

Female-biased dispersal in a bat with a female-defence mating strategy

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Abstract

The ultimate causes for predominant male-biased dispersal (MBD) in mammals and female-biased dispersal (FBD) in birds are still subject to much debate. Studying exceptions to general patterns of dispersal, for example, FBD in mammals, provides a valuable opportunity to test the validity of proposed evolutionary pressures. We used long-term behavioural and genetic data on individually banded Proboscis bats (*Rhynchonycteris naso*) to show that this species is one of the rare mammalian exceptions with FBD. Our results suggest that all females disperse from their natal colonies prior to first reproduction and that a substantial proportion of males are philopatric and reproduce in their natal colonies, although male immigration has also been detected. The age of females at first conception falls below the tenure of males, suggesting that females disperse to avoid father–daughter inbreeding. Male philopatry in this species is intriguing because Proboscis bats do not share the usual mammalian correlates (i.e. resource-defence polygyny and/or kin cooperation) of male philopatry. They have a mating strategy based on female defence, where local mate competition between male kin is supposedly severe and should prevent the evolution of male philopatry. However, in contrast to immigrant males, philopatric males may profit from acquaintance with the natal foraging grounds and may be able to attain dominance easier and/or earlier in life. Our results on Proboscis bats lent additional support to the importance of inbreeding avoidance in shaping sex-biased dispersal patterns and suggest that resource defence by males or kin cooperation cannot fully explain the evolution of male philopatry in mammals.

Keywords: female age at first conception, inbreeding avoidance, local mate competition, male philopatry, male tenure, *Rhynchonycteris naso*

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Introduction

Dispersal is an almost ubiquitous phenomenon in animals affecting the demography and genetic structure of populations as well as the evolution of social behaviour (e.g. Clobert *et al.* 2001). Natal dispersal, that is, dispersal from the natal group or area prior to sexual maturity, is usually sex biased in birds and mammals (Greenwood 1980; Dobson 1982). Female-biased dispersal (FBD) prevails in the majority of bird species,

whereas male-biased dispersal (MBD) is the rule in mammals (Greenwood 1980; Dobson 1982; Clarke *et al.* 1997). The main evolutionary forces shaping dispersal patterns include the avoidance of inbreeding (e.g. Waser *et al.* 1986; Pusey 1987; Clutton-Brock 1989; Perrin & Mazalov 2000), the avoidance of local mate competition (e.g. Hamilton 1967; Dobson 1982; Perrin & Goudet 2001), the avoidance of local resource competition (e.g. Clarke 1978; Greenwood 1980; Sterck *et al.* 1997) and kin cooperation (Perrin & Goudet 2001; Le Galliard *et al.* 2006). Though, there is still much disagreement about the relative importance of these ultimate causes for sex-biased dispersal (SBD; e.g. reviewed in Lawson Handley & Perrin 2007).

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There are several mechanisms how a species' mating system may ultimately affect the direction of SBD (Greenwood 1980; Dobson 1982; Perrin & Goudet 2001). First, Greenwood (1980) hypothesized in his seminal article on the resource-defence hypotheses that the philopatric sex in birds (males) and mammals (females) corresponds to the sex that benefits most from familiarity with the local area. The sex involved less in resource acquisition should then disperse to avoid inbreeding. In accordance with Greenwood's resource-defence hypotheses, most birds are socially monogamous, male birds mostly follow a resource-defence strategy, and thus, dispersal is predominantly female biased (e.g. Greenwood 1980). In contrast, the majority of mammals exhibit MBD because they have socially polygynous or promiscuous mating systems where males defend females directly (e.g. Dobson 1982; Lawson Handley & Perrin 2007). Additional support for the resource-defence hypothesis comes from species with an atypical mating strategy and a reversed dispersal pattern [i.e. MBD in birds with female defence (e.g. in the Anatidae Greenwood 1980; White-throated Magpie-jay *Calocitta formosa* Langen 1996) and FBD in mammals with resource defence by males (e.g. Kinkajou *Potos flavus* Kays *et al.* 2000; Greater sac-winged bat *Saccopteryx bilineata* Nagy *et al.* 2007)]. However, some exceptions to the general dispersal patterns cannot be explained by the resource-defence hypothesis. This includes mammalian species with FBD where males pursue a female-defence strategy (e.g. Spider monkeys *Ateles paniscus* McFarland Symington 1987; Horses *Equus caballus* Monard & Duncan 1996) and no bias in dispersal in spite of resource-defence polygyny (e.g. Roe deer *Capreolus capreolus* Coulon *et al.* 2006; Gaillard *et al.* 2008).

Second, mating systems have been proposed to shape dispersal patterns through differences in the intensity of local mate competition relative to local resource competition (Dobson 1982; Perrin & Mazalov 2000; Perrin & Goudet 2001). While one can assume that the sexes compete approximately for the same items in monogamous systems, this is not the case in polygynous or promiscuous systems. In the latter, females are the ones that usually bear the whole burden of parental care and compete primarily for access to resources, whereas competition among males is mainly for access to mating partners (Dobson 1982; Clutton-Brock 1991). When local competition equally affects both sexes, as it is assumed to be the case in monogamous systems, Perrin & Mazalov's (2000) model predicts dispersal to be unbiased. Owing to the relatively greater potential reproductive rate of male mammals, theory predicts that local mate competition among males should exceed local resource competition among females and that dispersal should therefore be mediated by males (Perrin & Mazalov

2000). The fact that MBD predominates in polygynous and promiscuous mammals, whereas generally no bias in dispersal is found in socially monogamous mammals, supports the prediction that asymmetries in the intensity of local mate competition and local resource competition between the sexes affect SBD (Dobson 1982). However, since Dobson's seminal article (1982), a number of monogamous mammals have been shown to exhibit SBD (e.g. MBD in Fork-marked lemurs *Phaner furcifer* Schülke 2003; FBD in Greater white-toothed shrews *Crocidura russula* Favre *et al.* 1997) and monogamous birds generally have FBD (e.g. Clarke *et al.* 1997). This contrasts with the prediction that local resource competition should equally affect both sexes in monogamous mammals (Perrin & Mazalov 2000).

