

## SONGS, SCENTS, AND SENSES: SEXUAL SELECTION IN THE GREATER SAC-WINGED BAT, *SACCOPTERYX BILINEATA*

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Like many other mammals, *Saccopteryx bilineata* exhibits a polygynous mating system, in which each male defends a group of females called a harem. Colonies consist of several harems, and nonharem males roost adjacent to harems. Unlike most other mammals, females disperse from their natal colony and most juvenile males remain in it. Thus, colonies consist of patriline, which promotes intense local mate competition. Females are in estrus during a few weeks at the end of the rainy season. Mating is most likely initiated by females and preceded by intense courtship displays of males. Forty percent of colony males do not sire any offspring during their tenure in the colony, whereas a few males can sire up to 6 offspring in a single year. Males use olfactory, visual, and acoustic signals for courtship, and they demonstrate territory ownership by scent marks, low-frequency calls, and visual displays. Harem males sire on average more offspring than do nonharem males but produce only 30% of the offspring within their own harem territory, with 70% being sired by other harem males or nonharem males. Reproductive success of males increases with decreasing size, fluctuating asymmetry, and fundamental frequency of territorial calls. In addition, females that are closely related to the harem holder are more likely to mate with other males than with the harem holder. Sexual selection in *S. bilineata* is most likely influenced by intense local mate competition caused by scarce roosts and the patrilineal organization of colonies.

Key words: acoustic signals, female choice, harem, olfactory signals, polygynous mating system, sex-biased dispersal, visual signals

The extent of sexual selection in animals is usually seen as a function of the divergent potential reproductive rates of males and females (Clutton-Brock and Parker 1992; Trivers 1972). According to this idea, females are the choosier sex because their ability to enhance their Darwinian fitness is constrained by their large energetic investment in their current offspring. By contrast, males usually invest little more in their offspring than ejaculate (Clutton-Brock 1991), and, therefore, males could potentially sire more offspring than females (Clutton-Brock and Parker 1992).

Male parental care is rare among mammals (Clutton-Brock 1991), and virtually absent among bats (Kunz and Hood 2000). Most often, male mammals either monopolize a resource to which females may gain access, or they monopolize groups of females directly (Clutton-Brock 1989a; Clutton-Brock and Harvey 1978). The ability of males to monopolize groups of females recently has been questioned for some mammals (Clutton-Brock and Isvaran 2006) because it is becoming clear that so called extradominant paternities, that is, paternities by males other than the dominant male in a group, are more abundant than previously envisaged. Thus, sexual conflicts are common in mammalian mating systems, although often subtle and unnoticed.

Bats are no exception to the overall mammalian pattern that females choose the mating partner and males compete over access to resources or groups of females (Bradbury 1977a; McCracken and Wilkinson 2002). Sexual selection is common among bats, and most obvious in, for example, lek-displaying

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species such as *Hypsignathus monstrosus*, which exhibits strong sexual dimorphism in head morphology and vocalizations, among other traits (Bradbury 1977b). Emballonurid species have been one of the 1st groups of bats that were intensively studied with respect to their social organization (Bradbury and Emmons 1974; Bradbury and Vehrencamp 1976, 1977). The studies of Bradbury and coworkers have stimulated more than 20 papers about the social life of *Saccopteryx bilineata*, making it one of the best-studied mating systems within the order Chiroptera. The goal of this paper is to review our current knowledge about the sexually selected traits and the underlying mechanisms of sexual selection in the mating system of *S. bilineata*. First, we provide an overview about the taxonomy, geographic distribution, and major morphological traits of *S. bilineata*. Then we summarize the major aspects of the species' biology, that is, roosting behavior and reproductive biology, and discuss how social and dispersal behavior may set the framework for sexual selection. We summarize the findings with respect to sexually selected traits of males, such as male morphology and male acoustic, visual, and olfactory signals, and end with an outlook about where to go next in the study of sexual selection in *S. bilineata*.

Greater sac-winged bats (*S. bilineata*) belong to the family of sheath-tailed bats (Emballonuridae). Emballonuridae occur both in the Old and New World, but exhibit their highest species richness in circumtropical regions (Voigt 2003). The genus *Saccopteryx* includes 5 species (Lim et al. 2008; Muñoz and Cuartas 2001). The closest relative of *S. bilineata* is *S. leptura* (Lim et al. 2008). *S. bilineata* has a geographical distribution range from southern Brazil to southern Mexico, and it usually inhabits forested lowland regions (Voigt 2003). *S. bilineata* is an aerial hawking insectivorous bat that emits echolocation calls at 45 and 47 kHz while hunting for small insects at night (Barclay 1983; Jung et al. 2007).

