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**Behavioral Ecology and Sociobiology**

ISSN 0340-5443

Behav Ecol Sociobiol

DOI 10.1007/s00265-014-1702-2



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# Dispersal and social organization in the Neotropical Grey sac-winged bat *Balantiopteryx plicata*

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Received: 3 November 2013 / Revised: 22 February 2014 / Accepted: 24 February 2014  
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**Abstract** Recent evidence suggests that tropical bats may frequently depart from the predominant mammalian male-biased dispersal pattern. So far, two emballonurid bat species that are closely related to our study species (Grey sac-winged bat, *Balantiopteryx plicata*) have been found to exhibit exceptional female-biased dispersal that is in accordance with father–daughter inbreeding avoidance. In contrast, using a combination of long-term behavioral observations of banded bats and DNA sequencing of the mitochondrial d-loop, our results suggest that *B. plicata* is the first Neotropical emballonurid with female philopatry and frequent male dispersal. However, just like in the other emballonurids, the age of females at first conception fell below the tenure of males. Thus, philopatric *B. plicata* females might face a father–daughter inbreeding risk if mating with males from their roosts. Such risk could be circumvented if mating occurs outside the nursing roost, e.g., in male mating aggregations. In contrast to other Neotropical emballonurid bats, the Grey sac-winged bat forms colonies with a greatly male-biased sex ratio (only 5 and 21 % females). Males of such colonies showed high roost fidelity and the sex ratio did not change throughout the year and for up

to many years, suggesting an important role in mating. We conclude that studying the diverse mating and dispersal patterns of Neotropical emballonurids shows great potential to enlarge our understanding on how the proposed ultimate causes (i.e., avoidance of inbreeding and local competition between kin) affect the evolution of sex-biased dispersal.

**Keywords** d-Loop · Emballonuridae · Inbreeding avoidance · Male-biased dispersal · Mating system · Sex ratio

## Introduction

Dispersal is a key life history trait that has profound effects on the genetic structure and demography of populations (Clobert et al. 2001). In general, dispersal is sex-biased in birds and mammals such that female-biased natal dispersal prevails in birds and male-biased natal dispersal is the rule in mammals (Greenwood 1980; Dobson 1982; Clarke et al. 1997). The evolution of sex-biased dispersal has received much attention, both in terms of empirical and theoretical endeavors (e.g., Greenwood 1980; Dobson 1982; Perrin and Mazalov 2000; Perrin and Goudet 2001). However, there is still much disagreement regarding the relative importance of proposed evolutionary mechanisms (e.g., reviewed in Lawson Handley and Perrin 2007). The main selective pressures suggested to explain the evolution of sex-biased dispersal patterns include inbreeding avoidance (e.g., Waser et al. 1986; Pusey 1987; Clutton-Brock 1989; Perrin and Mazalov 2000), the avoidance of local mate competition (e.g., Hamilton 1967; Dobson 1982; Perrin and Goudet 2001), the avoidance of local resource competition (e.g., Clarke 1978; Greenwood 1980; Sterck et al. 1997), and the benefits of cooperation between kin (Perrin and Goudet 2001; Le Galliard et al. 2006).

Mating systems are believed to exert decisive influence on the direction and extent of sex-biased dispersal. A species' mating system may determine the identity of the dispersing

Communicated by G. S. Wilkinson

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and faithful sex by means of the male mating strategy (female defense vs. resource defense; Greenwood 1980), the differences concerning the intensity of local mate competition relative to local resource competition (Dobson 1982; Perrin and Mazalov 2000; Perrin and Goudet 2001) and the length of male breeding tenures and longevity, which determines whether females face a risk of father daughter inbreeding (Clutton-Brock and Isvaran 2007; Clutton-Brock 2009; Clutton-Brock and Lukas 2011). These three hypotheses predict that dispersal should be mediated by males in the predominantly polygynous and promiscuous social systems of mammalian species, and this is in agreement with general mammalian dispersal patterns (Greenwood 1980; Dobson 1982; Lawson Handley and Perrin 2007). The resource-defense hypothesis by Greenwood (1980) is able to explain some cases where polygynous mammals have female biased dispersal (resource defense for example by males in Kinkajous *Potos flavus* Kays et al. 2000), but does not account for mammalian species where males defend females directly but dispersal is females biased like in the Proboscis bat (*Rhynchonycteris naso*, Nagy et al. 2013). In contrast, habitual female dispersal in plural-breeding mammals (i.e., species living in stable social groups that include several breeding females) has been found to be consistently associated with male breeding tenures that exceed the age of females' first conception, suggesting that females disperse to avoid the risk of father–daughter inbreeding (Lukas and Clutton-Brock 2011).

