

# Chapter 3

## Sex-Biased Dispersal and Social Systems of Neotropical Emballonurids

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**Abstract** The most common pattern of sex-biased dispersal in mammals including temperate bats is that females remain philopatric and males disperse from their natal groups. In contrast, sex-biased dispersal patterns in tropical bat species appear much more variable, ranging from all-offspring dispersal to female-biased dispersal and male-biased dispersal. The identity of the philopatric sex is essential for the kin structure of social groups (i.e. matrilineal relatives in species with female philopatry and patrilineal relatives in species with male philopatry) and thus for the evolution of social behavior. This book chapter contrasts sex-biased dispersal and the social systems of three well-studied Neotropical bat species of the family Emballonuridae. Two of these Neotropical Emballonurids exhibit exceptional female-biased dispersal and male philopatry in combination with resource-defense polygyny (greater sac-winged bat *Saccopteryx bilineata*) or female-defense polygyny (proboscis bat *Rhynchonycteris naso*). However, in the gray sac-winged bat (*Balantiopteryx plicata*) females are the more philopatric sex and the social system involves some sort of sexual segregation with mating probably taking place at male mating aggregations. To conclude, we discuss the evolutionary pressures driving the observed dispersal patterns and how sexual selection in Neotropical Emballonurids with male philopatry might shape bat sociality.

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### 3.1 Sex-Biased Dispersal in Neotropical Bats

Studies from the past decade revealed an astonishing diversity in dispersal patterns among Neotropical bats. Although to date only a handful of Neotropical bat species have been studied with respect to their dispersal behavior, the reported dispersal patterns span the whole spectrum of possible sex-biased and unbiased dispersal patterns. The predominant mammalian dispersal pattern of male-biased dispersal (i.e. dispersal is more prevalent in males and females tend to be faithful to their place or area of birth, termed philopatry) has been detected in common vampire bats (*Desmodus rotundus* Wilkinson 1985) and in gray sac-winged bats (*Balantiopteryx plicata*, Nagy et al. 2014). Thus far, these are the only examples of Neotropical bats that possess a dispersal behavior similar to temperate bats and the majority of mammals (Moussy et al. 2012; Lawson-Handley and Perrin 2007). In contrast, the remainder of Neotropical bats to which information on dispersal are available, exhibit rather exceptional dispersal patterns. Female-biased dispersal (i.e. dispersal is more prevalent in females and males tend to be philopatric) has been reported from two Emballonurid bats (greater sac-winged bat, *Saccopteryx bilineata*, Nagy et al. 2007; proboscis bat, *Rhynchonycteris naso*, Nagy et al. 2013) and from two Phyllostomid bats (Seba's short-tailed bat, *Carollia perspicillata* Fleming 1988; Cosson 1994; greater spear-nosed bat, *Phyllostomus hastatus* McCracken and Bradbury 1981). Two other species of Neotropical bats show a dispersal behavior without sex-bias; in the white-throated round-eared bat (*Lophostoma silviculum*) all offspring disperse from their natal colonies (Dechmann et al. 2007) and in Spix's disc-winged bats (*Thyroptera tricolor*) offspring of both sexes are philopatric to their natal groups (Chaverri and Kunz 2011).

The diversity in sex-biased dispersal patterns of Neotropical bats is paralleled by a similarly astonishing diversity in mating and social systems (McCracken and Wikinson 2000; Zubaid et al. 2006). Mating systems are widely believed to decisively influence the extent and direction of sex-bias in dispersal and, in general, dispersal in the polygynous and promiscuous social systems of mammals is assumed to be mediated by males (e.g. Greenwood 1980; Dobson 1982; Clutton-Brock and Lukas 2011). Female dispersal and male philopatry in mammals is frequently correlated with a rather rare mammalian male mating strategy of resource defense (Greenwood 1980). The mating system has also been proposed to influence the length of male breeding tenures and their longevity, whereby it determines whether females face a risk of father-daughter inbreeding, the latter of which should prompt females to disperse (Clutton-Brock and Isvaran 2007; Clutton-Brock 2009; Clutton-Brock and Lukas 2011). The unusual dispersal patterns in Neotropical Emballonurids provide us with the unique opportunity to test the validity of existing hypotheses on sex-biased dispersal and to gain new insights into the evolution of this important life history trait. In the remainder of this book chapter, we want to summarize what is known on the social systems and dispersal patterns of three well-studied Neotropical Emballonurids and on the evolutionary pressures that shape these patterns.