Individuals of *S. bilineata* from Central American populations weigh between 7 and 9 g. In general, males are smaller than females by approximately 15% (Voigt et al. 2005b). The morphological structure from which the genus name was derived is a pouch (sac, from Latin *saccus*) in the antebrachium or propatagium (wing, from Greek *peron*—Scully et al. 2000; Starck 1958). The species name *bilineata* refers to 2 wavy white lines that reach from the shoulders dorsally to the edge of the uropatagium. *S. bilineata* also has been called the greater white-lined bat because of these white lines, but we will continue to use the common name greater sac-winged bat because other emballonurid bats such as *Rhynchonycteris naso*, and non-emballonurid bats, such as the phyllostomid genera *Uroderma*, *Chiroderma*, and others, also have 1 or 2 dorsal lines.

### ROOSTING, REPRODUCTIVE, AND SOCIAL BEHAVIOUR

*Roosting behavior.*—*Saccopteryx bilineata* roosts in cavities formed by buttress roots of large rain-forest trees and in the well-lit parts of hollowed trees, as well as in the interior or exterior of buildings (Bradbury and Emmons 1974; Tannenbaum 1975; Fig. 1). Contrary to most other bat species, *S. bilineata* clings to



FIG. 1.—Harem of *Saccopteryx bilineata* consisting of 1 male and 4 females at the well-lit basal portion of a large tree (Costa Rica, June 2007, photo courtesy of M. Knörnschild).

vertical rather than to horizontal surfaces and individuals maintain a minimum distance of 5–8 cm from each other, a distance that is rigorously maintained by agonistic behaviors (Bradbury and Emmons 1974). Some colonies have persisted for more than a decade (e.g., 15 years—Bradbury and Emmons 1974; Voigt et al. 2006). The traditional use of particular sites seems to be related to the specific roosting preferences of these bats and the overall rarity of large trees (Bradbury and Emmons 1974).

*Reproductive biology of males and females.*—In Central America, copulations have been observed in colonies of *S. bilineata* at the end of the rainy season during late November or December (Tannenbaum 1975; Voigt and Schwarzenberger 2008); sometimes even in January (Tannenbaum 1975). Females come into estrus for 1 or 2 days as shown by measurements of estrogen and 20-oxo-pregnane metabolites in fecal samples collected daily during the mating season (Voigt and Schwarzenberger 2008). Behavioral estrus seems to occur at the same time as physiological estrus, because copulations were only observed in females with high fecal estrogen metabolite levels. Most estrous events were detected during times of heavy precipitation coinciding with a drop in ambient temperature, which suggests that external factors may tune the timing of estrus (Voigt and Schwarzenberger 2008). But synchronization of physiological estrus also could be a tactic used by females to reduce sexual harassment or to undermine male surveillance. Tannenbaum (1975) recorded embryos in female *S. bilineata* during January and February, and, therefore, it is unlikely that sperm is stored or implantation delayed. After, on average,  $169 \pm 2$  days (mean  $\pm$  SE) of pregnancy, females of *S. bilineata* give birth to a single young each year (Bradbury and Emmons 1974; Voigt and Schwarzenberger 2008).

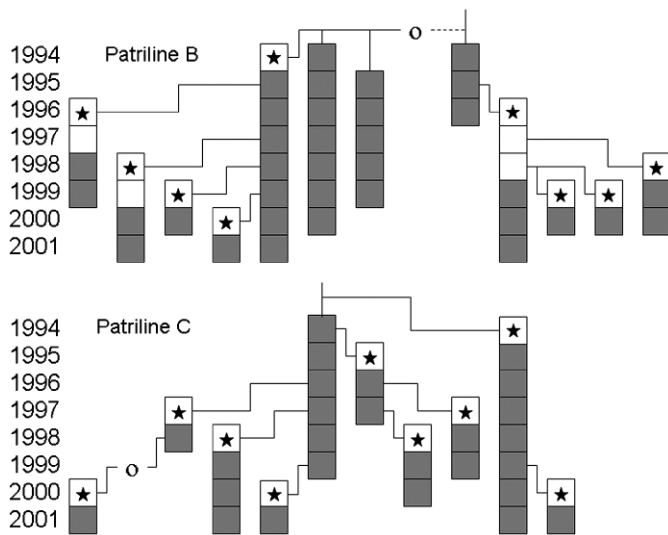


FIG. 2.—Two of 12 patrilineal pedigrees for *Saccopteryx bilineata*, inferred from paternity analysis and significant pedigree relationship tests in a colony. Each column depicts an individual male and each cell of the column a year for which paternities were determined (from 1996 until 2001) or reconstructed (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). In some years, grandfathers, fathers, sons, brothers, and cousins compete for colony females at the same time, suggesting a high level of local mate competition.