Finally, the prevalence of female philopatry in mammals has been suggested to result from lower relative breeding tenures and longevity of males in polygynous mating systems. If the breeding tenures of males or of male kin groups fall below the age of females at first conception, then philopatric females do not risk inbreeding with their fathers, because the reproductive tenure of their fathers will have ended by the time females start breeding in their natal groups (Clutton-Brock & Isvaran 2007; Clutton-Brock 2009; Clutton-Brock & Lukas 2011). In plural-breeding mammals (i.e. species living in stable social groups that include several breeding females), habitual female dispersal (i.e. most or all females leave their natal group before reproducing and breeding females in groups are unrelated immigrants) is consistently associated with male breeding tenures that commonly exceed the age of females' first conception because of the risk of father-daughter inbreeding associated with philopatry (Clutton-Brock 1989; Clutton-Brock & Lukas 2011). Moreover, phylogenetic reconstructions suggest that in plural-breeding mammals, the transition from habitual female philopatry to habitual female dispersal is correlated with an increase in relative male tenure and inbreeding risk (Lukas & Clutton-Brock 2011).

Examples of mammalian species with FBD are scarce (e.g. Chimpanzees *Pan troglodytes* Pusey & Packer 1987; Hamadryas baboons *Papio hamadryas* Hammond *et al.* 2006; Greater sac-winged bat *Saccopteryx bilineata* Nagy *et al.* 2007) but represent an excellent opportunity to test the validity of existing hypotheses for SBD. They may provide unique insights into more general explanations of SBD (e.g. Greenwood 1980; Clarke *et al.* 1997; Lawson Handley & Perrin 2007). One well-studied mammalian species with FBD is the bat *S. bilineata*. Here, habitual female dispersal is associated with male tenure durations that exceed the age of females' first conception and male philopatry correlates with a resource-defence mating system corroborating Greenwood's (1980) theory (Bradbury

& Emmons 1974; Nagy *et al.* 2007). The Proboscis bat (*Rhynchonycteris naso*) is a closely related, sympatric emballonurid bat in which offspring of both sexes supposedly disperse from their natal colonies at 2–4 month of age and males have been reported to follow a female-defence mating strategy (Bradbury & Vehrencamp 1976, 1977a). These observations and the assumption that MBD is the ancestral dispersal pattern in mammals (Clutton-Brock & Lukas 2011) suggest that assumed all-offspring dispersal in *R. naso* might represent an intermediate evolutionary stage towards the evolution of FBD. However, detailed studies that combine long-term behavioural observations of individually recognizable group members with molecular parentage and kinship analysis, which are essential to gain a reliable estimate of dispersal patterns and for testing ultimate causes of dispersal or philopatry (Lawson Handley & Perrin 2007; Harris *et al.* 2009; Clutton-Brock & Lukas 2011), are currently lacking in *R. naso*.

The Proboscis bat is a small insectivorous bat distributed in lowland rainforests between the south of Mexico, the south of Brazil and the east of the Andes to Peru and Columbia (Hall 1981). Roosting sites are exposed parts of tree trunks, branches, vines or man-made structures in the immediate vicinity of rivers (Bradbury & Emmons 1974). *Rhynchonycteris naso* space themselves at 5–10 cm from each other in the day roost and live year-round in stable social groups of 5–50 individuals with males and females at about equal numbers. The mating strategy of males has been reported to be one of direct female defence (Bradbury & Emmons 1974; Bradbury & Vehrencamp 1976, 1977a). These bats are physically cryptic in the day roost, which probably causes social interactions to be infrequent therein (Bradbury & Emmons 1974); this is in marked contrast to *S. bilineata* (e.g. Voigt *et al.* 2008). Even inconspicuous behaviours like grooming or urinating occur mostly accompanied by rocking and in synchrony with other bats in the colony and only when a gust of wind springs up, suggesting that bats are trying to resemble patches of vegetation swaying in a breeze to maintain their cryptic roosting habits (Knörnschild *et al.* 2009).

In this study, we used exhaustive long-term behavioural observations of individually banded Proboscis bats together with genetic parentage and kinship analysis to test whether dispersal is unbiased or sex biased in this bat. The result of Bradbury & Vehrencamp (1976) that all offspring disperse from their natal colonies is based on only 10 months of field data. According to Greenwood's hypothesis (Greenwood 1980), a female-defence strategy as exhibited by Proboscis bats should favour male dispersal. Thus, we predicted MBD if female age at first conception exceeds average male tenure duration and there is no risk of father–daughter inbreeding or all-offspring dispersal if female age at first concep-

tion falls below mean male tenure duration and there is a risk of father–daughter inbreeding (*sensu* Clutton-Brock 1989). All-offspring dispersal instead of FBD was predicted if male tenure duration exceeds female age at first conception, because male dispersal is supposedly driven by the avoidance of local mate competition in polygynous mammals (Dobson 1982; Perrin & Mazalov 2000).

