Female-biased dispersal and patrilocality in a mammal with resource-defence polygyny

Martina Nagy¹, Gerald Heckel², Christian C. Voigt³ and Frieder Mayer^{1,*}

¹Department of Zoology, University of Erlangen-Nuremberg, Staudtstraße 5, 91058 Erlangen, Germany

²Computational and Molecular Population Genetics, Zoological Institute, University of Bern, Baltzerstraße 6, 3012 Bern, Switzerland

³Leibniz Institute for Zoo and Wildlife Research, Alfred-Kowalke-Straße 17, 10315 Berlin, Germany

In most mammals, dispersal rates are higher in males than in females. Using behavioural and genetic data of individually marked bats, we show that this general pattern is reversed in the greater sac-winged bat (*Saccopteryx bilineata*). Dispersal is significantly female biased and male philopatry in combination with rare male immigration causes a patrilineal colony structure. Female dispersal helps avoid father–daughter inbreeding, as male tenure exceeds female age at first breeding in this bat species. Furthermore, our data suggest that females may engage in extra-harem copulations to mate with genetically dissimilar males, and thus avoid their male descendants as mating partners. Acquaintance with the natal colony might facilitate territory takeover since male sac-winged bats queue for harem access. Given the virtual absence of male immigration and the possible lower reproductive success of dispersing males, we argue that enhancing the likelihood of settlement of male descendants could be adaptive despite local mate competition. We conclude that resource defence by males is important in promoting male philopatry, and argue that the potential overlap of male tenure and female first conception is the driving force for females to disperse.

Keywords: female-biased dispersal; *Saccopteryx bilineata*; patrilineal; inbreeding avoidance; bat

1. INTRODUCTION

In most mammals and birds, dispersal is more prevalent in one sex, while a higher proportion of the other sex is faithful to its place of birth (Greenwood 1980). To date, a considerable amount of research has gone into uncovering the evolutionary forces that account for these sex-biased dispersal patterns. The main evolutionary explanations invoke the avoidance of inbreeding (e.g. Packer 1979; Dobson 1982; Waser *et al.* 1986; Pusey 1987; Clutton-Brock 1989; Wolff 1994; Perrin & Mazalov 2000) of local resource competition (Clarke 1978; Greenwood 1980) and of local mate competition (LMC; Dobson 1982; Moore & Ali 1984) as well as cooperative behaviour among kin (e.g. Perrin & Goudet 2001; Le Galliard *et al.* 2006). Evolutionary stable patterns of dispersal are assumed to result from a balance of the above-mentioned selective forces (Greenwood 1980; Dobson 1982; Perrin & Goudet 2001; Lawson Handley & Perrin 2007). Mating systems are widely accepted as fundamental determinants of the direction in sex-biased dispersal (Greenwood 1980; Dobson 1982; Perrin & Goudet 2001). Greenwood (1980) argued that dispersal in mammals and birds is tightly linked to male mating strategies. If males adopt a resource-defence strategy in order to attract females, familiarity with the natal area might be crucial in acquiring a territory and should therefore favour male philopatry. In accordance with the latter, dispersal is female biased in the majority of socially monogamous birds. Contrarily, in female-defence systems, which are most prevalent among polygynous mammals, males

predominantly compete for access to females and therefore the spatial distribution of females should determine male dispersion, and thereby promote male-biased dispersal (MBD, Greenwood 1980). However, MBD in polygynous mammals has also been argued to originate from avoidance of competition with kin (Dobson 1982). In polygynous systems, males and females compete for different items. While females compete for resources, males are expected to compete for access to females. The higher variance in male reproductive success compared with that of females is supposed to result in higher kin competition among males and should therefore promote MBD. This prediction is well supported by empirical data on polygynous mammals as well as by the fact that dispersal is not sex biased in the majority of monogamous mammals (Dobson 1982).

Female-biased dispersal (FBD) is rare among mammals (e.g. African wild dogs *Lycaon pictus*: Frame & Frame 1976; Chimpanzees *Pan troglodytes*: Pusey & Packer 1987) and its occurrence frequently correlates with resource-defence polygyny as proposed by Greenwood (1980). However, a resource-defence strategy does not necessarily lead to FBD (Coulon *et al.* 2006) and there are examples of mammals with FBD that do not follow a resource-defence mating strategy (e.g. Spider monkeys *Ateles paniscus*: McFarland Symington 1987; Horses *Equus caballus*: Monard & Duncan 1996). In a considerable number of polygynous mammalian species, females may disperse to avoid inbreeding with their fathers when male tenure exceeds female age at first conception (Clutton-Brock 1989). In the greater sac-winged bat (*Saccopteryx bilineata*), females have been reported to

* Author for correspondence (fmayer@biologie.uni-erlangen.de).

disperse from their natal colony, whereas at least some of the male progeny remain in their natal colony (Bradbury & Emmons 1974; Tannenbaum 1975). The mating system of this bat is best described as resource-defence polygyny (Bradbury & Vehrencamp 1977). Following Greenwood (1980), this would mean that females are assumed to disperse owing to the inbreeding risk arising from male philopatry. However, there are currently no studies investigating the causes for female dispersal in this species and if there is a risk of inbreeding arising from female breeding philopatry and male natal philopatry.