## 3.2 Female-Biased Dispersal in the Greater Sac-Winged Bat (*Saccopteryx bilineata*)

### 3.2.1 Social Organization and Mating System

*Saccopteryx bilineata* is a common inhabitant of lowlands between Southern Mexico and Southern Brazil. These bats use a number of different day roosts, all of which are generally well-lit. Day roosts (also referred to as colonies) include buttresses of large forest trees and cavities inside hollow trees, well-lit areas of caves, but also the inside or outside of abandoned and sometimes even inhabited human edifices (the most bizarre day roost we have ever witnessed was a group of about 30 *S. bilineata* roosting behind a fridge in a bar). Bats maintain a minimum distance of 5–8 cm to each other in the day roost. The basic social unit of *S. bilineata* is a one-male multifemale group that has been termed a ‘harem’. Year-round, males defend a harem territory (i.e. 1–2 m<sup>2</sup> of vertical surface in the day roost) that includes the roosting sites of up to 8 females and 2–3 females on average. Thus, *S. bilineata* has a socially polygynous mating system and males follow a resource-defense mating strategy to get access to females. A colony may contain only one harem, but large colonies can have up to 12 adjacent harems and up to 60 adult individuals (Bradbury and Emmons 1974; Voigt et al. 2008). Particularly, larger colonies also contain a varying number of nonharem males. Nonharem males roost outside of harem territories in the same colony or sometimes may even defend a territory of their own. However, territorial nonharem males only occasionally have females roosting in their territories (Bradbury and Emmons 1974; Bradbury and Vehrencamp 1976; Voigt et al. 2008). *Saccopteryx bilineata* males typically gain harem access by queueing. Voigt and Streich (2003) performed a removal experiment, temporality taking out harem holders of their territories to observe which of the nonharem males took over the vacant territory. Usurpers belonged to small groups of nonharem males that spent their daytime close to the respective harems. Moreover, these so-called peripheral groups appeared to have a hierarchical structure according to their tenure in the colony. Thus, the nonharem males with the longest tenure in a peripheral group will be the first in filling an arising harem vacancy (Voigt and Streich 2003).

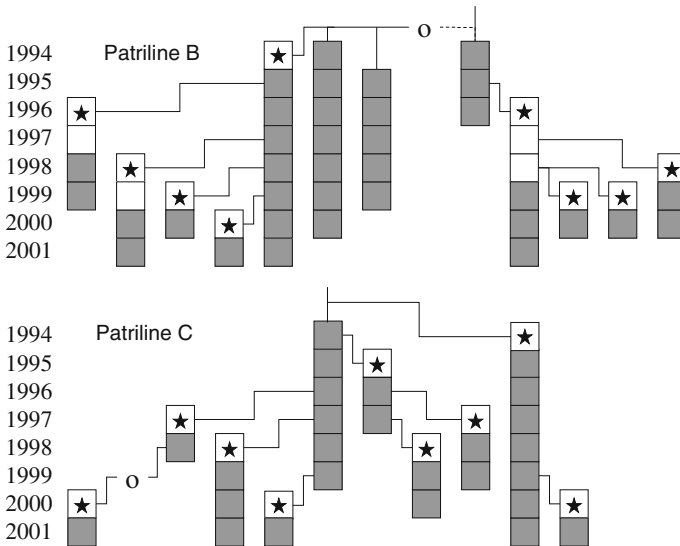
### 3.2.2 Female Dispersal

Female *S. bilineata* disperse from their natal colonies and immigrate into other colonies before they start reproducing; thus, female residents of a colony are unrelated immigrants (i.e. habitual female dispersal sensu Clutton-Brock and Lukas 2011). During a study period of 5 years (1996–2001) none of 71 juvenile females were observed to reproduce in their natal colony and 68 juvenile females (96 %) had already left their colony at an age of 6 months. The same study reported 37

female immigrants, none of which descended from members of the respective study colony (Nagy et al. 2007). Female dispersal in *S. bilineata* is very likely a strategy to avoid father-daughter inbreeding. In plural breeding mammals where several breeding females live in groups defended by one or more males, habitual female dispersal has been found to be consistently associated with male breeding tenures that exceed the females' ages at first conception. Therefore, if females were philopatric, they would risk inbreeding with their fathers, because the reproductive tenures of males will often not have ended before their daughters' onset of reproduction (Clutton-Brock 1989; Clutton-Brock and Lukas 2011). Age at first conception is about 7 months in *S. bilineata*, and females start reproducing the first mating season following their birth (Nagy et al. 2007). Mean tenure as a harem male based on data from 8 colonies was  $1.9 \pm 2.0$  years. Harem males in the smallest colonies with only one harem male and without permanent nonharem males had the shortest tenures with on average less than one year (range 0.6–1.2 years). Harem males in the largest colony under study that contained 9–12 harems and 7–12 nonharem males were able to hold their harems for on average 2.9 years and up to 9.2 years (Nagy et al. 2012). Thus, the age at females' first conception in *S. bilineata* falls below the tenure duration of harem males, suggesting that female dispersal is an inbreeding avoidance strategy.