There is increasing evidence that many tropical bats depart from the predominant mammalian dispersal pattern of male-biased dispersal. A surprising variety of differing dispersal patterns has been detected in tropical bats. These patterns range from unbiased dispersal such as all-offspring dispersal in for example the White-throated round-eared bat (*Lophostoma silviculum*, Dechmann et al. 2007) or all-offspring philopatry in Spix's disc-winged bats (*Thyroptera tricolor*, Chaverri and Kunz 2011) to female-biased dispersal in Greater sac-winged bats (*Saccopteryx bilineata*, Nagy et al. 2007) and Proboscis bats (*R. naso*, Nagy et al. 2013) and finally to male-biased dispersal in for example Common vampire bats (*Desmodus rotundus*, Wilkinson 1985). In contrast, most temperate bats have been found to possess the prevailing mammalian pattern of male-biased dispersal (e.g., Noctule bat *Nyctalus noctula*, Petit et al. 2001; Bechstein's bat *Myotis bechsteinii*, Kerth et al. 2002). There is evidence that dispersal patterns and mating systems are at least in part the result of a phylogenetic signal (Perrin and Mazalov 1999; Blomberg et al. 2003; Lukas and Clutton-Brock 2011). Thus, in contrast to most temperate bats studied that come predominantly from one family (Vespertilionidae) and have rather similar mating systems and dispersal patterns (McCracken and Wilkinson 2000; Moussy et al. 2012), the highly diverse mating and social systems and dispersal patterns of tropical bats provide an important opportunity to investigate whether

and how different mating systems may ultimately affect dispersal patterns or whether phylogenetic relatedness plays an important role. Neotropical emballonurids are particularly well suited for this undertaking. Mating systems range from possibly monogamous species to polygynous species with resource defense and female defense by males and supposedly to mating swarms or leks (Bradbury and Vehrencamp 1977a; Voigt et al. 2008; Nagy et al. 2013). Moreover, the two emballonurid species *S. bilineata* and *R. naso* have exceptional female-biased dispersal in accordance with a father–daughter inbreeding avoidance strategy because female age at first conception falls below the tenure of males and females mate almost exclusively with resident males (Nagy et al. 2007, 2013). To elucidate whether female dispersal is shaped by phylogeny or species-specific traits of the mating and social system, we chose a Neotropical emballonurid (Grey sac-winged bat *Balantiopteryx plicata*) for which current information suggests that it may have a social system that differs from other emballonurids; many of the social groups investigated so far possessed a large excess of males. It had been hypothesized that this species mates at male mating aggregations (López-Forment 1979; Bradbury and Vehrencamp 1976, 1977a).

*Balantiopteryx plicata* belongs to a sister lineage of *S. bilineata* and *R. naso* and occurs in sympatry with them (Lim et al. 2008). Grey sac-winged bats live in rather arid areas from western Mexico southward through most of central and southern Mexico along the Pacific to Costa Rica (Arroyo-Cabrales and Jones 1988). The social system of *B. plicata* is poorly studied. These bats form the largest colonies known among Neotropical emballonurids of up to 2,000 individuals (25 bats on average, López-Forment 1979; Bradbury and Vehrencamp 1976). They roost in the well-lit parts of caves, under boulders but also in buildings. The sexes roost intermixed and individuals do not have body contact but are spaced out at about 20-cm distance. The mating season is in January and February (López-Forment 1979), and females give birth to one pup per year in late June and early July (Bradbury and Vehrencamp 1976; López-Forment 1979). For *B. plicata*, it has been suggested that mating occurs at male mating aggregations, which are traditional or species specific sites that are visited by females only for mating (Bradbury and Vehrencamp 1977a). Males have been found to outnumber females in many colonies, such that the percentage of males caught from a roost ranged from about 30 to 100 % (López-Forment 1979). However, it is not yet clear whether such male mating aggregations form temporarily in the mating season in areas where many females roost or exist year round (corresponding to the large colonies with low percentages of females) and are visited by females during the mating season (Bradbury and Vehrencamp 1977a; López-Forment 1979).

Here, we used long-term behavioral observations in combination with genetic analysis to elucidate whether dispersal is unbiased or sex-biased in Grey sac-winged bats.

We hypothesized that dispersal should be female-biased if female age at first conception falls below male tenure durations. In this case, females should be the dispersing sex to avoid the inbreeding risk with their fathers. Otherwise, if female sexual maturity exceeds the tenure durations of males, females would not risk mating with their fathers. At the same time, females could benefit from associations with kin and familiarity with natal foraging areas by remaining philopatric. Thus, we predicted that females should then represent the philopatric sex. We further investigated the social structure of this species, attempting to get a better understanding of the reportedly rather unusual social organization of colonies (i.e., highly male biased sex ratios and potentially year round sexual segregation). Information on the social system of this species is essential in understanding the dispersal pattern.

## Methods

### Study sites and field methods

*Balantiopteryx plicata* was studied from 2006 to 2010 in three colonies in Guanacaste, Costa Rica. Our main study colony was located in the La Casona Museum in Santa Rosa National Park (Province Guanacaste, 10°50'2" N, 85°36'45" W). The main day roost of *B. plicata* in the La Casona colony was an approximately 16 m<sup>2</sup> large room on the second floor of the museum, where visitors were not permitted to enter. A small number of bats also used the exhibition rooms on the first floor as day roosts; however, the majority of bats (about 100–150) roosted upstairs. Bats used the La Casona Museum also as a night roost. We identified four night roosts in La Casona. Three night roost were situated on the first floor of the museum where Grey sac-winged bats clung to the wooden ceiling beams and the underside of a wooden staircase of the roofed gallery surrounding the exhibition rooms. The fourth night roost was located in the room on the second floor where bats roosted also during the day.