The greater sac-winged bat is a neotropical insectivorous member of the family Emballonuridae (Bradbury & Emmons 1974). Up to 50 adult individuals of this bat are associated year-round in colonies, which are situated on the buttresses of large trees, well-lit tree cavities, in abandoned buildings as well as on the outer walls of buildings (Bradbury & Emmons 1974). In a colony, several males defend each territories of approximately 1–2 m², occupied by on average 2–3 females, which results in up to 12 harem territories per colony. Peripheral males, which defend a territory without females or do not own a territory, roost adjacent to harems (Bradbury & Emmons 1974; Bradbury & Vehrencamp 1976; Heckel & von Helversen 2002). The pattern of harem succession is best explained by queuing for harem access, where the period of tenure in a given group of non-territorial males defines which male next occupies a vacant territory (Voigt & Streich 2003). Parentage analyses revealed that harem associations are not representative of the genetic mating system of the sac-winged bat, since 70% of the progeny are not fathered by the harem male of the mother (so called extra-harem young (EHY)), but predominantly by other harem or peripheral males of the colony (83% intracolony paternity, Heckel *et al.* 1999; Heckel & von Helversen 2003). Male reproductive success is not evenly distributed and was found to correlate with smallness, symmetry and acoustic parameters of territorial songs, which is indicative of an important role of sexual selection in male mating success (Voigt *et al.* 2005; Behr *et al.* 2006). For female mating decisions, the extensive male courtship efforts should be of major importance. Among these one can find complex male territorial and courtship songs (Behr & von Helversen 2004) as well as remarkable hovering flights, in which odour originating from a sexually dimorphic wing-sac is fanned towards individual females (Voigt & von Helversen 1999).

Here, we use behavioural observations and genetic analyses from a long-term study of a colony of *S. bilineata* to investigate the extent of female dispersal and male philopatry. In the light of the ambiguous role of male mating strategy in influencing mammal FBD, we test the hypothesis that female dispersal is a father-daughter inbreeding avoidance strategy (Clutton-Brock 1989) in a bat with FBD and resource defence by males. If so, female age at first conception should be lower than average male tenure. We further investigate the hypothesis that male natal philopatry in combination with long female and male breeding philopatry causes the risk of inbreeding between females and their male descendants. Finally, we test whether females avoid inbreeding by mating with genetically dissimilar males and thereby contribute to the high proportions of extra-harem paternities.

2. MATERIAL AND METHODS

(a) Field methods

The study colony was located in an abandoned building close to the 'La Selva' field station (10°25' N, 84°00' W) of the Organization for Tropical Studies, Costa Rica where it was monitored over a course of 8 years (1994–2001). Animals were captured, individually banded (coloured plastic bands: Hughes XCL) and a wing tissue sample was taken from each individual. Details on the study colony, marking techniques and DNA sampling can be found in Heckel *et al.* (1999), Voigt & von Helversen (1999) and Voigt *et al.* (2001). By the end of October 1995, all adult animals were individually banded and juvenile sampling began in summer 1996. The distribution of animals within the colony (social structure) was surveyed by direct observations of individually marked bats (Heckel *et al.* 1999) from September to October 1995, June to August 1996, October 1996 to February 1997, June to August 1997, June to August 1998, December 1998 to February 1999, June to August 1999, November to December 1999, June to August 2000, December 2000 to January 2001 and June to August 2001. During census observation, male status was determined based on territorial and courtship behaviours. Males defending a territory in which at least one female roosted were defined as harem males (HM). Female affiliation to certain harem territories was also determined via census observations (see Heckel *et al.* (1999), Voigt *et al.* (2001) and Heckel & von Helversen (2003) for details). Between 1996 and 2001, the study colony harboured 50–60 adult individuals spaced in 10–12 harem territories, which contained the 10–12 HM and all of the 27–40 female residents. Furthermore, 8–13 peripheral males, which did not defend any females, were present within this period. The parturition period of Costa Rican sac-winged bats lies between late May and end of July and is followed by the mating season, which is restricted to approximately three weeks in December and January (Voigt & Schwarzenberger 2008).

