Spec* 581:1–5