Methods

Field methods

The study was conducted from 2006 to 2012 in three main and 12 supplemental study colonies (day roosts) at the 'La Selva' field station of the Organisation for Tropical Studies (Costa Rica, Province Heredia, 10°25' N/84°00' W). The bats of two main study colonies (Cabina 5: C5 and Riverstation: RS) roosted on the outside, under the overhanging roof of two inhabited wooden station cabins and were thus well habituated to the presence of humans. The third main study colony roosted on the wooden ceiling beams inside an abandoned house (Casa Grande: CG). These roosting sites are known to have been occupied by Proboscis bats for at least 11 years. Bats were mist netted (Ecotone[®] monofilament, Gdynia, Poland) from the three main study colonies when emerging at dusk. Mist nets were set several metres away from the roosting bats to prevent bats from connecting the capturing event with a potential threat to their roosting site and to ascertain that captured bats return to their roosts. In addition to the three main study colonies, *Rhynchonycteris naso* were captured with a hand-held scoop net in 12 supplemental colonies, distributed approximately over 10 km along the banks of the Puerto Viejo River and the Sarapiquí River in 2006 and 2007. We took a small tissue sample from the plagiopatagium or chiropatagium (Stiefel[®] biopsy punch, 4 mm Ø) of each bat for genetic analysis (the resulting hole healed completely within 2–4 weeks) and individually marked each bat with coloured plastic bands on their forearms (AC Hughes[®] Ltd., UK, size XCS). Bands were attached to both forearms of bats through a small cut (ca. 3–4 mm) in the plagiopatagium. Males were banded with a unicoloured and numbered ring on the right forearm and with a bicoloured ring on the left forearm, whereas females were banded vice versa. Captured bats were weighed (16 g Pesola[®] spring scale), sexed, their age (juvenile, subadult or adult) and reproductive state were determined and their right forearm and third and fifth finger were measured (see supporting information for details on age determination). Table 1 provides details on the number of banded and genetically sampled bats.

Table 1 Number of banded and genetically sampled bats between 2006 and 2011

Age	Sex	Cabina 5		Riverstation		Casa Grande		Other colonies	
		Banded	Genetic. sampled	Banded	Genetic. sampled	Banded	Genetic. sampled	Banded	Genetic. sampled
Adult	Female	21	21	19	24	37	38	40	39
	Male	26	25	22	25	25	25	30	29
Subadult	Female	13	13	13	13	5	5	8	8
	Male	5	4	6	6	6	6	7	7
Juvenile	Female	11	13	7	8	3	3	0	6
	Male	12	14	2	5	8	12	0	5
Total		88	90	69	81	84	89	85	94

Group structure [colony size, number and identity of banded males and females, number of unbanded bats, number as well as motherhood of juveniles (i.e. banded pups were assigned to banded mothers by nursing observations)] was determined during daylight on a daily to at least monthly basis in the three main colonies with binoculars and digital pictures from a distance of approximately 5 m during the following periods: June–August 2006 (64–67 census days), June–August 2007 (68–74 census days), April–June 2008 (42–49 census days), August 2008 (2 census days), January–February 2009 (3 census days), March 2010 (1 census day), July–September 2010 (12–15 census days), April–May 2011 (29–32 census days), July 2011 (11–14 census days) and in July 2012 (19–22 census days). The exposed, light-tolerant roosting habits and the possibility to approach the bats of our three main colonies up to approximately 5 m permitted us to detect and, if banded, identify all present bats in a day roost during census observations. Table S1 (Supporting information) provides details on the numbers of bats per colony and year as well as the yearly genetic sample rate of colony members.

Census analyses

Overall, census data on group size and composition were collected on 275 (C5), 272 (RS) and 253 (CG) days (see also Table S1). Based on census observations, minimum tenure of adult females ($n = 68$) and males ($n = 54$) was calculated as the time interval between the day of banding and the last day of observation of the bat in its colony. The majority of bats were already adults when banded ($n = 55$ females and $n = 43$ males), so that the actual start of tenure in the respective colony was unknown. Moreover, the end of tenure of several bats remained undetermined, because these bats were still present in their resident colonies in our last field season in 2012 ($n = 20$ females and $n = 14$ males). Due to the lack of information on the beginning and ending

of tenure of a large number of bats in this study, the actual median tenures of adult *R. naso* surely exceed our median minimal tenure estimates. Only individuals that were observed also in the field season following the field season they had been banded in were included in the calculation of median minimal tenure ($n = 24$ females and $n = 32$ males were not included in median minimal tenure estimation). Our longest field season lasted for 74 consecutive days. Given that most individuals were already adult at capture and that the following field season often started a year later, the observation of an individual for only one field season would have greatly underestimated even the minimal tenure of individual *R. naso*.

Additionally, we calculated a fidelity index F (Heckel *et al.* 1999) of adult bats, which indicates the fidelity of each individual to its colony and thus the compositional stability of social groups. Unlike the calculation of tenure, F is calculated solely based on actual observation days and corresponds to the proportion of days a bat was present in its colony of residence between its first and last day of observation in the colony. F equals one if an individual was observed in its colony on every census day, and F equals 0.5 if a bat was present in a colony on half of census observations. A fidelity index was calculated only for individuals that were present at least until the end of the field season they had been banded in ($n = 71$ females and $n = 60$ males). Bats that disappeared before the end of the field season of their banding were not included in fidelity calculations ($n = 21$ females and $n = 26$ males), because their disappearance was most probably caused by a disturbance due to our repeated capture attempts.

Several bats were observed in two colonies. A bat was considered to have performed a permanent transfer to another colony if it was caught and banded in one colony (where it may or may not have been observed as a resident after banding) and was then observed to roost in another colony, without ever having been observed to return to its previous colony ($n = 5$). A

number of other bats were observed to transfer back and forth between two colonies. Some of these ($n = 5$) were residents of one colony and occasional visitors to another known colony (i.e. 1–15 days of observation in a second colony and no more than two consecutive days of presence per visit to the second colony). Other bats that were observed to transfer back and forth between two colonies were treated as residents of two colonies ($n = 3$) because they had been observed to roost for longer periods of consecutive observation days in two colonies (i.e. N_{\min} was 17 consecutive observation days). Also, while resident in one colony, these bats were observed as occasional visitors of the second colony. If bats were observed as residents of two colonies, we calculated minimal tenure and fidelity for both colonies of residence (i.e. for the period between the first and last day of observation in each colony) and averaged these values for their use in calculating median minimal tenure and median fidelity per colony.