### 3.2.3 Male Philopatry

Roughly, half of the juvenile males born in a colony are still present in their natal colonies, the mating season following their births (63 % in a Panamanian population and 45 % in a Costa Rican population, Tannenbaum 1975; Nagy et al. 2007). Almost all males that become new residents of a colony are natal and thus, philopatric males (27 of 29 males, Nagy et al. 2007). This is also reflected in the typically philopatric origin of males that gain a harem position. A long-term study on eight Costa Rican *S. bilineata* colonies found that 45 of 62 males that took over a harem were philopatric individuals that descended from females and males of their respective natal colonies (Nagy et al. 2012). Apparently, harem take-over by immigrant males is more frequent in colonies that occasionally do not harbor any nonharem males (55 % immigrant harem males) as compared to colonies with permanent nonharem males (12.5 % immigrant harem males, Nagy et al. 2012). As a consequence of male philopatry and high levels of intracolony paternity, colonies of *S. bilineata* have a patrilineal social organization (Heckel and von Helversen 2003; Nagy et al. 2007; Fig. 3.1). Typically, several closely related males (fathers with their sons and grandsons as well as brothers) will roost simultaneously in a colony and compete over access to harem territories and females. For example, up to 70 % of pups resulted from females mating with someone other than their own harem male (Heckel and von Helversen 2003; Nagy et al. 2007). For many of these males local mate competition must therefore be severe, raising the question of how *S. bilineata* cope with the costs related to local mate competition. The solution to this problem



**Fig. 3.1** Two of 12 patriline of *Saccopteryx bilineata* from a large colony in Costa Rica that continued up to twelve adjacent harems. Patriline were reconstructed based on paternity and kinship analysis. Each column depicts an individual male and each cell of the column a year for which paternities were determined (from 1996 until 2001) or reconstructed (before 1996). *Symbols*: star year of birth; gray cells years of presence in the colony; white squares years of presence outside the colony; open circle male from outside the colony; solid line relatedness of 0.5; dashed line relatedness of 0.25 (modified after Nagy et al. 2007). Patrilineal male kin, like grandfathers, fathers, sons, brothers, and cousins may roost simultaneously in a colony, competing over access to harem territories and females. Figure reproduced from Voigt et al. (2008), by courtesy of Oxford University Press

lies in the direct fitness benefits that males gain when living in multimale colonies. The reproductive tenure of harem males proved to increase with the number of male residents in a colony, whereas the number of breeding seasons a male succeeded in defending his harem was an important factor explaining variance in male lifetime reproductive success (Nagy et al. 2012). Intriguingly, in mammals evidence that male group size positively affects the reproductive tenure of males comes only from species where males are known or suspected to cooperate in female or territory defense (e.g., lions *Panthera leo* Bygott et al. 1979; red-fronted lemurs *Eulemur fulvus rufus*, Port et al. 2010). At present, evidence that male *S. bilineata* might likewise cooperate in excluding nonnatal males from settlement is only tentative. Because *S. bilineata* males profit from living in multimale colonies in terms of lifetime reproductive success, they should preferably immigrate into larger colonies. Immigration rate was, however, larger in smaller colonies. This suggests that resident males actively prevent immigration of nonnatal males and may be more effective in larger colonies with several resident males (Nagy et al. 2012). Excluding nonnatal males from settlement increases the chances that the patriline is maintained in a colony over large periods and therefore, can also assure future indirect fitness

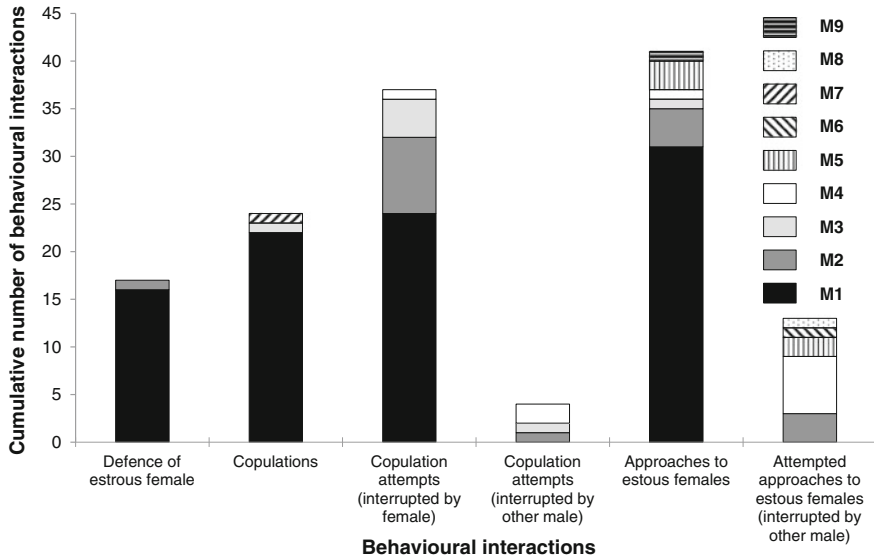
benefits (Nagy et al. 2007, Nagy et al. 2012). However, immigration attempts of nonresident males and/or attempts of immigrant males to expel harem males from their territories have only been documented anecdotally yet; such events are rare and, thus, difficult to observe. Further evidence for an active role of males in preventing settlement of nonnatal males comes from a learned vocal group signature in isolation calls that has been shown to reliably associate individuals with their natal colony. Isolation calls are usually used in mother-pup communication, but adult males of *S. bilineata* use isolation calls to appease more dominant males. Consequently, isolation calls may function as a ‘password’ allowing resident males to discriminate between natal and nonnatal males, but playback experiments are needed to verify this supposition (Knörnschild et al. 2012).