(b) Paternity and relatedness analysis

We used 11 highly polymorphic microsatellite markers for paternity and relatedness analyses (Heckel *et al.* 1999, 2000). A total of 50 adult females, 55 adult males and 183 juveniles were genotyped. This also includes individuals that were not observed to roost in the study colony, but were captured in the vicinity of the colony. Of the 183 juveniles, 160 were born in the study colony, and the sex of 179 was determined. Genotypes were not obtained from six females, one male and 10 juveniles that were observed but not caught between 1996 and 2001. We attempted to genotype each individual at 11 loci. In total, we obtained 98.9% of all possible genotypes and each individual was genotyped at least at 10 loci.

Paternity analysis was performed as described by Heckel & von Helversen (2003). We compared paternity data with harem affiliation of the parents during the mating season from December to January. If census data were not available from the mating season (1996 and 1998), we used census data from the following parturition period between June and August. Intra-harem young (IHY) were sired by parents who roosted in the same harem, while an EHY descended from a male that was not the harem male of its mother.

We used the program KINSHIP v. 1.3.1 (Goodnight & Queller 1999) to test pedigree relationships between pairs of individuals. We tested two hypotheses (father-offspring or half-siblings) as primary hypothesis versus the null hypothesis

Table 1. Dispersal and immigration occurrences of the study colony between 1996 and 2001.

dispersal	no. of juveniles born	dispersed prior to the next mating season
females	71	68 (96%)
males	87	48 (55%)
immigration	no. of newly established residents	no. of immigrated residents
females	40	37 (93%)
males	29	2 (7%)

of no relationship. In the case of a potential father–offspring relationship, we also tested against the null hypothesis of a half-sibling relationship. The significance of likelihood ratios ($p < 0.05$) was estimated with 100 000 simulations, using the allele frequencies obtained with CERVUS v. 2.0 (Marshall *et al.* 1998). Patriline were reconstructed on the basis of parentage analyses and the significant pedigree relationship tests were performed with the software KINSHIP.

We applied the program KINSHIP to determine pairwise relatedness between parents of an offspring as well as between females with EHY and their respective harem male. For statistical analyses, we divided our dataset into two groups, the first group consisting of females that reproduced with their harem male (IHY females, 54 incidences) and the second of females that reproduced with a male other than their harem male (EHY females, 77 incidences). For females that were present for more than 1 year, we averaged pairwise relatedness to account for pseudoreplication. We used only non-parametric tests for statistical analyses (SPSS v. 12) and tests were two-tailed unless otherwise specified. Mean values and one standard deviation are provided.

3. RESULTS

(a) Dispersal and immigration

Between 1996 and 2001, a total of 71 female juveniles and 87 male juveniles were born to colony females (table 1). Of the 71 females, only three (4%) were still present in their natal colony after a period of seven months and only one female was still present in the following parturition period, though not reproducing. Thus, 68 females (96%) dispersed or died prior to the next breeding season and none of the females reproduced in their natal colony. By contrast, 39 (45%) of the 87 juvenile males born in the colony were present in the mating season that followed their birth. This results in a significantly FBD (Chi-square test: $\chi^2_1 = 33.0$, $p < 0.001$).

A total of 37 females immigrated into the colony between 1996 and 2001, of which 14 females (38%) were juveniles at capture and 23 females (62%) were already adult. None of these females descended from members of our colony and three were born in three other colonies nearby. Until 2001 a total of 29 adult males have become resident as peripheral or HM. We found that 27 of them (93%) were born in our study colony and at least 25 males (86%) were fathered by a male resident in the colony. One of the two immigrating males was born in a neighbouring colony at a distance of 150 m. Only one male of unknown parents, and thus likely to be an offspring of another

colony, settled during the 6 years of the investigation in our study colony. The proportion of female immigrants among established individuals was significantly higher than the proportion of male immigrants (Chi-square test: $\chi^2_1 = 50.1$, $p < 0.001$).

(b) Female and male tenure

A total of 66 adult females roosted in our study colony between the years 1996 and 2001. Female tenure (total period of time individuals roosted in the colony) in the colony averaged 2.7 ± 2.0 years (range 0.05–7.6 years). Within the same period, 51 adult males were residents of our study colony. The average tenure in the colony was 2.7 ± 2.1 years (range 0.1–9.2 years) for males. Males that gained a harem position ($N = 30$) were present in the colony for 3.2 ± 2.4 years, whereas non-HM ($N = 21$) were present for only 2.0 ± 1.2 years. Thus HM had a longer tenure in the colony than non-HM (t -test: $T = 2.4$, d.f. = 42, $p = 0.019$).