Our second day roost was located at Playa Naranjo, which is also situated in Santa Rosa National Park (10°47'60" N, 85°40'55" W). Here, about 60 Grey sac-winged bats roosted against the inner sides of the two halves of a large rock that was cracked in the middle. Finally, we studied *B. plicata* at Finca Cañas Castillas (Province Guanacaste, 11°7'16" N, 85°35'37" W) where bats used a shed as their day roost.

Bats were mist netted (Ecotone® monofilament, Gdynia, Poland) when emerging at dusk from their day roosts or when returning to their day roost at dawn. We took a small tissue sample from the plagiopatagium (Stiefel® biopsy punch, 4 mm Ø) of each bat for genetic analysis and stored it in 80 % ethanol. The resulting small hole in the wing membrane healed completely within 2–4 weeks. We applied colored plastic bands (AC Hughes® Ltd., UK, size XCL) to the

forearms of each bat caught in La Casona and at Finca Cañas Castillas to make bats individually distinguishable from a distance. The banding procedure had been established in two closely related emballonurid species (since 1996 in *S. bilineata*, Heckel et al. 1999; since 2005 in *R. naso*, Nagy et al. 2013) and, to the best of our knowledge, has no negative effects on the bats' behavior or health. We weighed, sexed, determined the age (juvenile or adult) and reproductive state of captured bats, and finally measured their right forearm and third and fifth finger. Table 1 provides details on numbers of captured and banded bats and sizes of day roost colonies.

Group structure (total number of bats, number and identity of banded males and females, and number of unbanded bats) was determined on a daily to weekly basis with binoculars and digital pictures during the following periods in the La Casona day roost: August 2006 (10 census days), July to August 2007 (16 census days), July to August 2008 (12 census days), January to February 2009 (14 census days), and March 2010 (1 census day). The number of census days per season represents the number of census days, which were used for calculating tenure and fidelity (see below) of *B. plicata* males and females; however, at the beginning of each field season, bats were habituated to our presence in the day roost for 2–5 days, and these days were not used in calculations of fidelity. To determine the group structure of the left night roost in the La Casona colony, we took digital pictures on 11 nights in January to February 2009. Census pictures in the night roost were taken on average for 1.9 times per night (range one to three times per night), to increase our chances to detect members of the night roost that may be absent for foraging. Census pictures had also been taken in the other three night roosts; however, it was mostly not possible to approach the bats close enough, so that most pictures were blurry and did not allow the identification of bats.

At the Playa Naranjo day roost, bats were caught once with mist nets in August 2008. No census was conducted since the bats of this day roost had not been banded. At the Finca Cañas Castillas day roost, we captured and banded bats in March 2010 and in July 2010. The Finca Cañas Castillas day roost was censused on two occasions in March 2010 and on three occasions in July 2010.

### Census analyses

A total of 53 census days on group size and composition was collected from the La Casona day roost. Minimum tenure of adult females ( $N_f=7$ ) and adult males ( $N_m=97$ ) was calculated as the time interval between the day of banding and the last day a bat was detected in the day roost. Almost all bats were already adult at capture ( $N_f=6$ ,  $N_m=93$ ) so that the actual start of the bats' tenures remained unknown. In addition, a substantial number of banded bats was still present in our last field season in 2010 ( $N_f=4$ ,  $N_m=36$ ) so that the end of tenure of

**Table 1** Number of captured and banded bats, mean number of bats in the roosts studied (DR=day roost, NR=night roost) and sex ratio denoted as the percentage of banded females among all observed banded individuals of a roost

Roost and observation period	Number of captured (and banded) adult males	Number of captured (and banded) adult females	Number of observed (banded) adult females present <sup>a</sup>	Number of captured (and banded) juvenile males	Number of captured (and banded) juvenile females	Mean number of adult bats in roost	Sex ratio (% females)
La Casona DR August 2006	36 (35)	3 (3)	4 (3) <sup>a</sup>	0 (0)	1 (1)	55±4 (≈80–100) <sup>b</sup>	7.9
La Casona DR July–August 2007	46 (45)	2 (2)	7 (4) <sup>a</sup>	3 (3)	2 (2)	165±14	7.3
La Casona DR July–August 2008	88 (88)	3 (3)	8 (6) <sup>a</sup>	4 (1)	2 (1)	158±5	5.2
La Casona DR January–February 2009	0 (0)	0 (0)	6 (6)	0 (0)	0 (0)	116±10	7.0
La Casona DR 2006–2009	170 (168)	8 (8)	–	7 (4)	5 (4)	139±28	–
La Casona NR January–February 2009	–	–	2 (2)	–	–	≈53–83	6.7
Playa Naranjo DR August 2008	16 (0)	16 (0)	≥19 (0) <sup>c</sup>	11 (0)	5 (0)	≈58–63	50.0 <sup>d</sup>
Finca Cañas Castillas DR March 2010	17 (17)	6 (6)	6 (6)	0 (0)	0 (0)	≈25–30	26.1
Finca Cañas Castillas DR July 2010	5(5)	0 (0)	3 (3)	0 (0)	0 (0)	≈25–30	14.3