### 3.3 Female-Biased Dispersal in the Proboscis Bat (*Rhynchonycteris naso*)

#### 3.3.1 Social Organization and Mating System

*Rhynchonycteris naso* is the smallest Neotropical Emballonurid; it forages for insects over the surface of moving water and is widely distributed in the lowland rainforests ranging from the South of Mexico to the South of Brazil and East of the Andes to Peru and Columbia (Hall 1981; Bradbury and Vehrencamp 1976). Commonly used dayroosts include the exposed boles of trees, the sides of cliffs but also manmade structures (e.g. underneath the overhanging roofs of buildings), preferably in the immediate vicinity of waterways (Bradbury and Emmons 1974; Nagy et al. 2013). In the dayroost, bats keep an individual distance of approximately 2–4 cm to each other and are visually cryptic due to their woolly and mottled pelage and two pale wavy lines on their backs (Dalquest 1957; Bradbury and Vehrencamp 1976). Small groups with only three individuals have been reported, but large colonies can consist of up to 50 *R. naso* with males and females at about equal numbers (Bradbury and Emmons 1974; Bradbury and Vehrencamp 1976). Bradbury and Emmons (1974) reported quite high compositional variability of social groups in Trinidad (29–86 %). In contrast, a long-term study from Costa Rica found that social groups were highly stable over long periods and individuals to show high fidelity to their day roosts (89–100 % fidelity, N = 131 individually banded bats, Nagy et al. 2013).

The mating system of *R. naso* has been described as a female-defense polygyny (Bradbury and Vehrencamp 1977a). Bradbury and Vehrencamp (1976) reported that their study groups were never observed to be without at least one adult male. This most-constant male was also the one that frequently returned to the roost at night, whereas other male group members rarely did so (Bradbury and Vehrencamp 1976). Their observations led them to suggest that there is some sort of dominance structure between the males of a colony (Bradbury and Emmons 1974, Bradbury and Vehrencamp 1976). Behavioral observations during the postpartum estrus of female



**Fig. 3.2** Behavioral interactions (copulations, copulation attempts and defense of females) of *Rhynchonycteris naso* males with estrus females or competing males. Individual males (M1–M9) are represented by different colors or patterns. The majority of copulations, copulation attempts, and female defenses were performed by one most dominant male (M1). Figure reproduced from Nagy et al. (2013), by courtesy of John Wiley and Sons

*R. naso* in one Costa Rican colony showed that one of ten resident males performed the majority of copulations (92 %), copulation attempts (65 %), and defenses of estrus females (94 %, Nagy et al. 2013, Fig. 3.2). However, this apparently most dominant male sired just four of the 12 pups (33 %) fathered in the mating season preceding the observations. The remaining eight pups descended from five other males, four of which were also residents of the colony (Nagy et al. 2013). Admittedly, the surprisingly low fathering success of the by far most dominant male in the day roost might reflect differences in the males' dominance hierarchy of the preceding mating season, when the pups were sired. However, an alternative explanation could also be that direct defense of females in the day roost is not the only male mating strategy. There is preliminary, hitherto unpublished evidence from an ongoing PhD-thesis of Linus Günther on reproductive strategies of *R. naso* indicating that some sort of territorial defense might also be part of male mating strategies.

### 3.3.2 Female Dispersal

Just like in *S. bilineata*, all female offspring of *R. naso* leave their natal colonies before sexual maturity to disperse and immigrate into another social group. Evidence

for female dispersal comes from the observation that 21 females banded as juveniles disappeared from their natal colonies within their first year of life. Furthermore, genetic paternity analysis on females captured and banded as subadults revealed that only 2 of 39 of them descended from adult members of their resident colonies (Nagy et al. 2013).

Females typically give birth the year following their own birth and first conception is rather early in life, at an age of about 10 months (Nagy et al. 2013). The median minimum tenure of males (1.65 years) was found to exceed the age of females at first conception. The actual tenure of males surely exceeds the minimal tenure estimate, because many bats were captured as adults or were still present in the social groups at the end of the study (Nagy et al. 2013). Natal dispersal of females in *R. naso*, therefore, has probably evolved to avoid father-daughter inbreeding (Clutton-Brock 1989; Clutton-Brock and Lukas 2011).