(c) Female and male age at first breeding

We obtained data on the reproduction of 11 females that were banded as juvenile immigrants in our study colony and were still present at the next parturition period. All of these females gave birth to a juvenile at an age of 1 year. Thus, female sac-winged bats conceived first at an age of approximately seven months, in the mating season following the summer of their own birth. Only two of the 39 males, which were present during the mating season following their birth, fathered one offspring each at half a year of age. Male sac-winged bats seemed to have reached sexual maturity at six months, even though they rarely father offspring at that age.

(d) Patriline and LMC

The combination of rare male immigration and high levels of intracolony paternity led to lineages of closely related males. The 51 resident males observed between 1996 and 2001 in the colony could be allotted to 12 patriline by genetic kinship analysis (figure 1). Some or even all of these patriline are likely to coalesce before 1994 owing to the common male ancestors that lived prior to our study in the same colony. The patriline were composed of 1–12 males. The majority of resident males (40, 78%) belonged to four patriline, whereas each of the remaining eight patriline consisted of one or two individuals. Closely related sexually mature males are commonly observed simultaneously in the colony, since male tenure is extensive (see above) and young males may father offspring already at an age of 0.5 years (see above). One adult male, for example, was observed to roost together with up to three sexually mature sons and one grandson (figure 1c), which results in severe LMC.

(e) Inbreeding avoidance

Male natal philopatry, female breeding philopatry and the coexistence of overlapping generations caused by the bats' longevity promote the risk of mother–son or mother–grandson inbreeding. Eighteen mothers roosted simultaneously with 1–3 sons of an age of at least 1.5 years in the colony. Four of these mothers were even members of their son's harem. Another four females were found to roost in the same colony with their grandsons. Of 160 juveniles, none was found to result from a mating between mothers

Figure 1. Affiliation of the 51 adult males to 12 patriline (a–l). Each column represents an individual male, with every cell depicting a year from summer 1996 (uppermost cell) to summer 2001 (lowest cell). The year of birth is labelled by an asterisk, while a grey background indicates the residence period of adult males. Empty columns represent males that were not present in the colony during the study period, but were present or caught until 1995 or were resident in a neighbouring colony. Solid lines denote a relatedness of 0.5, dashed lines show that of 0.25.

and their sons or grandsons. Females with an extra-harem young (EHY females) were more closely related to their harem male than females with an intra-harem young (IHY females; figure 2; Mann–Whitney U -test, $n_1 = 31$, $n_2 = 38$, $U = 380$, $p = 0.012$). Furthermore, EHY females and the fathers of their offspring were genetically more dissimilar than EHY females and their respective HM (figure 2; one-tailed Wilcoxon signed-rank test: $N = 38$, $Z = -1.954$, $p = 0.026$). Moreover, EHY females were still more closely related to their harem male than IHY females after removing the four females that roosted in their sons' harem from the analysis (figure 2; one-tailed Mann–Whitney U -test $n_1 = 31$, $n_2 = 36$, $U = 411$, $p = 0.033$). Therefore, familiarity of mothers with their sons cannot explain mating of EHY females with genetically more dissimilar males. The relatedness between parents of EHY and parents of IHY was not significantly different (figure 2; Mann–Whitney U -test: $n_1 = 31$, $n_2 = 38$, $U = 503.5$, $p = 0.302$).

4. DISCUSSION

Dispersal of greater sac-winged bats is significantly female biased (FBD). All female juveniles of our study colony dispersed or died prior to reproduction and all reproducing females that newly established were immigrants not

Figure 2. Boxplots showing pairwise relatedness values between parents of IHY, between females with extra-harem young (EHY females) and their HM, between parents of EHY and between EHY females and their HM after removing relatedness values of EHY females that roosted in their son's harem (HM^A). Boxes represent the interquartile range, bars within boxes are median values, whiskers indicate the 10th and 90th percentiles and individual data point outliers. Results of statistical tests are indicated as not significant (NS) or significant at the 5% level (*). See text for details.

descending from colony members. By contrast, we found the majority (93%) of newly established males to be born in the colony, leading to a patrilineal social organization of the colony. However, we also detected a large proportion of males (55%) that either had left the natal colony or died before reaching half a year of age.