<sup>a</sup> Here, the number of observed females is composed of the number of banded females plus the number of unbanded females, whose sex was identified by the observation of pup nursing

<sup>b</sup> Many bats were not visible during census observations in 2006 because they roosted behind two open doors. Total number of bats was determined on three occasions and was between 80 and 100 individuals

<sup>c</sup> Here, the number of females was assessed based on three days of census pictures by counting the number of pups in the colony. Because pups were already quite large, some may have escaped correct identification as pups, and it is probable that the number of females was larger

<sup>d</sup> Bats were not banded in the Playa Naranjo day roost. Thus, sex ratio was assessed based on the number of bats of each sex that had been captured with mist nets at the day roost

several bats remained undetermined. Due to the lack of information concerning the beginning and the ending of the tenure of a large number of bats, the actual tenures of adult Grey sac-winged bats surely exceed our minimal tenure estimates. A total of 26 males that had been caught in the vicinity of the La Casona day roost had never been observed in the day roost and were not included in the calculation of minimal tenure. Furthermore, we excluded bats from the calculation of minimal tenure if they were observed only in the field season they had been banded in. Our longest field season lasted for 25 consecutive days. Given that almost all individuals were already adult at capture and that the following field season mostly started 1 year later, the observation of an individual for only one field season would have underestimated even the minimal tenure of individual *B. plicata*.

We calculated two fidelity indices  $F$ , to examine the compositional stability of *B. plicata* groups in the day roost. One fidelity index represents the fidelity of an adult bat to its day roost ( $F_{DR}$ ) and the second fidelity index represents the fidelity of an adult bat to a social group within the day roost ( $F_{SG}$ ). Fidelity of bats to their day roost ( $F_{DR}$ ) was calculated as the proportion of days a bat was observed in the La Casona day roost between its first and last day of observation in the day roost and was based on the total number of census days in the day roost. Only for the days a bat was observed in the day roost,  $F_{SG}$  was calculated as the proportion of days a bat was observed in the social group where it roosted the majority of days during one field season. Fidelity indices were only calculated for individuals for whom we had at least 5 days on which a bat was observed in the day roost ( $F_{SG}$ ) and/or at least five census days after the banding of a bat ( $F_{DR}$ ).

#### Genetic analyses

DNA was isolated with the salt-chloroform procedure by Miller *et al.* (1988) and modified by Heckel *et al.* (1999). We used primers E: 5'-CCTGAAGTAGGAACCAGATG-3' (Wilkinson and Chapman 1991) and P\*: 5'-CCCCACCATC AACACCCAAAGCTGA-3' (Wilkinson *et al.* 1997) to amplify the mitochondrial d-loop region with polymerase chain reaction (PCR) following a protocol by Wilkinson *et al.* (1997). PCR started with denaturation phase of 4 min at 94 °C followed by 25 cycles of 30 s at 94 °C, 45 s at the annealing temperature of 55 °C, and 1 min at 72 °C and followed by a final elongation phase of 20 min at 72 °C. PCR products were sequenced with Primer P\* and BigDye Terminator Cycle Sequencing Kit version 1.1 on an ABI Prism Genetic Analyzer 3130 XL (following the manufacturer's protocol). Sequences were checked and aligned with CodonCode Aligner 4.0.4 (CodonCode Corporation, Dedham, MA, USA). The number of different haplotypes ( $K$ ) was counted with DAMBE 5.3.0 (Xia and Xie 2001), and

minimum spanning trees were generated with HapStar 0.5 (Teacher and Griffiths 2011). The sequences of six unique haplotypes were deposited in GenBank (accession numbers: KJ438792-KJ438797). We used Arlequin 3.5 (Excoffier *et al.* 2005) to calculate genetic diversity indices for both sexes from all three colonies and to calculate genetic differentiation among males and among females from different colonies using pairwise fixation indices ( $F_{ST}$ ).  $F_{ST}$  values can range from zero to one, with an  $F_{ST}$ -value of zero indicating no genetic differentiation and an  $F_{ST}$  value of one indicating that the two compared samples do not share any genetic diversity. If gene flow into colonies is higher in males than in females, we anticipated that mitochondrial genetic diversity within a colony should be higher in males than in females and that genetic differentiation among colonies should be higher for females than for males. As a measure of genetic diversity, we established (1) gene diversity  $\hat{H}$ , the probability that two randomly chosen haplotypes in a sample are different, (2) nucleotide diversity  $\pi$ , equivalent to gene diversity but at the nucleotide level and corresponding to the probability that two randomly chosen homologous nucleotide sites are different in a sample, and (3) theta ( $k$ )  $\theta_k$ , a diversity estimator based on the number of different haplotypes. Arlequin 3.5 (Excoffier *et al.* 2005) was also used to test for differentiation between the two sexes within each day roost based on haplotype frequencies by calculating an exact test following Raymond and Rousset (1995).

#### Statistical analyses

All Fisher's exact tests were calculated with Preacher and Briggs' (2001) online interactive calculation tool. Post hoc power analyses were conducted with G\*Power 3 (Faul *et al.* 2007). Bonferroni corrections were applied following Holm (1979). All statistical tests were two-tailed and means are shown  $\pm$ one standard deviation (SD).