Average age at females' first conception was estimated from 10 females caught as subadults (all banded juvenile females dispersed to unknown colonies or disappeared). Female *R. naso* may give birth to two pups per year. In the first parturition period in April, the majority of females have a single pup, whereas some females may also have a second pup per year between July and October (Bradbury & Vehrencamp 1976, 1977b). Females were excluded from the calculation of age at females' first conception if it was probable that we had missed their first reproductive event ($n = 11$ excluded females). The first reproductive event of a female was considered to have been missed if we lacked data from a female's first possible parturition in April and if the female did not have a pup in June, July or August of the same year. To estimate the date of a female's first conception, the average gestation period in *R. naso* (4 months, Bradbury & Vehrencamp 1977b) was subtracted from the birth date of its first juvenile. The age of females at first conception was then calculated as the difference between the date of first conception and the female's own birth date. The female's own birth date was conservatively assumed to be the earliest possible date (beginning of April, Bradbury & Vehrencamp 1976, 1977b) in the same year it was caught as a subadult.

Copulations and defence of oestrous females by males

We observed the behaviour of *R. naso* in one of the main study colonies (C5) during a period of 18 consecutive days (*ad libitum* sampling for 65:08 h on 16 individual days) in April and May 2011. Within this period, five females gave birth to juveniles and apparently came into post-partum oestrus. Those females and the

11 adult males that were present in the colony were the focal bats of our behavioural observations. All focal bats were present throughout the entire observation sessions. We defined different behavioural interactions. Copulations started with a male approaching a female crawling towards her from behind. Subsequently, the male mounted the back of the female until their heads were almost at the same level. We considered a copulation to have been successful if we observed the male flattening its interfemoral membrane, giving several short thrusts and finally tapping the female with his chin on her back. Copulation attempts also started with a male approaching a female from behind and with the male mounting the back of the female but were interrupted either by the female hitting the male with a wing and/or flying away or by another male that quickly approached the couple, prompting the male that was trying to copulate to move away from the female. Approaches to oestrous females were defined when a male left his roosting position in the colony to move and stay in close spatial proximity to a female that had given birth within the preceding days. Attempted approaches to oestrous females were interrupted by another male that moved towards the male approaching an oestrous female, sometimes hitting him with his wing, which prompted the approaching male to move or fly away from the oestrous female. Males that interrupted copulation attempts or attempts to approach an oestrous female were considered to have performed an act of female defence.

Genetic analyses

Tissue samples were preserved in 80% ethanol, and DNA was isolated with the salt–chloroform procedure by Miller *et al.* (1988) modified by Heckel *et al.* (1999) [for details on PCR conditions, see Heckel *et al.* (2000) and Nagy *et al.* (2009)]. We used the DNA Analyser 4300 (LI-COR®; Biosciences) and the SAGA^{GT} (LI-COR®; Biosciences) allele scoring software to genotype a total of 354 individuals (Table 1) at nine highly polymorphic microsatellite loci (Heckel *et al.* 2000; Nagy *et al.* 2009) caught in the three main study colonies and 12 additional colonies between 2005 and 2011 (nine *R. naso* were sampled genetically in 2005, before the beginning of this study, and no genetic analysis were performed for the year 2012). All individuals were genotyped at least at eight loci, and genotypes were 99.8% complete. Table S2 shows allele numbers per locus, results of Hardy–Weinberg tests, null allele frequencies and nonexclusion probabilities for the nine microsatellite markers.

Parentage analysis was performed with CERVUS v. 3.0 (Kalinowski *et al.* 2007) for 128 potential colony

offspring, consisting of 66 bats caught as juveniles and 62 bats caught as subadults in our study colonies. Maternity of 38 *R. naso* caught as juveniles was determined by nursing observations in the field and confirmed with genetic analysis. Maternity of 28 juvenile and 62 subadult individuals was analysed entirely with CERVUS v. 3.0 (Kalinowski *et al.* 2007). All males caught as adults ($n = 104$) and resident males that matured during this study ($n = 13$) were treated as putative fathers for paternity assignment of pups with known ($n = 71$) and with unknown mothers ($n = 57$). Simulations were run with 100 000 cycles, a genotyping error of 1.1% (estimated with CERVUS v. 3.0 and based on five mismatches between 38 known mother offspring pairs), a proportion of 60% sampled candidate fathers and a proportion of 14.5% candidate fathers that were relatives, related to the true father by $r = 0.5$. The percentage of relatives among candidate fathers was estimated based on the results of the kinship analysis between adult males. Although on average we had sampled 70% of the individuals in our study colonies, we attempted to account for possible extra-colony paternities by choosing a lower sampling rate of 60% candidate fathers. Simulations were performed for two confidence levels (80% and 95%). We accepted one mismatch per parent–offspring dyad, thus two independent mismatches between an offspring and each of its parents to account for genotyping errors. Forty-nine parent pairs were assigned at 95% confidence, and three parent pairs were assigned at 80% confidence. Eight fathers and 19 mothers were assigned at 95% confidence, and six fathers were assigned at 80% confidence. In contrast to all other loci, the locus Sb85 showed significant evidence for null alleles (Table S2). Therefore, we ran parentage analyses with and without the locus Sb85, which resulted in 22 differently assigned mothers or fathers (10 additional mothers, 10 additional fathers and two differently assigned fathers). In 17 of these 22 cases, there was no evidence for null alleles at locus Sb85 (candidate offspring was heterozygous); therefore, we used results from paternity analysis with all loci. For five candidate offspring, results of paternity analysis without the locus Sb85 were used.

Additionally, to find parent–offspring dyads among adults, we analysed kinship among all adults across all colonies (135 females and 117 males) with the software KINGROUP v2 (Konovalov *et al.* 2004) that is based on the likelihood-calculation algorithm of the software KINSHIP (Goodnight & Queller 1999). Here, we tested the primary hypothesis of parent–offspring relatedness against the null hypothesis of full siblings using 100 000 simulations to assess the significance of likelihood ratios ($P < 0.05$). We used the closest degree of relatedness between the primary and the null hypothesis, to achieve

a high discriminatory power for distinguishing parent–offspring dyads from other kinship relationships (Konovalov *et al.* 2004).