Testes of male *S. bilineata* are noticeable only before and during the mating season. One of us (CCV) observed that testes mass of male *S. bilineata* peaks at 0.5% of body mass shortly before the mating season, which is less than in similarly sized vespertilionid bats. Given the small testes of males and the lack of sperm storage in the female reproductive tract, we consider sperm competition not to be relevant in the mating system of *S. bilineata*. As the mating season progresses, testes decrease in size until they are not apparent by external manipulation (Voigt et al. 2007). Although harem males perform courtship hovering displays and territorial behaviors more frequently during than after the mating season (Voigt et al. 2007), both activities are exhibited throughout the entire year (Voigt 2003). Contrary to our expectation, courtship activity by harem males was not related to fecal testosterone metabolite levels, which should parallel seasonal testes mass changes (Voigt et al. 2007).

**Social organization.**—Colonies of *S. bilineata* consist of single-male-multiple-female groups, which are stable year-round. In the remainder of the text, we will refer to these groups as harems for simplicity. Harem males each defend a territory of 1–2 m<sup>2</sup>, in which, on average, 2 or 3 females roost, entailing a harem-polygynous social system. Colonies can comprise up to 60 adult individuals distributed in 1–12 such harems. Adult nonharem males that roost adjacent to harem territories also are present in the colony (Bradbury and Emmons 1974; Voigt and Streich 2003). The term nonharem male is synonymous with satellite male. Additionally, some male offspring up to the age of 6–8 months roost close to their

mothers within the boundaries of their natal harem territory (cryptic males, sensu Tannenbaum [1975]). Such cryptic males are usually ignored by the harem holder. Cryptic males do not court females, but will occupy vacant harems when the respective harem male disappears or is temporarily removed (Tannenbaum 1975; Voigt and Streich 2003).

Harem groups have been categorized as stable in their male attendance, but less stable in their composition of females, at least when adjacent harems were present. During the mating season, harem and cryptic males were almost always encountered at their harem territory (98% presence probability for harem males and 85% for cryptic males—Voigt et al. 2007). Females were similarly loyal to their roosting territory (91% presence probability at a given day during the mating season—Voigt and Schwarzenberger 2008). Males or females of *S. bilineata* almost never switched between neighboring colonies (Bradbury and Emmons 1974). This is also emphasized by the fact that female tenure in a colony is long. During a 6-year census study, females remained on average for  $2.7 \pm 2.0$  years (mean  $\pm 1$  SD; range 0.05–7.6 years,  $n = 66$ ) in the colony, whereas harem males held tenure for on average  $3.2 \pm 2.4$  years (range 0.2–9.2 years,  $n = 30$ —Nagy et al. 2007).

**Dispersal.**—Unlike the majority of species of mammals, in which dispersal is predominantly undertaken by males (Greenwood 1980), *S. bilineata* exhibits female-biased dispersal. In a population in Panama, Tannenbaum (1975) observed that 84% of young females dispersed from the study area or died within the 1st year, whereas 63% of young males remained at least for 1 year in the natal colony. Intercolony genetic heterogeneity was higher among males than among females in Trinidad populations, indicating that males of a colony are more related to each other than are females (McCracken 1984). The majority of males (40 of 52 males; 78% of all recorded males) roosting over a 6-year period in a colony belonged to only 4 patrilineal groups, indicating a patrilocal organization of colonies (Fig. 2). Consequently, closely related males compete for harem territories and access to females, which results in intense local mate competition (Nagy et al. 2007).