## Results

#### Study colonies

Our main study colony, the La Casona day roost, contained on average  $139 \pm 28$  bats between 2006 and 2009. Sex ratio in the La Casona day roost was highly male-biased as only 8 of 176 banded bats were females (5 %, Table 1). The Finca Cañas Castillas day roost contained about 25–30 adult bats, and sex ratio was also highly male-biased (21 % females, Table 1). In the third study day roost (Playa Naranjo), the bat population comprised 58–63 adult individuals and 50 % of the captured adult bats were females. Sex ratio within a day roost did not change between different months of the year (Fisher's exact test: La Casona day roost July–August vs. January–February,

$df=1$ ,  $p=0.999$ ; Finca Cañas Castillas day roost March vs. July,  $df=1$ ,  $p=0.46$ ; Table 1). However, we found different day roosts to have dissimilar sex ratios during the same season of the year (Fisher's exact test: La Casona day roost vs. Playa Naranjo day roost in July–August,  $df=1$ ,  $p<0.001$ ,  $\alpha=0.071$ ; Finca Cañas Castillas day roost vs. Playa Naranjo day roost in July–August,  $df=1$ ,  $p=0.0078$ ,  $\alpha=0.0083$ ).

*Balantiopteryx plicata* were also observed in four night roosts in La Casona. Here, we observed on average  $34.2 \pm 13.3$  bats (range, 17–52;  $N=11$  observation nights, left night roost),  $2.5 \pm 1.9$  bats (range, 0–4;  $N=8$  observation nights, middle night roost),  $18.7 \pm 5.6$  bats (range, 10–27;  $N=11$  observation nights, right night roost), and  $16.7 \pm 2.5$  bats (range, 14–19;  $N=3$  observation nights, second floor night roost). Thus, we observed on average 72.1 bats roosting in the four night roosts, of which a mean of 34.4 individuals had bands on their forearms (50.5 %). During the same observation period (January–February 2009), the percentage of banded bats in the La Casona day roost averaged  $51.4 \pm 4.2$  %, suggesting the same population of bats inhabited both the La Casona day and night roost. We were able to identify the exact color combinations of bands only for bats roosting in the left night roost. Thirty of the bats (28 males and 2 females) roosting in the left night roost had bands on their forearms allowing their identification as individuals and as residents of the La Casona day roost. Sex ratio in the La Casona night roost was not different from the sex ratio encountered in the La Casona day roost (Fisher's exact test: La Casona night roost January–February vs. La Casona day roost January–February and July–August, both  $df=1$  and  $p=0.999$ , Table 1).

#### Minimum tenure of adult bats in the day roost

Between 2006 and 2010, median minimal tenure of adult females was 2.00 years ( $N_f=7$ ; interquartile range, 1.50–2.31 years; range, 0.59–2.62 years). Median minimal tenure of adult males was 1.56 years ( $N_m=97$ ; interquartile range, 0.59–1.99 years; range, 0.54–3.94 years). Because almost all males and females were adult at capture ( $N_f=6$ ,  $N_m=93$ ) and because many of our study objects were still present in the study colony in 2010 when the last census was conducted ( $N_f=4$ ,  $N_m=36$ ), the actual tenure of male and female *B. plicata* exceeds our minimal tenure estimates.

#### Fidelity of adults to the day roost

Most bats showed high fidelity to their day roost. Median fidelity of adult females to the day roost was 0.76 ( $N_f=8$ ; interquartile range, 0.68–0.90; range, 0.30–0.96) and median fidelity of adult males to the day roost was 0.80 ( $N_m=134$ , interquartile range 0.60–0.92; range, 0.07–1.00).

Bats in the La Casona day roost were distributed over 8–10 spatially separated groups. Both females and males exhibited high fidelity to individual groups within the day roost. Within observation periods, females had a median fidelity to individual groups of 0.78 ( $N_f=7$ ; interquartile range, 0.70–0.95; range, 0.65–0.98), and the male's median fidelity to a group was 0.90 ( $N_m=121$ ; interquartile range, 0.80–1.00; range, 0.38–1.00), suggesting that the day roost included several social groups with constant membership of bats. Most bats that were observed over two to four observation periods roosted in the same social group throughout the entire study, i.e., across years ( $N_f=2$ , 29 %;  $N_m=50$ , 63.3 %). Some bats changed social group membership from one observation period to the next. Four females (57 %) and 28 males (35.4 %) were observed to roost in two different social groups, and one female (14 %) and one male (1.3 %) were observed to roost in three different social groups. The mean percentage of banded adult females that remained in the La Casona day roost from one field season to the next (76 %, range 67 %–83 %,  $N=8$  females) was similar to the respective percentage in males (74 %; range, 67–77 %,  $N=142$  males), suggesting similar survival of females and males.