FBD is exceptional among mammals, and so far primates account for the majority of cases (64% of mammals with FBD, Lawson Handley & Perrin 2007). The avoidance of LMC is regarded as an important ultimate cause, inducing MBD among polygynous/promiscuous mammals (Dobson 1982; Perrin & Goudet 2001; Coulon *et al.* 2006). With male philopatry, the impact of LMC should be highest in mammals associated with polygynous/promiscuous multi-male groups, in which several related males may reproduce simultaneously. The incidence of male philopatry under such conditions is known from highly social primate species (Lawson Handley & Perrin 2007) and now also from a bat species. Single males are associated with on average 2–3 females in harems (one-male units) and a colony may consist of up to 12 such adjacent harems in addition to queuing non-territorial males (Voigt & Streich 2003). Extra-harem paternities can reach values up to 70% in the sac-winged bat, but reproduction occurs almost exclusively between the male and female residents of a colony (83% intracolony paternity, Heckel & von Helversen 2003). With respect to this specific mating pattern, colonies of the greater sac-winged bat closely resemble multi-male groups in primates (e.g. Alaotran gentle lemur *Haplorhina griseus*: Mutschler *et al.* 2000; Chimpanzee *P. troglodytes*: Vigilant *et al.* 2001). A patrilineal organization entails that several closely related males compete for harem territories and according to the high proportions of EHY (up to 70%) also for mates (Heckel & von Helversen 2003). This results in severe LMC, which is similarly high as in multi-male groups of male philopatric primates. Thus, the potentially high impact of LMC raises the question of why dispersal is female-biased in the greater sac-winged bat.

In their recent review, Lawson Handley & Perrin (2007) point out that inbreeding avoidance and co-operation are among the most important factors leading to FBD in mammals with high LMC. In social mammals, female dispersal from the natal group as a means of inbreeding avoidance has been predicted for situations where the average residence of males or of resident male kin groups exceeds the average age of females at first conception (Clutton-Brock 1989). This applies to the greater sac-winged bat, since females start to reproduce at approximately half a year of age, when their fathers are most likely to be still present in the colony. Therefore, in the greater sac-winged bat female dispersal probably stems from father–daughter inbreeding avoidance. At this point, it is important to realize that female dispersal is not necessarily linked to male philopatry, because the risk of father–daughter inbreeding is not generated by male natal philopatry but by male tenure. Although female dispersal reduces the problem of inbreeding, males in polygynous systems still need to overcome the costs of LMC if male philopatry is to be promoted. In several mammalian species, where female dispersal is assumed to be an inbreeding avoidance strategy, both sexes commonly transfer from their natal groups (e.g. plain zebra,

Equus burchelli; red howler monkey, *Alouatta seniculus*, reviewed in Clutton-Brock (1989)). Moreover, in two other closely related polygynous emballonurid species (*Rhynchonycteris naso* and *Balantiopteryx plicata*: Bradbury & Vehrencamp 1976), all juveniles of both sexes disperse from natal colonies. So far *S. bilineata* is the only known species in the family of Emballonuridae with female dispersal and male philopatry and might have the most derived dispersal pattern, which evolved from a state of all offspring dispersal. Only recently a study on another neotropical bat (*Lophostoma silviculum*) showed that all offspring disperse from their natal colony. Female dispersal was also suggested to originate from father–daughter inbreeding avoidance, but males dispersed despite resource-defence polygyny (Dechmann *et al.* 2007), which indicates that LMC plays an important role. These dispersal patterns of neotropical bats contrast with the matrilineal colony structures of temperate zone bats including several vespertilionid species (Kerth *et al.* 2000; Castella *et al.* 2001; Petit *et al.* 2001) and the greater horseshoe bat (Rossiter *et al.* 2005).

Generally, natal philopatry is thought to be favoured in cases where familiarity with the natal area facilitates the acquisition of a resource crucial to reproduction and when individuals can take advantage of the benefits of kin cooperation (Greenwood 1980; Perrin & Mazalov 2000; Lawson Handley & Perrin 2007). In the greater sac-winged bat, both mechanisms might apply. Male sac-winged bats queue for harem access, and male philopatry might be favoured as males need to establish familiarity with nearby territories and consequently acquire site dominance as early as possible (Voigt & Streich 2003). Also female sac-winged bats seem to influence their sons' chance to settle in the natal colony. Unlike all other bat species studied so far, female greater sac-winged bats are known to defend their own roosting site inside a harem territory, in which their sons may roost cryptically up to an age of eight months (Tannenbaum 1975; Voigt & Streich 2003). Delayed dispersal of sons but not of daughters from the mother's territory may enhance the likelihood of these cryptic males in taking over a nearby vacant territory at a young age (Tannenbaum 1975; Voigt & Streich 2003). However, 17 out of 22 observed males (77%) became resident without prior cryptic status, which makes it unlikely that only mothers influence their sons' success.