### 3.3.3 *Male Philopatry*

Evidence that males are faithful to their natal colonies in *R. naso* is provided by both observational and genetic evidence. Ten of 22 male pups (46 %) were still roosting in their natal colonies at an age of one year and a substantial proportion of males captured as subadults roosted together with one or both parents in the same colony (71 %, Nagy et al. 2013). Notwithstanding the high rate of male philopatry, immigration of males into established colonies is apparently not uncommon in *R. naso*. Several males transferred back and forth and were residents of two colonies or relocated permanently to another colony. In addition, philopatric and immigrant males were identified as sires of colony offspring (Nagy et al. 2013). So far data on the frequency of male immigration, degree of relatedness of males in colonies (i.e. patrines) and success of males' reproductive strategies is lacking for *R. naso*.

## 3.4 Male-Biased Dispersal in the Gray Sac-Winged Bat (*Balantiopteryx plicata*)

### 3.4.1 *Social Organization and Mating System*

*Balantiopteryx plicata* live mostly in arid to semiarid areas with pronounced seasonality and all sites studied in Guerrero (Mexico) and Guanacaste (Costa Rica) underwent strong seasonal changes in rainfall (Bradbury and Vehrencamp 1976; López-Forment 1979; Arroyo-Cabrales and Jones 1988). These bats are distributed from Western Mexico along the Pacific to Costa Rica (Arroyo-Cabrales and Jones 1988). Day roosts used by *B. plicata* include well-lit parts of caves, crevices, mines, cliffs, the underside of boulders and also buildings (Arroyo-Cabrales and Jones 1988,



López-Forment 1979). Colonies can contain up to 2,000 individuals (25 bats on average) and are the largest social groups known among Neotropical Emballonurids (Bradbury and Vehrencamp 1976; López-Forment 1979). As is typical for many Emballonurids, individuals roost without body contact and maintain a distance of about 20 cm to one another in the day roost (López-Forment 1979).

Information on the social system of *B. plicata* is still rather scarce, and thus at this point conclusions on the social organization and mating system of this bat are often deduced from circumstantial evidence. Females and males have been reported to roost intermixed in their colonies, and no subdivision of the roosting area into territories was observed (Bradbury and Vehrencamp 1976). However, in our main study colony, located in the La Casona Museum in Santa Rosa National Park in Costa Rica, the few females (4–8) present tended to roost close to each other (MN and MK unpublished observation) and census data on banded individuals suggest that day roosts contain several social groups with constant membership of bats (Nagy et al. 2014). The same population of bats also returned to the La Casona Museum at night. Likewise, bats were highly faithful to their social groups at night, but surprisingly membership to social groups in the day roost was not in accordance with nightly social group membership. Bats roosting together in the night roost originated from different social groups of the day roost. At present, the significance of these changes in social group membership between day and night roost remains unknown (Nagy et al. 2014).

Social behavior within the day roost is dominated by unusually high levels of aggression between males as reflected in an almost fourfold higher percentage of aggressive events in *B. plicata* males (9.2 % of total time, Table 3.1) as compared to for example males of *S. bilineata* (2.5 % of total time per hour in the state ‘aggression’; MK unpublished data). Males spent significantly more time in aggressive interactions than females (Mann-Whitney U test:  $U = 0$ ,  $N_1 = 10$ ,  $N_2 = 4$ , exact  $P = 0.002$ , corrected  $\alpha = 0.025$ ; Table 3.1) and displayed significantly more aggressive events than females (Mann-Whitney U test:  $U = 0$ ,  $N_1 = 10$ ,  $N_2 = 4$ , exact  $P = 0.002$ , corrected  $\alpha = 0.05$ ; Table 3.1). During our observation, pups displayed no aggressive behavior at all (Table 3.1).

In polygynous *S. bilineata* and *Artibeus jamaicensis*, aggressive interactions among males are often associated with competition for preferred roosting space in the day roost (Voigt et al. 2008; Ortega et al. 2008). We investigated whether the same could be the case in *B. plicata* by monitoring all aggressive interactions on twelve successive days for 60 min after 30 min of habituation (ad libitum sampling sensu Altmann 1974). Aggressive interactions among males often forced the inferior bat to relocate in the day roost. Thus, we monitored the spatial position of the aggressor prior to displacements to test whether dominant bats were predominantly found in the center or periphery of bat groups or alone. The spatial position of the aggressor after displacements was monitored to investigate whether the displacement occurred in the context of competition for preferred roosting places. If this was the case, we expected the aggressor to occupy the spatial position of the displaced conspecific. The aggressor’s behavior was monitored to assess the most prevalent behavior causing displacements. In total, we monitored 494