#### Fidelity of adults to the night roost

Fidelity to the left night roost appeared to be low ( $N=30$ , median  $f=0.55$ ; interquartile range, 0.36–0.64; range, 0.09–1.00). However, because bats forage at night, it is well possible that absent bats were foraging at the time when census pictures were taken. In contrast, fidelity of individual bats to social groups within the left night roost was high, with a median fidelity of 1.00 ( $N=30$ ; interquartile range, 1.00–1.00; range, 0.67–1.00). **Membership to social groups in the day roost was not in accordance with membership to social groups in the left night roost to the effect that bats that roosted in the same social group in the night roost mostly originated from different social groups of the day roost (Table 2).**

#### Age of females at first conception

Since no data on reproduction of previously banded juvenile females was available, age of females at first conception was estimated based on parturition rates. All females for which reproductive state was inspected at capture during the parturition period in July and August were lactating ( $N=25$ ). Bradbury and Vehrencamp (1976) reported 97 % parturition rates in their study and all of 26 dissected females from Mexico had implanted embryos (López-Forment 1979). Parturition rates between 97 and 100 % thus suggest that young females do not forgo reproduction in their first year and that females start reproducing in the first mating season following their birth at half a year of age.



**Table 2** Census of bats observed in the left night roost in 2009 ( $N=11$  nights). The majority of bats roosting together in the same group of the left night roost were not found roosting together in the same social group during the day

Social group in left night roost	1							2							3	4							5
Social group in day roost	5	6	7	5	5	6	7	8	7	5	7	7	8	9	1	7	7						
Bat ID	173	187	165	111	109	71	110	191	65	184	53	133	182	66	148	143	193						
Social group in left night roost	6							7							8	9	11	12					
Social group in day roost	1	5	8	1	6	1	1	2	3	7	1	5	9										
Bat ID	82	176	171	20	174	112	131	121	183	128	89	150	64										

Observations of natal philopatry

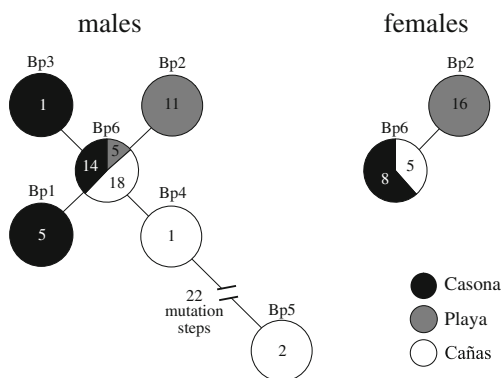
In total, we caught 12 juvenile *B. plicata*, of which eight juveniles (4 males and 4 females) were large and heavy enough to be banded with one bicolored plastic ring. All males and two of the four females were classified as philopatric individuals, since they were present for at least half a year in the day roost. Five of the six philopatric pups remained not only in their natal day roost but roosted as adults in the same social group in which they had roosted as pups. One philopatric individual changed social groups. However, it is possible that this philopatric male moved to another social group together with its unbanded mother. In 2008, the unbanded mother of the philopatric male in question roosted close to another banded female. In 2009 and 2010, the philopatric male roosted in the same social group with the banded female that had formerly been a fellow group member of its unbanded mother.

Genetic structure of day roosts

We sequenced a 239-bp fragment of the mitochondrial d-loop region in adult females (La Casona:  $N=8$ ; Playa Naranjo  $N=16$ ; Finca Cañas Castillas  $N=6$ ) and males (Playa Naranjo:  $N=16$ ; Finca Cañas Castillas:  $N=22$ ; La Casona:  $N=20$  randomly selected). Twenty-six polymorphic sites resulted in six different haplotypes (Fig. 1). All six haplotypes were found

among males, but only two among females (Fig. 1). For all three day roosts, genetic variation within a day roost was always higher in males than in females (Table 3), suggesting that gene flow is mediated by males. Within colonies, number of haplotypes ranged between two and three for males while females did not show any variation. Differences in haplotype frequencies between sexes were significant only in the colony Playa Naranjo (PN; Fischer's exact test:  $p=0.04$ ) but not in La Casona (LC;  $p=0.37$ , post hoc power=0.11) and Finca Cañas Castillas (FCC;  $p=1.00$ , post hoc power<0.001); however, due to the small sample sizes of females in the two nonsignificant colonies (Fig. 1), the statistical power was very low. To account for the problem of small sample sizes in females, we pooled our results concerning haplotype frequencies for the three study colonies. Per colony, we classified haplotypes into two categories: Haplotype category 1 comprised the females' haplotype of the respective colony and haplotype category 2 contained all haplotypes not found in females of the respective colony. Only one haplotype was found in the females of any given colony (Fig. 2). A Fisher's exact test showed that males had significantly more often haplotypes that were not detected in the females they resided with ( $p=0.002$ ).

Males and females within a colony shared always the same most frequent haplotype (Fig. 1). For females, the pairwise  $F_{ST}$  value was large between the colonies LC and PN and between PN and FCC, but not between LC and FCC (Table 4). In the latter case, females from both colonies likely shared the same haplotype by chance.  $F_{ST}$  was higher for females than for males (Table 4), suggesting more gene flow between colonies by males.



**Fig. 1** Haplotype network of males and females from the three day roosts

Discussion

Dispersal

Evidence for female philopatry in *B. plicata* is provided by our analysis of mitochondrial DNA, which revealed no genetic variation among females within day roosts, i.e., all females of a given day roost shared the same mitochondrial haplotype. Female philopatry is also supported by direct observations.