In consideration of the low proportion of immigrant males, one might speculate that resident males also may have an active role in the settlement of new males. They might level their aggression predominantly against unfamiliar and thus probably unrelated males. Young males of the colony and thus familiar males could be the offspring of any resident male, considering the high levels of EHY (70%) and intracolony paternity (83%; Heckel & von Helversen 2003). The indirect fitness gained by tolerating the reproductive success of male kin might overcome the costs arising due to LMC, if dispersing males have little perspective to settle and reproduce in other colonies. This is indicated by rare male immigration into our study colony. One chance that a dispersing male might have is the establishment of a new colony. However, sac-winged bats have very specific roost preferences (Bradbury & Emmons 1974; Tannenbaum 1975) and suitable roosts might be a scarce resource. Although we do not have information on the

fate of young males that dispersed from our study colony, we suppose that the reproductive success of dispersing males should be lower on average than that of philopatric males. The benefits of such local resource enhancement have only recently found attention as a potentially potent factor in the evolution of sex-biased dispersal (e.g. Perrin & Mazalov 2000; Le Galliard *et al.* 2006).

Our results on the mating pattern of female sac-winged bats are in line with those from other studies indicating that extra-pair/extra-group paternities may function as an important inbreeding avoidance mechanism (e.g. Blomqvist *et al.* 2002; Tarvin *et al.* 2005; Muniz *et al.* 2006). The role of inbreeding avoidance in shaping dispersal patterns has been controversially discussed, since in polygynous systems females pay a higher cost to inbred matings than males and since females rather than males should therefore be the dispersing sex (Waser *et al.* 1986). However, Lehmann & Perrin (2003) showed in a modelling approach that female choosiness to mate with unrelated males should boost male dispersal. Our results provide evidence of an opposite effect. Female sac-winged bats seem to have evolved a kin-recognition mechanism and thus avoid mating with male descendants. This does not prevent male philopatry, it might even be important in maintaining it. The proximate mechanisms enabling female sac-winged bats to evaluate relatedness between themselves and potential mates beyond mother-son recognition are currently unknown and a possible role of immune genes and associated olfactory cues, as shown in a few other mammals (Piertney & Oliver 2006), remains speculative.

We conclude that resource defence by male sac-winged bats does play an important role in promoting male philopatry. We argue that female dispersal originates from the potential overlap between the time of females' first conception and male tenure. It remains questionable whether FBD would have evolved merely with resource defence by males and without a different incentive for females to disperse.

We are thankful to S. Meister, M. Brandt, B. Caspers and A. Brunner who contributed to field and laboratory work. M. L. East, H. Hofer, O. v. Helversen, M. Knörnschild, O. Behr and O. Höner made most helpful comments on the manuscript. We are grateful to the Costa Rican authorities, especially Javier Guevara, for support and research permits. This work was funded by the Deutsche Forschungsgemeinschaft (DFG).