Other statistical analyses

We used SPSS (version 20.0) to perform statistical tests. We tested data for a Gaussian distribution with Kolmogorov–Smirnov tests. Comparisons of non-normally distributed data were performed with Mann–Whitney *U*-tests. To test divergence between observed and expected frequencies of normally distributed data, we used Pearson's chi-square test if all expected frequencies were above five and Fisher's exact test if at least one expected value was below five. All tests were two-tailed, and means are presented with 1 standard deviation (\pm SD).

Results

Minimum tenure and fidelity of adults to colonies

Between 2006 and 2012, the median minimum tenure of 68 adult females was 1.27 years (interquartile range 0.98–2.58 years) and the median minimum tenure of 54 adult males was 1.65 years (interquartile range 0.69–2.56 years), with no significant difference between sexes (Mann–Whitney *U*-test: $n_f = 68$, $n_m = 55$, $U = 1921.5$, $P = 0.66$). Because most females ($n = 55$) and males ($n = 43$) were adult at capture and because many of the bats banded before July 2011 were still present at the end of the observation period in July 2012 ($n = 20$ females, $n = 14$ males), the actual average tenure of adult colony members exceeds our minimal tenure estimates.

Adult male and female *Rhynchonycteris naso* were present in their resident colonies almost every day within the respective observation periods. Median fidelity to study colonies was 0.99 (interquartile range 0.89–1.00) in adult males and 1.00 (interquartile range 0.97–1.00) in adult females. Males tended to have lower fidelity indices than females (Mann–Whitney *U*-test: $n_f = 71$, $n_m = 60$, $U = 2548.5$, $P = 0.05$). Although adult individuals generally showed long-term tenure and high fidelity to their resident colonies, we observed several cases of transfers of adults between colonies. Four adult females and one adult male were observed to perform a permanent transfer (i.e. secondary dispersal) to another of our main study colonies, where they became residents. In addition, we observed several adult males ($n = 8$) to transfer back and forth between two main colonies. Five of these males were residents of one colony and occasional visitors of another colony, and three of these males were residents of two colonies. Another

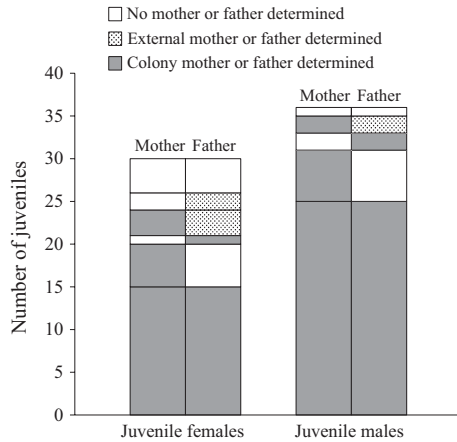


Fig. 1 Results of paternity analysis for juveniles ($n = 30$ females and $n = 36$ males). Bars for juvenile females and males are split to show whether a mother and/or father has been assigned, and if so, whether the mother and/or father was a resident of the same or another colony compared to the juvenile bat. [Correction after online publication 18 February 2013: the figure was replaced to correctly show where no mother or father has been assigned.]

29 adult females (F_f range: 0.79–0.99) and 25 adult males (F_m range: 0.27–0.99) had fidelity indices lower than one but were not observed while absent from their colony and might thus be occasional visitors of unknown colonies or have a second residency in another, unknown colony.

Age of females at first conception

We were able to estimate the age of first conception for 10 females, which were banded as subadults (see Methods for details). They all gave birth to a juvenile the year following their own birth, which resulted in a mean age at first conception of 10 ± 2 months (range 8–14 months). Thus, the median minimum tenure of adult males (1.65 years) exceeded the age of females at first conception.

Parentage of juveniles

Genetic parentage analysis was performed for 66 *R. naso* pups of which 36 were males and 30 were females. Overall, we were able to assign both parents to 68% of juveniles ($n = 45$, Fig. 1). We determined only the mother ($n = 11$) or the father ($n = 5$) of 24% of juveniles. We were not able to determine any parents for 8% of juveniles ($n = 5$). Our ability to determine at least one parent (i.e. both parents or the mother/father) did not differ between males (97%, $n = 35$ juvenile males with at least one parent) and females (87%, $n = 26$ juvenile females; Fisher's exact test: $\chi^2 = 2.60$, d.f. = 1,

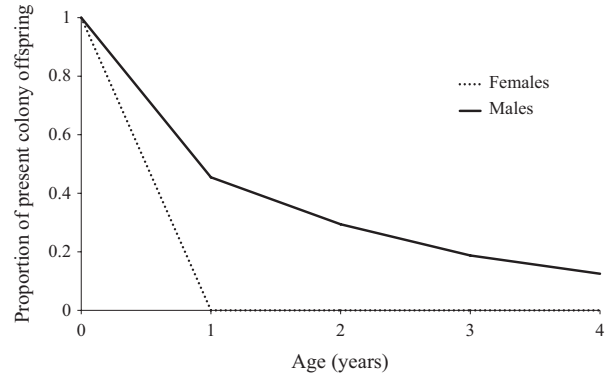


Fig. 2 Post-natal residence of male (solid line) and female (dashed line) offspring in their natal colonies. $n = 21$ females and $n = 22$ males at 1 year of age; $n = 13$ females and $n = 17$ males at 2 years of age and $n = 13$ females and $n = 16$ males at three and 4 years of age. Please note that the difference in sample sizes for males and females drops from age 1 to age 4, because some bats were observed for <4 years (i.e. when they were born 1, 2 or 3 years before the end of the study).

$P = 0.17$). Four of 10 observed philopatric males (see next paragraph) were found to have fathered 1–4 offspring in their respective colonies of birth before the end of this study. Two males were determined to be immigrants, and one of these males (a resident of two colonies) fathered two pups in its colony of immigration. One other male fathered a pup in the colony it occasionally visited. Because the bats in our study colonies were not completely banded and genetically sampled (Table S1), we were not able to determine the dispersal status of all other males that fathered offspring.