**Table 3** Mitochondrial DNA diversity in males and females of the three day roosts

Colony	Sex	<i>n</i>	<i>K</i>	$\hat{H} \pm SD$	$\pi \pm SD$	$\theta_k$
La Casona	Males	20	3	0.4684±0.1045	0.0020±0.0020	0.7185
	Females	8	1	0.0000±0.0000	0.0000±0.0000	0.0000
Playa Naranjo	Males	16	2	0.4583±0.0954	0.0019±0.0020	0.3472
	Females	16	1	0.0000±0.0000	0.0000±0.0000	0.0000
Finca Cañas Castillas	Males	21	3	0.2667±0.1197	0.0177±0.0102	0.7035
	Females	5	1	0.0000±0.0000	0.0000±0.0000	0.0000

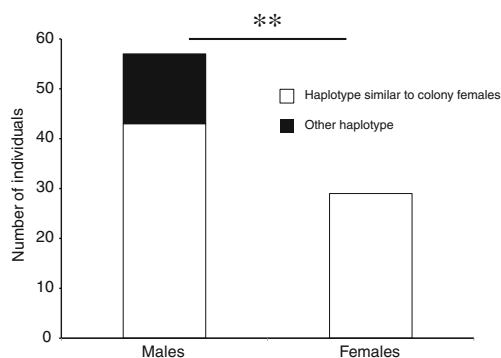
*n* sample size, *K* number of different haplotypes,  $\hat{H}$  gene diversity,  $\pi$  nucleotide diversity,  $\theta_k$  theta estimator based on the number of different haplotypes

Two of four banded female pups were still roosting in their natal day roost upon reaching sexual maturity, and one of these philopatric females was also observed to bear a pup in its natal day roost. The fact that the single haplotype present among females of a day roost was in all three day roosts also the most frequent haplotype among resident males suggests that these males might descend from colony females and might thus be philopatric. This is in accordance with our direct behavioral observations. However, because of the limited periods of observation and because not all bats in the La Casona day roost were banded, we were not able to observe immigrants. Evidence for higher gene flow by males and thus male immigration into day roosts comes from the mitochondrial d-loop analysis that showed higher diversity indices for males than for females and a lower genetic structure between males of different day roosts than between females from different day roosts. In addition, and considering that only four to eight females but on average 139 males (Table 1) roosted in the La Casona day roost, it is highly improbable that all of these males descended from the few female residents. It is much more likely that the male residents of the La

Casona day roost were composed of philopatric and immigrant individuals.

*Balantiopteryx plicata* is the first member of the studied Neotropical emballonurids that exhibits the prevailing mammalian male-biased dispersal pattern (e.g., Dobson 1982; Lawson Handley and Perrin 2007). In closely related Greater sac-winged bats (*S. bilineata*) and Proboscis bats (*R. naso*), the exceptional female dispersal is consistent with a father-daughter inbreeding avoidance strategy because the tenure durations of individual males or of male kin groups exceed the age of females at first conception (Clutton-Brock 1989; Nagy et al. 2007, 2013; Clutton-Brock and Lukas 2011; Lukas and Clutton-Brock 2011). Interestingly, female *B. plicata* are philopatric in spite of an apparently existing risk of inbreeding with closely related males, since median minimal male tenure of 19 months exceeds the age of females at first breeding (about half a year of age; Bradbury and Vehrencamp 1976; López-Forment 1979).

In a recent seminal paper on the evolution of habitual female dispersal in mammals, the authors found that where females start breeding such early that their fathers might still reproduce in their social groups, females in only 4 of 22 species (18 %) are philopatric in spite of the inbreeding risk (Lukas and Clutton-Brock 2011). The authors suggested that where males are not able to monopolize females and females



**Fig. 2** Pooled distribution of haplotypes in males and females from the three day roosts. Haplotype data was pooled over the three day roosts and haplotypes were allocated to two categories: Haplotype category 1 comprised the females' haplotype of the respective colony and haplotype category 2 all haplotypes not found in females of the respective colony. Please note that all analyzed females shared one single haplotype per day roost and thus were all allotted to category number 1. The result of the Fisher's exact test is shown as significant on a 0.01 significance level (\*\*)

**Table 4**  $F_{ST}$  values and significance levels of pairwise comparisons of colonies for each sex separately

Sex	Comparison	Pairwise $F_{ST}$	
		$F_{ST}$	<i>p</i> value
Females	LC/PN	1.00	<0.001
	PN/FCC	1.00	<0.001
	LC/FCC	0.00	0.999
Males	LC/PN	0.41	<0.001
	PN/FCC	0.52	<0.001
	LC/FCC	0.08	0.058

LC La Casona, PN Playa Naranjo, FCC Finca Cañas Castillas

stand a chance of recognizing their fathers and other male kin, philopatry of females can be maintained despite an inbreeding risk (Lukas and Clutton-Brock 2011). During their extremely long tenure of up to 17 years, alpha male White-faced capuchins (*Cebus capucinus*) accumulate a number of daughters in their social groups, the latter of which mate with subordinates to avoid mating with their fathers (Muniz et al. 2006, 2010). Female-mate choice maintains female philopatry and drives male dispersal also in Spotted hyenas (*Crocuta crocuta*). Here, females preferably mate with males that were born into their clan or immigrated therein after their own birth (Höner et al. 2007). In the temperate bat species *Plecotus auritus*, the long-term stable maternity colonies contain males and females, both of which can be philopatric to the maternity colony. However, females have been demonstrated to mate with males from outside their own maternity colony (Burland et al. 2001).