**Table 3.1** Time-budget data for different behavioral states and events exhibited by *B. plicata* in the day roost

Behavioral states	Males	Females	Pups
	States per hour [%]		
Resting	84.5	90.1	95.2
Aggression	9.2	1.1	0.0
Grooming	5.9	7.6	3.9
Rocking	0.4	0.5	0.2
Shaking and resistance	0.0	0.7	0.7
Behavioral events	Nr. of events per hour		
Crawling position change	1.7	1.7	0.3
Flying position change	2.2	0.6	0.2
Wing flick	1.5	1.3	0.1
Wing blow	2.2	0.3	0.0
Bite	0.8	0.1	0.0
Aerial chase	1.7	0.0	0.0
Collision	1.8	0.0	0.0
Yawn	0.4	0.2	0.1
Push-up	0.4	2.0	0.3
Teat switch	0.0	0.0	1.6

Mean values for ten males, four females and their volant, nursing pups are shown

**Table 3.2** Count data on aggressive interactions of *B. plicata* bat dyads in the day roost resulting in displacements (720 min of total observation time)

Position of aggressor prior to displacement	Position of aggressor after displacement				
	Return to previous position	Remain at position of displaced bat	Move to new position	No movement	Sum
Center of bat group	72	64	82	30	248
Periphery of bat group	37	40	100	2	179
Alone	4	17	46	0	67
Sum	113	121	228	32	494

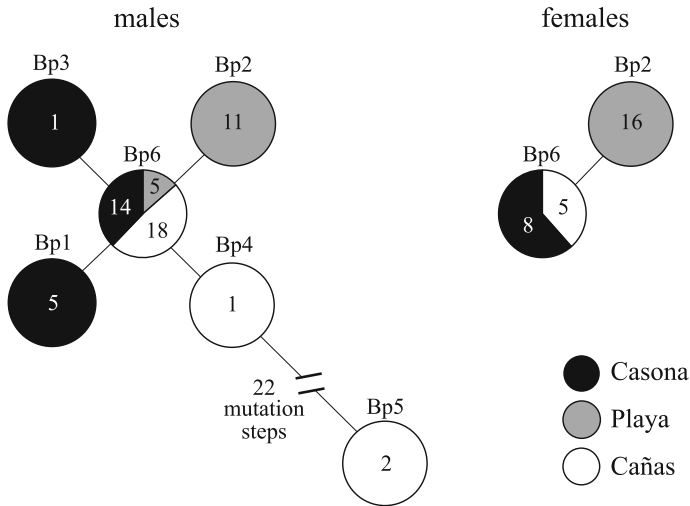
displacements in 720 min of observation (Table 3.2). Aggressors usually approached their opponents on the wing landing next to or directly on them, but displacements were also caused by bats crawling or stationary flicking their wings (flying: 329; crawling: 133; stationary: 32; Chi-Square test:  $\chi^2 = 276.98$ ,  $df = 2$ ,  $p < 0.0001$ ; corrected  $\alpha = 0.0167$ ). Prior to displacements, the majority of aggressors were roosting in the center of a bat group, not at its periphery or alone (Chi-Square test:  $\chi^2 = 101.35$ ,  $df = 2$ ,  $p < 0.0001$ ; corrected  $\alpha = 0.025$ ; Table 3.2). After displacements, aggressors moved to a new roosting position significantly more often than they remained at the position of the displaced opponent or returned

to their previous position (Chi-Square test:  $\chi^2 = 53.55$ ,  $df = 2$ ,  $p < 0.0001$ ; corrected  $\alpha = 0.05$ ; Table 3.2). On rare occasions (6.5 % of cases), the aggressor displaced a conspecific without an accompanying position change; this happened mainly when the aggressor was roosting in the center of a bat group and displaced a fellow group member by flicking its wing (30 of 32 cases; Table 3.2). Thus, competition for preferred roosting places is an unlikely explanation for the unusually high level of male aggression in the day roost. In 2009, when the aggression observations took place, the La Casona colony contained 116 bats on average, six of which were females (Nagy et al. 2014). Therefore, it is also unlikely that the more than 100 resident males were competing for access to the few female residents. One possibility is that male aggression in the day roost serves to establish some sort of dominance that might become important in the mating season. 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, see also next paragraph).

Many colonies of *B. plicata* have highly male-biased sex-ratios and the proportion of males in a colony has been found to range from 30–100 % (López-Forment 1979; Bradbury and Vehrencamp 1976; Nagy et al. 2014). The sex-ratio in a colony did not change from the parturition period (July and August) to the mating period (January and February) and also remained unchanged over several years, suggesting that in some *B. plicata* colonies males constantly prevail (Nagy et al. 2014). It has been suggested that the male-bias in colonies is caused by high female mortality leading to a male-biased population sex-ratio (López-Forment 1979). However, recent evidence shows that male and female tenure as well as survival from one year to the next are comparatively similar among the sexes (Nagy et al. 2014) and, in fact, López-Forment (1979) also caught almost equal numbers of males and females during his study. Thus, a population sex-ratio biased towards males appears improbable. Instead, a more plausible explanation could be that highly male-biased colonies represent year-round male mating aggregations that are visited by females during the mating season (potentially lek arenas; Bradbury and Vehrencamp 1977a; Nagy et al. 2014). Male calling activity has been noted to be increased and well audible from a distance in large colonies during the copulation period (Bradbury and Vehrencamp 1977a, MN and MK unpublished data) and might serve for attracting females to male mating aggregations during the mating season.

