Female-biased dispersal and patrilocal kin groups in a mammal with resource-defence polygyny

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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; patrilines; 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
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 98.8% 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.
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 ($\lambda$ < 0.05) was estimated with 100,000 simulations, using the allele frequencies obtained with CERVUS v. 2.0 (Marshall et al. 1998). Patrilines 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 group consisting 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 mating 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: $\chi^2 = 33.0, p < 0.001$).

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: $\chi^2 = 50.1, p < 0.001$).

(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 ($C = 2.4, d.f. = 42, p = 0.019$).

(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 offspring 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) Patrilines 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 patrilines by genetic kinship analysis (figure 1). Some or even all of these patrilines are likely to coalesce before 1994 owing to 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.
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 son’s 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 1. Affiliation of the 51 adult males to 12 patrilines (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.

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*). 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.
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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. Alotran gentle lemur Hapalemur 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 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.

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