Natal philopatry and dispersal

Observations of banded juveniles. Between 2006 and 2012, we captured and banded 43 juveniles (22 males and 21 females) in the three main study colonies. Subsequent census observations revealed that all female offspring disappeared from their natal colonies within their first year of life (Fig. 2). In contrast, 10 of 22 male offspring (46%) were present in their birth colony at an age of 1 year. Subsequently, the proportion of philopatric males dropped to 2 of 16 (13%) until the age of four (Fig. 2). Thus, within the first year of life, dispersal rates of females were much higher than in males and natal dispersal was significantly female biased (Fisher's exact test: $\chi^2 = 12.44$, d.f. = 1, $P < 0.001$).

Parentage of subadults. In addition, we also used paternity analysis attempting to determine the dispersal status (philopatric or immigrant) of subadult females ($n = 39$) and males ($n = 35$; 12 males were caught as

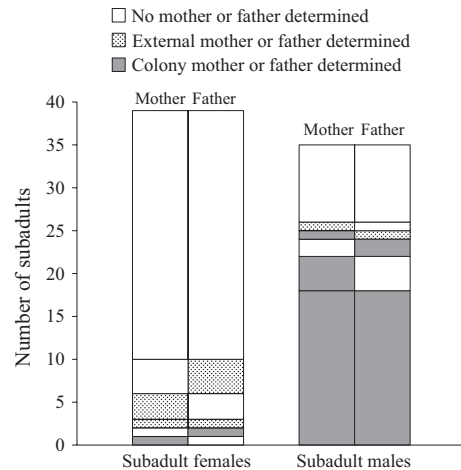


Fig. 3 Results of paternity analysis for bats that were present as subadults in our study colonies ($n = 39$ females and $n = 35$ males). Please note that results for males include 12 males that were captured as juveniles and were later present as subadults in our study colonies and 23 males that were captured as subadults. Bars for subadult females and males are split to show whether a mother and/or father has been assigned, and if so, whether the mother and/or father was a resident of the same or another colony compared to the subadult bat. [Correction after online publication 18 February 2013: the figure was replaced to correctly show where no mother or father has been assigned.]

juveniles and were still present as subadults, and 23 males were caught as subadults) of our study colonies. Only 2 of 39 subadult females (5%, Fig. 3) descended from adult members of their colony of residence. In contrast, we found that 25 of 35 subadult males (71%) roosted in the same colony with either both parents or at least one parent. Thus, the number of parents (mother, father or both parents) that roosted together with their subadult son in the same colony was significantly higher than the number of parents that roosted together with their subadult daughter in the same colony (χ^2 -test: $\chi^2 = 37.51$, d.f. = 1, $P < 0.001$). Furthermore, this analysis revealed eight subadult females and only two subadult males that descended from male and female residents of other colonies (Fig. 3).

Parent-offspring relationships among adults. Finally, a genetic kinship analysis was performed among adult bats from all 15 colonies (135 females and 117 males) to identify possible parent-offspring relationships among them. In total, 48 significant parent-offspring relationships were determined with the software KINGROUP v2 ($n = 10$, $P < 0.001$; $n = 24$, $P < 0.01$ and $n = 14$, $P < 0.05$). Because the majority of bats were already adults at first capture ($n = 227$), we lacked information on their birth date. In these cases, we were not able to determine the direction

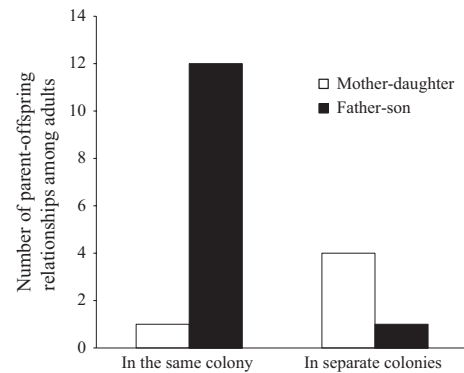


Fig. 4 Number of mother-daughter and father-son relationships found among adults in the same colony ($n = 13$) or in two different colonies ($n = 5$).

of the parent-offspring relationship (who is parent and who is offspring). Therefore, we restricted our analysis to pairs of the same sex (mother-daughter and father-son pairs). Within a colony, 92% of the determined same-sex parent-offspring relationships (12 of 13, Fig. 4) were father-son relationships and only 8% mother-daughter relationships (1 of 13, Fig. 4). In addition, we found a reversed ratio in the number of parent-offspring relationships among adult individuals that roosted in separate colonies (20% father-son and 80% mother-daughter relationships, Fig. 4). These reversed and significantly different patterns of mother-daughter and father-son relationships within and between colonies (Fisher's exact test: $\chi^2 = 9.41$, d.f. = 1, $P < 0.01$) indicate that females disperse at a higher rate from their natal colony than males and that some males remain in their natal colonies.

Copulations and defence of oestrous females

Nine of the 11 colony males were observed to participate in behavioural interactions with oestrous females (Fig. 5). Interactions of males with females took place for 3–5 days after parturition, suggesting a short female oestrus. Three males were observed to copulate with females; however, copulations were dominated by one male (M1: 92% of copulations, Fig. 5). The same male was also observed to perform the majority of copulation attempts that were interrupted by females (65%), approaches to oestrous females (76%) and defences of females (94%). Likewise, the apparently most dominant male was never interrupted by other males when approaching oestrous females or when attempting to mate with them. Furthermore, our behavioural observations fit well with paternity of pups caught in one main colony (C5) in 2011, although these pups were fathered in the mating season preceding our observations. Seven of 12 pups (58%) were fathered by the two males that were most frequently involved in interactions with oestrous females (M1: 4 pups, M2: 3