The sex-specific dispersal patterns of birds and mammals are assumed to have resulted from an interaction between inbreeding and kin competition avoidance as well as from cooperation among kin (Lawson Handley and Perrin 2007). In *S. bilineata* as well as in some other polygynous mammals, avoidance of father-daughter inbreeding is assumed to be an ultimate explanation for female dispersal (see also Dechmann et al. 2007). Female mammals commonly transfer to breed in other groups, when the average residence of males or of male kin-groups exceeds the average age of females at 1st conception (Clutton-Brock 1989b). Females of *S. bilineata* breed 1st at an age of 6 months and male tenure averaged  $2.7 \pm 2.1$  years (range 0.1–9.2 years—Nagy et al. 2007). Harem succession follows a queuing pattern, because the longest tenured male will occupy the next vacant harem territory (Voigt and Streich 2003). Males need to enter a queue and consequently establish site dominance as early as possible, because familiarity with the natal colony facilitates acquisition of harem territory. Thus, the observation of queuing nonharem

males is in line with the genetic data indicating male philopatry. Females of *S. bilineata* also may influence the probability of their male offspring to establish a harem territory in the colony by allowing their sons to roost cryptically close to them. Consequently, mothers might enhance the likelihood of cryptic males acquiring a nearby vacant harem territory at a young age. However, in the study conducted by Nagy and coworkers (2007), 17 (77%) of 22 males became resident without prior cryptic status, which makes it unlikely that only cryptic roosting enhances the likelihood of harem acquisition. The same study showed that immigration of males was rare, because  $\leq 2$  of 29 males that became resident in the colony over a 6-year period were not born to colony females. Low levels of immigration might indicate that dispersing males have little prospect of settling and reproducing in another colony. The scarcity of suitable roosts also may make the establishment of new colonies difficult. Therefore, resident males also may play an active role in the settlement of new males, by directing their aggression predominantly against unfamiliar or unrelated males. Thus, the indirect fitness benefits gained by tolerating reproduction of male kin in the colony might overcome the costs arising by local mate competition. However, cooperation among related males has not been observed in colonies of *S. bilineata* and given that males may increase their fitness more efficiently by siring offspring (direct fitness gain) than by helping related males (indirect fitness gain), we consider male cooperation to be unlikely in the social system of *S. bilineata*.

*Potential for mate surveillance by males.*—In larger colonies, females may switch harem territories during the daytime. Usually, harem males follow these females, but mostly fail to gain control over the movements of females within the colony. A previous study proposed that females of a given harem use neighboring foraging areas at night, which altogether are defended by the respective harem male. This pattern was considered responsible for the year-round harem association of females with males in daytime roosts (Bradbury and Vehrencamp 1976). However, with home-range areas of males overlapping by approximately 60% with those of females of their own harem and the employment of different night roosts by males and females of the same harem territory, it is likely that the haremlike spatial distribution of colony members in the daytime roosts is not maintained at night (Hoffmann et al. 2007). Thus, males are mostly unaware of the whereabouts of their females when foraging at night.

*Extraharem paternities.*—Extradominant paternities (sensu Clutton-Brock and Isvaran 2006) are common in the mating system of *S. bilineata*. In *S. bilineata*, extradominant paternities have been referred to as extraharem paternities, and the offspring sired by other than the dominant male as extraharem young (Heckel et al. 1999). A genetic study of paternity patterns based on all colony males and all colony offspring revealed that harem males sired, on average, more offspring than did nonharem males (Heckel and von Helversen 2002). However, harem males sired only a minority of the offspring within their own harem territory (Heckel et al. 1999; Heckel and von Helversen 2002). A recent paternity survey of 6 juvenile cohorts (159 juveniles) yielded 56 juveniles sired by