REFERENCES

- Behr, O. & von Helversen, O. 2004 Bat serenades—complex courtship songs of the sac-winged bat (*Saccopteryx bilineata*). *Behav. Ecol. Sociobiol.* **56**, 106–115. (doi:10.1007/s00265-004-0768-7)
- Behr, O., von Helversen, O., Heckel, G., Nagy, M., Voigt, C. C. & Mayer, F. 2006 Territorial songs indicate male quality in the sac-winged bat *Saccopteryx bilineata* (Chiroptera, Emballonuridae). *Behav. Ecol.* **17**, 810–817. (doi:10.1093/beheco/arl013)
- Blomqvist, D. *et al.* 2002 Genetic similarity between mates and extra-pair parentage in three species of shorebirds. *Nature* **419**, 613–615. (doi:10.1038/nature01104)
- Bradbury, J. W. & Emmons, L. H. 1974 Social organization of some trinidad bats I. Emballonuridae. *Z. Tierpsychol.* **36**, 137–183.
- Bradbury, J. W. & Vehrencamp, S. L. 1976 Social organization and foraging in emballonurid bats I. Field studies. *Behav. Ecol. Sociobiol.* **1**, 337–381. (doi:10.1007/BF00299399)
- Bradbury, J. W. & Vehrencamp, S. L. 1977 Social organization and foraging in emballonurid bats IV. Parental investment patterns. *Behav. Ecol. Sociobiol.* **2**, 19–29. (doi:10.1007/BF00299285)
- Castella, V., Ruedi, M. & Excoffier, L. 2001 Contrasted patterns of mitochondrial and nuclear structure among nursery colonies of the bat *Myotis myotis*. *J. Evol. Biol.* **14**, 708–720. (doi:10.1046/j.1420-9101.2001.00331.x)
- Clarke, A. B. 1978 Sex ratio and local resource competition in a prosimian primate. *Science* **201**, 163–165. (doi:10.1126/science.201.4351.163)
- Clutton-Brock, T. H. 1989 Female transfer and inbreeding avoidance in social mammals. *Nature* **337**, 70–72. (doi:10.1038/337070a0)
- Coulon, A., Cosson, J. F., Morellet, N., Angibault, J. M., Cargnelutti, B., Galan, M., Aulagnier, S. & Hewison, A. J. M. 2006 Dispersal is not female biased in a resource-defence mating ungulate, the European roe deer. *Proc. R. Soc. B* **273**, 341–348. (doi:10.1098/rspb.2005.3329)
- Dechmann, D. K. N., Kalko, E. K. V. & Kerth, G. 2007 All-offspring dispersal in a tropical mammal with resource defense polygyny. *Behav. Ecol. Sociobiol.* **61**, 1219–1228. (doi:10.1007/s00265-007-0352-z)
- Dobson, F. S. 1982 Competition for mates and predominant juvenile male dispersal in mammals. *Anim. Behav.* **30**, 1183–1192. (doi:10.1016/S0003-3472(82)80209-1)
- Frame, L. & Frame, G. W. 1976 Female African wild dogs emigrate. *Nature* **263**, 227–229. (doi:10.1038/263227a0)
- Goodnight, K. F. & Queller, D. C. 1999 Computer software for performing likelihood tests of pedigree relationship using genetic markers. *Mol. Ecol.* **8**, 1231–1234. (doi:10.1046/j.1365-294x.1999.00664.x)
- Greenwood, P. J. 1980 Mating systems philopatry and dispersal in birds and mammals. *Anim. Behav.* **28**, 1140–1162. (doi:10.1016/S0003-3472(80)80103-5)
- Heckel, G. & von Helversen, O. 2002 Male tactics and reproductive success in the harem polygynous bat *Saccopteryx bilineata*. *Behav. Ecol.* **13**, 750–756. (doi:10.1093/beheco/13.6.750)
- 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. (doi:10.1046/j.1365-294X.2003.01722.x)
- Heckel, G., Voigt, C. C., Mayer, F. & von Helversen, O. 1999 Extra-harem paternity in the white-lined bat *Saccopteryx bilineata* (Emballonuridae). *Behaviour* **136**, 1173–1185. (doi:10.1163/156853999501829)
- Heckel, G., Achmann, R. & Mayer, F. 2000 Highly polymorphic microsatellite markers in the white-lined bat (*Saccopteryx bilineata*). *Mol. Ecol.* **9**, 242–244. (doi:10.1046/j.1365-294x.2000.00804-4.x)
- Kerth, G., Mayer, F. & König, B. 2000 Mitochondrial DNA (mtDNA) reveals that female Bechstein's bats live in closed societies. *Mol. Ecol.* **9**, 793–800. (doi:10.1046/j.1365-294x.2000.00934.x)
- Lawson Handley, J. L. & Perrin, N. 2007 Advances in our understanding of mammalian sex-biased dispersal. *Mol. Ecol.* **16**, 1559–1578. (doi:10.1111/j.1365-294X.2006.03152.x)
- Le Galliard, J. F., Gundersen, G., Andreassen, H. P. & Stenseth, N. C. 2006 Natal dispersal, interactions among siblings and intrasexual competition. *Behav. Ecol.* **17**, 733–740. (doi:10.1093/beheco/arl002)