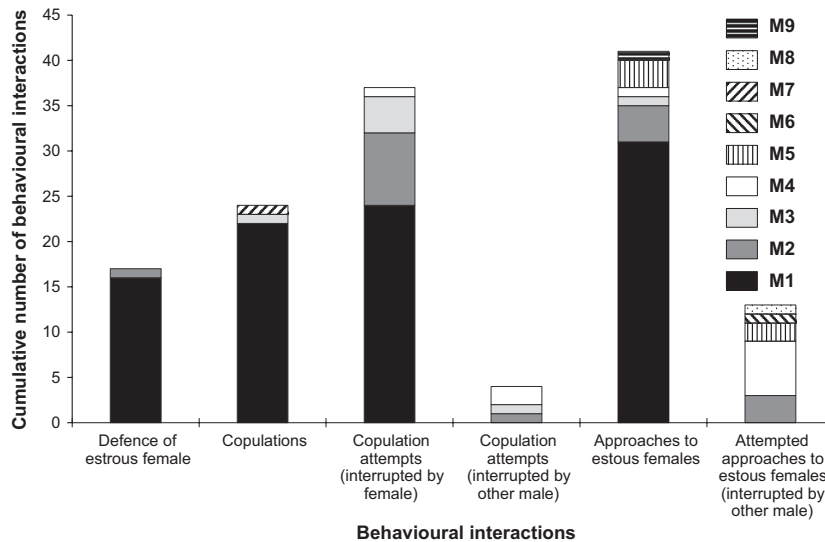


Fig. 5 Cumulative number of behavioural interactions of males with oestrous females or competing males. Individual males (M1–M9) are represented by different colours or patterns. Details on the definition of behavioural interactions can be found in the methods section.

pups). Another two pups were fathered by the two males that were not involved in interactions with females. One pup was fathered by a male that was absent in 2011, but present in 2010, and finally one pup descended from an external father.

Discussion

Both our long-term observations of individually banded bats and genetic paternity and kinship analyses clearly show that dispersal is female biased in the Proboscis bat. Different lines of evidence testify to habitual female dispersal (*sensu* Clutton-Brock & Lukas 2011). All female offspring emigrated from their natal colonies or disappeared within their first year of life before reaching sexual maturity and none reproduced in its colony of birth. Also, only 5% of subadult females in our colonies were found to descend from an adult member of the respective colony. The two subadult females for which we determined a colony parent were not present in their colonies of capture the following field season when they were adult, indicating that they had dispersed at a later stage. Finally, we found only one mother–daughter pair within a colony. These results suggest that the vast majority if not all reproducing females in a colony are immigrants.

In contrast to the majority of mammals where dispersal is male biased (e.g. Dobson 1982; Lawson Handley & Perrin 2007), the Proboscis bat is among the still few exceptions where virtually all females disperse to a new social group before reproducing. Usually, philopatry is assumed to be the optimal strategy for female mammals (reviewed in Clutton-Brock & Lukas 2011). For example, philopatric female mammals have been reported to benefit from higher feeding efficiency

(Young & Monfort 2009), earlier breeding and higher reproductive potential (Ronce 2007; Fisher *et al.* 2009) as well as from improved fecundity or breeding success when associating with kin (e.g. Kawata 1990; König 1994). One hypothesis to explain the evolution of habitual female dispersal in plural-breeding mammals states that females habitually disperse to avoid father–daughter inbreeding if the tenure durations of individual males or of male kin groups exceed the age at which females commonly start to reproduce (Clutton-Brock 1989; Clutton-Brock & Lukas 2011; Lukas & Clutton-Brock 2011). Our results suggest that father–daughter inbreeding avoidance might be the cause for female dispersal in *Rhynchonycteris naso* because the mean age of females at first conception (10 months) fell below the median minimum tenure duration of individual males (20 months). Bradbury & Vehrencamp (1976) suggested that the age at females' first reproduction might be up to 18 months. However, the earlier study was conducted for only 10 months and the estimation of females' age at first conception was extrapolated from only two nulliparous females that failed to reproduce during the study (Bradbury & Vehrencamp 1976). Until now, female dispersal as a means to avoid father–daughter inbreeding has been shown to prevail in the three great apes, a number of other primates, all social equids and in two other Neotropical bats, namely the closely related emballonurid *Saccopteryx bilineata* (FBD; Nagy *et al.* 2007) and *Lophostoma silvicolum* (all-offspring dispersal; Dechmann *et al.* 2007; Lukas & Clutton-Brock 2011). Although there is evidence for female dispersal in other tropical bats (e.g. *Phyllostomus hastatus* McCracken & Bradbury 1981; *Cynopterus sphinx* Storz *et al.* 2000), long-term studies on marked individuals in combination with paternity and kinship analysis that

are necessary for reliably estimating dispersal patterns and tenure duration of males are still scarce and thus do often not allow to estimate whether female dispersal is associated with a father–daughter inbreeding risk. In this context, longitudinal studies incorporating genetic methods would surely be worthwhile, especially because bats are long-lived, highly social mammals and females in most studied tropical bats start breeding in their first year of life, in some phyllostomid bats even at an age as early as 3 months (Barclay & Harder 2003; Chaverri & Kunz 2006). These life history traits of tropical bats could well indicate that a large number of tropical bats may have dispersal patterns that differ from the majority of mammals.

Male philopatry is an even rarer life history trait in mammals than female dispersal (Clutton-Brock 1989). In the Proboscis bat, three lines of evidence suggest that many young males remain in their natal colonies until adulthood and that they also become reproducing residents therein. First, almost half of the male colony offspring were observed as adult residents in our main study colonies and four of these 10 philopatric males reproduced in their natal colony before the end of this study. Second, a minimum of 71% of subadult males had at least one colony parent. Finally, several father–son dyads were found among the adult residents of study colonies. This is in contrast to an earlier study reporting that all male offspring disperse at 2–4 month of age (Bradbury & Vehrencamp 1976). However, the latter study was based on only 10 months of observation and it is not clear how many, if any juvenile males were banded in the former study (Bradbury & Vehrencamp 1976). A similar proportion of natal males faithful to their natal colonies as in Proboscis bats (46%) were found in Greater sac-winged bats, *S. bilineata* (45%, Nagy *et al.* 2007). However, our results suggest male immigration might be more common or easier to accomplish in *R. naso* when compared to *S. bilineata*, where up to 93% of resident males are natal males (Nagy *et al.* 2007). In the Proboscis bat, evidence that male immigration might be common despite a proportion of 46% of males that are philopatric comes from the observation that several males transferred back and forth and were residents of two social groups or even permanently transferred to another social group, which was never observed in *S. bilineata* (Nagy *et al.* 2012). Also, our ability to find parents for subadult males was significantly lower than for juvenile males, suggesting that some subadult males are immigrants. At present, we are not able to estimate the frequency of male immigration into *R. naso* colonies because the incomplete banding of our study colonies (Table S1) prevented us from systematically recognizing immigrants.