Philopatry is assumed to be the optimal strategy in female mammals and benefits to females involve for example higher feeding efficiency (Young and Monfort 2009), earlier breeding and higher reproductive potential (Ronce 2007; Fisher et al. 2009) but also improved fecundity and breeding success when associating with kin (e.g., Kawata 1990; König 1994). Among Neotropical emballonurids, *B. plicata* inhabits the most seasonal and arid areas and individuals have been observed to forage up to 12 km away from the day roost. Especially in the dry season, when food availability is low and females are gestating, females might profit greatly from remaining philopatric and having access to nearby foraging grounds (Bradbury and Vehrencamp 1976, 1977b; López-Forment 1979).

### Social organization

One peculiarity of the social system of this species is the existence of some colonies where males prevail. Of 285 *B. plicata* caught in a cave roost in Costa Rica, inhabited by 1,500–2,000 bats of this species, only 66 (23 %) were females, whereas a census at a nearby boulder revealed a female proportion of 46 % (Bradbury and Vehrencamp 1976). Our results are in accordance with these findings as we noted a proportion of 5, 21, and 50 % of females in our day roosts (Table 1). Previous studies claimed that the frequently male biased sex ratio of some colonies may be the result of a male biased population sex ratio, the latter of which was supposedly caused by high female mortality (López-Forment 1979; Bradbury and Vehrencamp 1976). Our results contradict this suggestion. We found that females and males had rather similar minimal tenure durations and that similar proportions of males and females survived from one field season to the next. In fact, although López-Forment (1979) proposed that the population sex ratio is biased towards males in *B. plicata*, the author caught almost equal numbers of males and females during his study ( $N=501$ , 51 % males and 49 % females; calculated

based on Fig. 5 in López-Forment 1979). Thus, in the light of López-Forment's (1979) and our results, it is improbable that the population sex ratio in this species is biased towards males and it appears most likely that *B. plicata* exhibits some kind of year-round sexual segregation.

Evidence for sexual segregation being persistent throughout the year is provided by the fact that males and females were highly faithful to their day roost and night roost and even to specific social groups within these roosts. Regarding the day roost, this was true for up to several years and throughout the parturition and mating season. Concerning the La Casona colony, our results suggest that the same population of bats is present in the day roost and in the night roost during the mating season. The percentages of banded bats were very similar between the day and the night roost in the mating season of 2009. Although we observed fewer bats in total in the La Casona night roost (72 bats on average) than in the day roost (116 bats on average), this might be explained by bats being absent for foraging at night and/or by additional night roosts in La Casona that were not located by us. The lack of change in the sex ratio over the course of the year within day roosts in combination with differing sex ratios between individual day roosts in the same months of the year further supports the idea that this species possesses colonies where males constantly predominate. The role of colonies where males predominate is not yet clear. It has been suggested that they might represent year round male mating aggregations (potentially lek arenas; Bradbury and Vehrencamp 1977a). However, this speculation can only be resolved with further field studies involving more colonies and more data on individuals' behavior.

If further studies will be able to confirm that highly male biased colonies in *B. plicata* are truly male mating aggregations that may be visited by females for mating, then this could explain why in contrast to other emballonurids *B. plicata* exhibits male-biased dispersal. If females visit specific sites for mating, the fathers of philopatric females would not reside in the natal colonies of females and female philopatry would not create an inbreeding risk. Furthermore, if mating takes place at male mating aggregations, males could profit from immigrating into such colonies by getting access to female mating partners.

### Conclusions

In conclusion, our study together with earlier papers showing female-biased dispersal in *S. bilineata* and *R. naso* (Nagy et al. 2007, 2013) suggests that dispersal patterns in closely related bat species of the family Emballonuridae are not caused merely by a phylogenetic signal, but that dispersal patterns in this bat family are probably shaped by differences concerning the social system and possibly also the species'

**ecology.** Thus, current and further studies focusing on the highly diverse dispersal patterns and social systems of the Neotropical Emballonuridae promise to greatly enhance our understanding on the interplay of ultimate causes in shaping sex-biased dispersal patterns.

**Acknowledgments** We thank the Costa Rican authorities, especially Javier Guevara for support and research permits and Santa Rosa National Park (Area de Conservación Guanacaste Costa Rica, ACG), especially Roger Blanco Segura for technical assistance. We are grateful to Isabelle Kühndahl for contributing to lab analysis. This work was funded by the Deutsche Forschungsgemeinschaft (DFG, FM: MA1737/8-1), the National Geographic Society (NGS), by the German Academic Exchange Service (DAAD; MN), the Ilse & Dr. Alexander Mayer Stiftung (MN), and the German Merit Foundation (MK).

**Ethical standards** All field work was approved by the Costa Rican authorities (MINAET Ministerio del Ambiente, Energía y Telecomunicaciones and SINAC Sistema Nacional de Areas de Conservación) and was in compliance with the current laws of Costa Rica and Germany.

**Conflict of interest** The authors declare that they have no conflict of interest.

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