### 3.4.2 Female Philopatry

Genetic and behavioral data provide evidence of female philopatry in *B. plicata*. A fragment of the mitochondrial d-loop region was sequenced for bats of three day roosts, revealing that all females of a given day roost shared the same haplotype (Fig. 3.3). The same study reported that two of four female pups were observed to roost in their natal colony as adults, and that one of these females gave birth to a



**Fig. 3.3** Haplotype network of *Balantiopteryx plicata* males and females based on a 239 bp fragment of the mitochondrial d-loop region and on data from three day roosts (Casona, Playa and Canas) from Costa Rica. Circles depict individual haplotypes and numbers inside of circles indicate how often a haplotype was detected per day roost. Genetic variation within a day roost was always higher in males than in females, suggesting that gene flow is mediated by males. Figure reproduced from Nagy et al. (2014), by courtesy of Springer

pup in its colony of birth (Nagy et al. 2014). In contrast, and based on considerably larger sample sizes of banded female pups, reproduction of females in their natal colonies has never been witnessed in *S. bilineata* nor in *R. naso* (Nagy et al. 2007; Nagy et al. 2013).

Philopatry is usually considered the optimal strategy for female mammals (Clutton-Brock and Lukas 2011). Dispersing females frequently incur substantial fitness costs because of lower feeding efficiency (Young and Monfort 2009) and because the energetic costs of dispersal may delay breeding and reduce reproductive potential (Ronce 2007; Fisher et al. 2009). Furthermore, philopatric females can profit from improved fecundity and breeding success when associating with kin (e.g. Kawata 1990; König 1994). Bradbury and Vehrencamp (1977b) compared costs of parental investment among female *B. plicata*, *R. naso*, *S. leptura*, and *S. bilineata* and found *B. plicata* to incur the highest parental costs. Among the studied Neotropical Emballonurids, *B. plicata* experiences the highest seasonality in food supplies with a marked minimum during the dry season that coincides with females' gestation and the lowest adult survival rates (López-Forment 1979, Bradbury and Vehrencamp 1976). In Guanacaste, Costa Rica, males of this species had a 23 % lower body weight during the dry season as compared to the rainy season (Bradbury and Vehrencamp 1976). Therefore, environmental constraints might have favored female *B. plicata* to remain philopatric. By settling in the natal group, females can profit from knowledge of and access to nearby foraging grounds.

Tenure of males exceeds the age of females at first conception (average 1.56 versus 0.5 years, respectively, Nagy et al. 2014). Thus, it appears that female *B. plicata* are philopatric despite the risk of father-daughter inbreeding. However, possibly female philopatry does not create an inbreeding risk in *B. plicata*. This would be the case if further studies can corroborate that male-biased colonies function as male mating aggregations that are visited by females for mating. Then philopatric females would not roost with their fathers in the same colonies, and female philopatry would not cause an inbreeding risk.

### 3.4.3 Male Dispersal and Philopatry

Genetic and behavioral data suggest that the males of a given day roost constitute both philopatric and immigrant individuals. The analysis of the mitochondrial d-loop revealed higher diversity indices in males than in females and lower genetic structure between the males of various day roosts than between the females of various day roosts. This suggests that gene flow is higher among males and that males thus mediate dispersal (Nagy et al. 2014). However, the most frequent haplotype among males of a colony was in all colonies identical to the single haplotype females of a colony shared (Fig. 3.3), indicating that some males might descend from colony females and might therefore be philopatric. In accordance with genetic data, all four males banded as pups settled in their natal colony (Nagy et al. 2014). However, immigration of males could not be observed because of incomplete banding of bats (Nagy et al. 2014).

## 3.5 Conclusion

Female age at first conception falls below the breeding tenures of males in all three Neotropical Emballonurids contrasted in this book chapter, but only in *S. bilineata* and *R. naso* females disperse in accordance with a father-daughter inbreeding strategy (Nagy et al. 2007, 2013). We believe that female philopatry in *B. plicata* is probably favored by environmental constraints, because of a marked insect shortage during gestation in the arid and semiarid areas inhabited by this species (Bradbury and Vehrencamp 1976; 1977b; López-Forment 1979, Arroyo-Cabrales and Jones 1988). At present, male mating aggregations that females visit during the copulation period are the most likely mating system for *B. plicata* (Bradbury and Vehrencamp 1977a; Nagy et al. 2014). In such a scenario, philopatric females would not roost together with their fathers in a colony and no inbreeding risk would arise from female philopatry in *B. plicata*. In two other bat species (*Plecotus auritus* and *Thyroptera tricolor*), colonies contain philopatric individuals of both sexes and females have been demonstrated to mate with males from outside their own colonies (Burland et al. 2001; Buchalski et al. 2014). Thus, it appears that inbreeding

avoidance plays an important role in shaping female dispersal and mating decisions in bats. Considering that longevity, year-round stable mixed-sex groups and the onset of female reproduction within the first year of life are traits shared among many Neotropical bats (Barclay and Harder 2003, McCracken and Wilkinson 2000), we predict that many Neotropical bats may in fact have dispersal patterns that deviate from typical mammalian male-biased dispersal.