Male philopatry in mammals has been attributed to the unusual mammalian mating strategy of resource defence, where philopatric males gain considerable benefits from familiarity with the local resources and the benefits of kin cooperation (Greenwood 1980; Perrin & Mazalov 2000; Lawson Handley & Perrin 2007). None of these correlates of mammalian male philopatry seem to apply to the Proboscis bat. In contrast to Greater sac-winged bats where males exhibit resource-defence polygyny, *R. naso* males have never been observed to defend territories in the day roost for mate attraction. The mating system of the Proboscis bat has been classified as one of direct female defence (Bradbury & Vehrencamp 1977b). Our observations that males defend oestrous females (Fig. 5) corroborate Bradbury & Vehrencamp's (1977b) classification of a male mating strategy based on direct female defence. Given that male immigration of males appears common in *R. naso*, it is unlikely that male kin cooperate in attracting and retaining females in the colony and thus that kin cooperation has played a role in the evolution of male philopatry in Proboscis bats. Another explanation for male philopatry in mammals lately been proposed by Clutton-Brock & Lukas (2011) is that once female dispersal has evolved due to relatively long tenures of resident males and the risk of father–daughter inbreeding, philopatry might be the optimal strategy for males if they are tolerated by resident males. As all young female *R. naso* disperse, the risk of inbreeding is averted. Thus, philopatry might be an optimal strategy for male Proboscis bats because, for example, in contrast to dispersing male *R. naso*, philopatric males might profit from acquaintance with and access to the natal group's foraging grounds (Bradbury & Vehrencamp 1976; see also e.g. Greenwood 1980; Watson *et al.* 1994). In addition, philopatric *R. naso* males might be able to attain dominance easier or earlier in life and thus gain higher reproductive success than immigrant males (e.g. Bensch *et al.* 1998). Bradbury & Vehrencamp (1976) suggested that male Proboscis bats have a dominance hierarchy. This suggestion fits well with our own observations that copulations and defence of females were dominated by one of 11 colony males. Further studies will have to determine the correlates of male reproductive success and whether there are fitness differences between natal and immigrant *R. naso* males. Nonetheless, the existence of male philopatry in Proboscis bats contrasts with the hypothesis that local mate competition should be severe in female-defence systems, thereby leading to male-biased dispersal (Dobson 1982; Perrin & Goudet 2001). The question is thus how severely *R. naso* males may suffer from local mate competition. At present, we can only speculate but due to the presence of several adult males per colony and the

fact that females and thus mothers of philopatric males are unrelated, a philopatric male will most probably compete with much more unrelated or distantly related males than with close kin (Lukas *et al.* 2005). If local mate competition does not have high costs for philopatric *R. naso* males, remaining in the natal colony might indeed be the better strategy.

Our study adds to the growing evidence that inbreeding avoidance has played a significant role in the evolution of female dispersal and thus in the evolution of SBD patterns in mammals (e.g. Pusey 1987; Lukas & Clutton-Brock 2011). Interestingly, male philopatry evolved in *R. naso* although there is no evidence for the usual correlates (i.e. resource-defence polygyny or kin cooperation) of male philopatry shared by other mammals (Greenwood 1980; Lawson Handley & Perrin 2007). Along with similar evidence from other mammalian species (e.g. Spider monkeys *Ateles paniscus* McFarland Symington 1987), this raises the question of whether male philopatry in mammals indeed evolves as a result of resource defence and cooperation between male kin. While a resource-defence mating strategy is also generally assumed to drive FBD in birds (Greenwood 1980), an alternative hypothesis proposed by two recent articles is that the evolution of FBD in group-living birds stems from father–daughter inbreeding avoidance, as many female group-living birds start reproducing in their second year of life and tenure of males is often longer than 2 years (Clutton-Brock & Lukas 2011; Lukas & Clutton-Brock 2011). As yet, we can only speculate that male tenure may be longer in mammalian species with a resource-defence mating system than in mammals with a female-defence mating strategy. Because one important factor affecting the risk of father–daughter inbreeding is the length of male tenure, we propose that the chance that female dispersal evolves as a means to avoid father–daughter inbreeding may be higher in polygynous mammalian species with a resource-defence mating strategy. Once female dispersal has evolved, male philopatry may be the optimal strategy for males (Clutton-Brock & Lukas 2011). Thus, one alternative to the hypothesis that the frequent correlation between FBD and male resource defence in mammals is caused by the benefits of familiarity for philopatric males (Greenwood 1980) may be that longer tenures of male mammals in resource-defence systems compared to female-defence systems increase the chance that female dispersal evolves to avoid father–daughter inbreeding.

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F.M., M.N. and M.K. conceived and designed the study. M.N., M.K. and L.G. performed the field work. L.G. performed the lab work. L.G. and M.N. analyzed the data. M.N. and L.G. wrote an initial draft of the manuscript and all authors finalized it.

Data accessibility

Colony group structure: Supporting Information Table S1.

Microsatellite data and details of typed individuals (ID, capture date, capture locality, sex, age at capture): Dryad doi:10.5061/dryad.nv5r5.

Supporting information

Additional supporting information may be found in the online version of this article.

Table S1 Details on yearly mean \pm SD colony sizes, numbers and means \pm SD of banded and unbanded bats as well as yearly genetic sample rate.

Table S2 Results from allele frequency calculations with CERVUS v. 3.0 (Kalinowski *et al.* 2007).

Appendix S1 Field methods.