- Lehmann, L. & Perrin, N. 2003 Inbreeding avoidance through kin recognition: choosy females boost male dispersal. *Am. Nat.* **162**, 638–652. (doi:10.1086/378823)
- Marshall, T. C., Slate, J., Kruuk, L. E. & Pemberton, J. M. 1998 Statistical confidence for likelihood-based paternity inference in natural populations. *Mol. Ecol.* **7**, 639–655. (doi:10.1046/j.1365-294x.1998.00374.x)
- McFarland Symington, M. 1987 Sex ratio and maternal rank in wild spider monkeys: when daughters disperse. *Behav. Ecol. Sociobiol.* **20**, 421–426. (doi:10.1007/BF00302985)
- Monard, A. M. & Duncan, P. 1996 Consequences of natal dispersal in female horses. *Anim. Behav.* **52**, 565–579. (doi:10.1006/anbe.1996.0198)
- Moore, J. & Ali, R. 1984 Are dispersal and inbreeding avoidance related? *Anim. Behav.* **32**, 94–112. (doi:10.1016/S0003-3472(84)80328-0)
- Muniz, L., Perry, S., Manson, J. H., Gilkenson, H., Gros-Louis, J. & Vigilant, L. 2006 Father–daughter inbreeding avoidance in a wild primate population. *Curr. Biol.* **16**, 156–157. (doi:10.1016/j.cub.2006.02.055)
- Mutschler, T., Nievergelt, C. M. & Feistner, A. T. C. 2000 Social organization of the Alaotran gentle lemur (*Haplemur griseus alaotrensis*). *Am. J. Primatol.* **50**, 9–24. (doi:10.1002/(SICI)1098-2345(200001)50:1<9::AID-AJP2>3.0.CO;2-2)
- Packer, C. 1979 Inter troop transfer and inbreeding avoidance in *Papio anubis*. *Anim. Behav.* **27**, 1–36. (doi:10.1016/0003-3472(79)90126-X)
- Perrin, N. & Goudet, J. 2001 Inbreeding, kinship and the evolution of natal dispersal. In *Dispersal* (eds J. Clobert, E. Danchin, A. A. Dhondt & J. D. Nichols), pp. 123–142. Oxford, UK: Oxford University Press.
- Perrin, N. & Mazalov, V. 2000 Local competition, inbreeding and the evolution of sex-biased dispersal. *Am. Nat.* **155**, 116–127. (doi:10.1086/303296)
- Petit, E., Balloux, F. & Goudet, J. 2001 Sex-biased dispersal in a migratory bat: a characterization using sex-specific demographic parameters. *Evolution* **55**, 635–640. (doi:10.1554/0014-3820(2001)055[0635:SBDIAM]2.0.CO;2)
- Piertney, S. B. & Oliver, M. K. 2006 The evolutionary ecology of the major histocompatibility complex. *Heredity* **96**, 7–21.
- Pusey, A. E. 1987 Sex-biased dispersal and inbreeding avoidance in birds and mammals. *Trends Ecol. Evol.* **2**, 295–299. (doi:10.1016/0169-5347(87)90081-4)
- Pusey, A. E. & Packer, C. 1987 Dispersal and philopatry. In *Primate societies* (eds B. B. Smutts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham & T. T. Struhsaker), pp. 250–266. Chicago, IL: University of Chicago Press.
- Rossiter, S. J., Ransome, R. D., Faulkes, C. G., Le Comber, S. C. & Jones, G. 2005 Mate fidelity and intra-lineage polygyny in greater horseshoe bats. *Nature* **437**, 408–411. (doi:10.1038/nature03965)
- Tannenbaum, B. R. 1975 Reproductive strategies in the white-lined bat. PhD thesis, Cornell University, NY.
- Tarvin, K. A., Webster, M. S., Tuttle, E. M. & Pruett-Jones, S. 2005 Genetic similarity of social mates predicts the level of extrapair paternity in splendid fairy-wrens. *Anim. Behav.* **70**, 945–955. (doi:10.1016/j.anbehav.2005.01.012)
- Vigilant, L., Hofreiter, M., Siedel, H. & Boesch, C. 2001 Paternity and relatedness in wild chimpanzee communities. *Proc. Natl Acad. Sci. USA* **98**, 12 890–12 895. (doi:10.1073/pnas.231320498)
- Voigt, C. C. & Schwarzenberger, F. 2008. Female reproductive endocrinology of a small tropical bat (*Saccopteryx bilineata*; Emballonuridae) monitored by fecal hormone metabolites. *J. Mammal.*
- Voigt, C. C. & Streich, W. J. 2003 Queuing for harem access in colonies of the greater sac-winged bat. *Anim. Behav.* **65**, 149–156. (doi:10.1006/anbe.2002.2031)
- Voigt, C. C. & von Helversen, O. 1999 Storage and display of odour by male *Saccopteryx bilineata* (Chiroptera, Emballonuridae). *Behav. Ecol. Sociobiol.* **47**, 29–40. (doi:10.1007/s002650050646)
- Voigt, C. C., von Helversen, O., Michener, R. & Kunz, T. H. 2001 The economics of harem maintenance in the sac-winged bat, *Saccopteryx bilineata* (Emballonuridae). *Behav. Ecol. Sociobiol.* **50**, 31–36. (doi:10.1007/s002650100337)
- Voigt, C. C., 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. (doi:10.1007/s00265-004-0874-6)
- Waser, P. M., Austad, S. N. & Keane, B. 1986 When should animals tolerate inbreeding? *Am. Nat.* **128**, 529–537. (doi:10.1086/284585)
- Wolff, J. O. 1994 More on juvenile dispersal in mammals. *Oikos* **71**, 349–352. (doi:10.2307/3546284)