Male philopatry seems to occur in *S. bilineata*, *R. naso*, and *B. plicata*, although in the latter species dispersal is more prevalent in males than in females (i.e. male-biased dispersal in *B. plicata*). This stands in contrast to the substantial differences in the mating systems and male mating strategies of these species. Whereas, *S. bilineata* males clearly follow a resource-defense mating strategy, with possible cooperation between related colony males (Nagy et al. 2012), it appears that direct female defense plays an important role in *R. naso* (Nagy et al. 2013) and that *B. plicata* probably form year-round male mating aggregations (possibly resembling lek arenas, Nagy et al. 2014). Thus, the common correlates of male philopatry in mammals (resource-defense by males and/or cooperation between males, Greenwood 1980, Lawson Handley and Perrin 2007) are apparently not sufficient to explain the prevalence of male philopatry in Neotropical Emballonurids. However, we must admit that to date for example, cooperation between related *R. naso* males has not yet been considered and that the mating system of *B. plicata* is poorly understood. Only long-term studies on banded bats that involve estimates of males' lifetime reproductive success with genetic tools will help us to understand which selective pressures are important in shaping male philopatry in these and other species.

Bats are exceptionally long-lived, social mammals and the majority of bats live in groups (McCracken and Wilkinson 2000, Kunz and Lumsden 2003). However, the reasons for bat sociality are still subject to much debate: proposed causes such as ecological constraints (e.g. roost limitation), physiological demands (e.g. thermoregulation), and demographic traits (e.g. longevity) do not seem to be able to fully explain why bats are social (Kerth 2008). Much of what we know about bat sociality is based in studies of female bats from the temperate zone (but see e.g. Dechmann et al. 2010) and thus typically focuses on naturally selected traits that enhance the fitness of females (but see Safi and Kerth 2007, reviewed in Kerth 2008). In contrast, Neotropical bats often permanently live in polygynous/promiscuous mixed-sex groups and kin structures may often differ from temperate bats because of female dispersal and male philopatry (Bradbury and Vehrencamp 1977a, McCracken and Wilkinson 2000, Kunz and Lumsden 2003). This raises the question of how sexual selection in addition to natural selection may shape sociality of bats in the Neotropics.

One possible explanation for how sexual selection might shape bat sociality may constitute in the benefits of cooperating with other males in female defense. For example in *S. bilineata*, males gain direct and indirect fitness from roosting in multimale groups, and may even form cooperative alliances (Nagy et al. 2012). In *A. jamaicensis*, dominant males with large harems profit from the presence of related subordinates in their harems (Ortega et al. 2003). Female choice plays an

important role in *S. bilineata* (Voigt et al. 2008) and although females can choose freely among the males in a colony, they generally mate with the males of their resident colony (Heckel and von Helversen 2003). Female *R. naso* probably also mate only with colony males (Nagy et al. 2013). If the males of a colony represent the pool of males available for mating, females should have a vital interest to immigrate into colonies that contain several males, thereby possibly selecting males to be more social. Due to frequent female philopatry maternal support is largely directed at daughters in mammals (e.g. in cercopithecine primates, Silk 2009) and support of sons is rare due to the general absence of male philopatry. In mammals, maternal support of sons has been documented from bonobos and chimpanzees, both of which have female-biased dispersal (Boesch 2009; Surbeck et al. 2011). Female support of daughters is also known from bats (e.g. allogrooming between mother daughter pairs, Kerth et al. 2003), but female support of sons in male philopatric species of bats has not yet been considered. For example, *S. bilineata* mothers could gain substantial inclusive fitness by promoting their sons' establishment in the natal colony. Immigration of males into new colonies is rare and suitable roosts to establish new colonies are probably rare as well (Nagy et al. 2007, Nagy et al. 2012).

In conclusion, we propose that studying the diverse social systems and frequently exceptional sex-biased dispersal in Neotropical bats will contribute to our understanding of how evolution has shaped sex-biased dispersal patterns in mammals. Overall inbreeding avoidance seems well in accordance with female dispersal in Neotropical bats, but the factors driving male philopatry are less evident. There is a clear need for more longitudinal studies that incorporate genetics to study social systems and dispersal in Neotropical bats. In addition, a better understanding of social organization, mating systems, male mating strategies, and social interactions of Neotropical bats might grant us a better understanding on sexually and naturally selected causes of bat sociality.

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