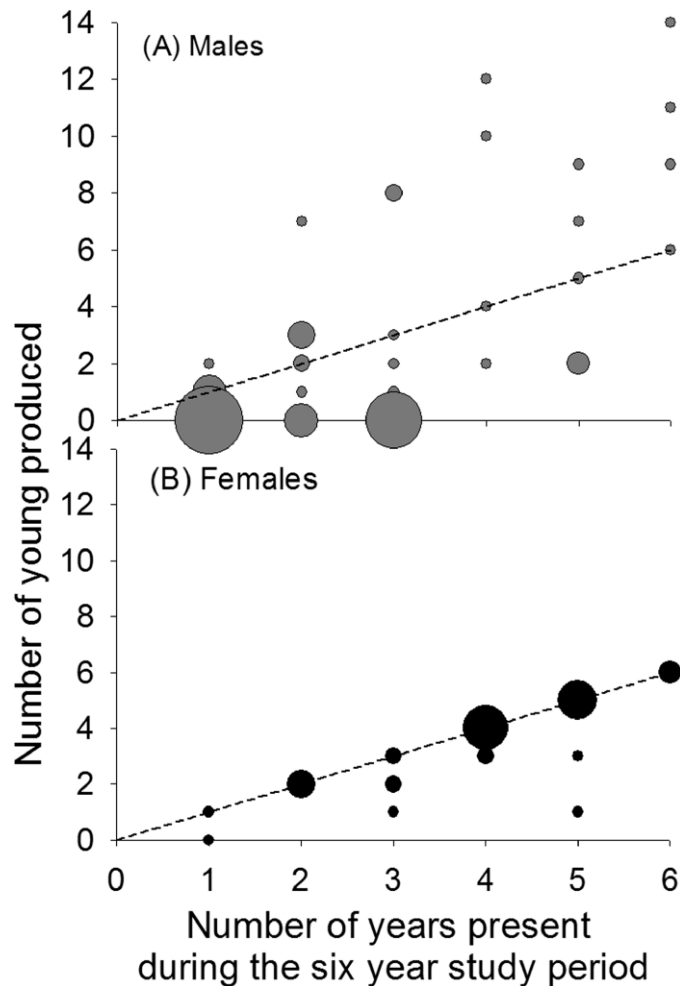
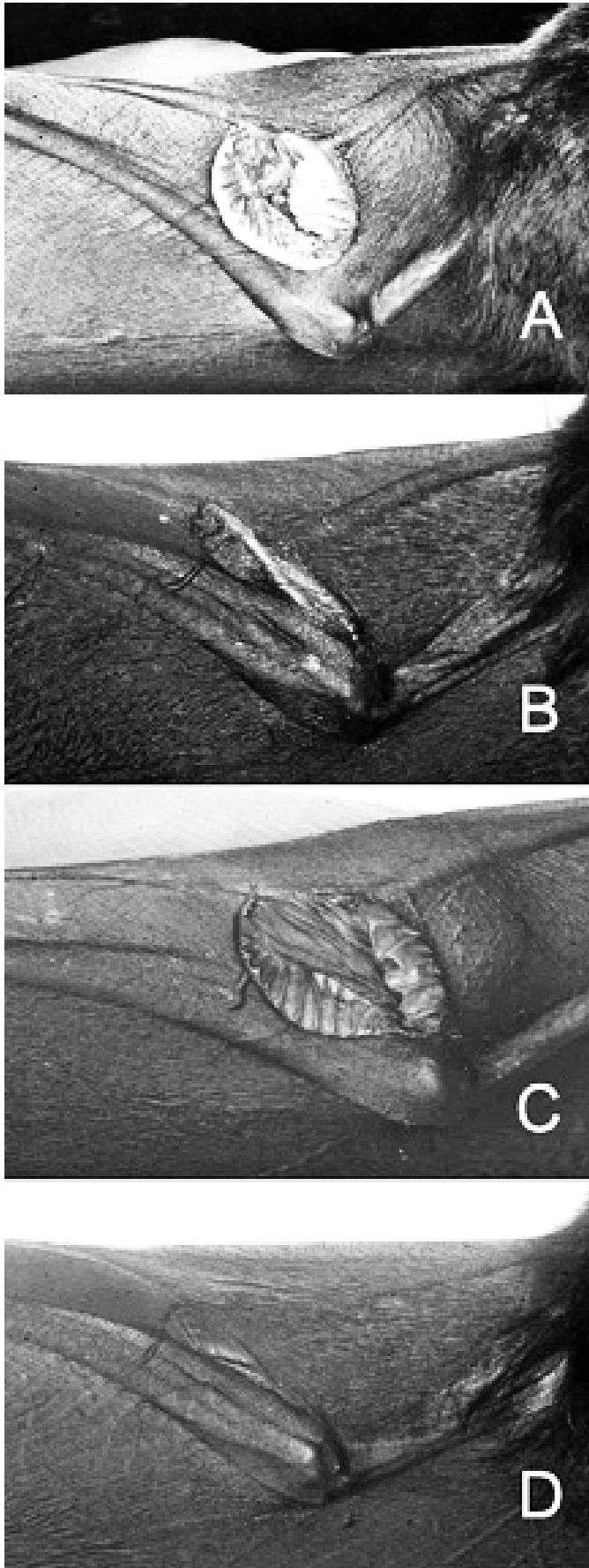


FIG. 3.—Realized reproductive rate of *Saccopteryx bilineata* during a 6-year study period, measured as the number of young produced for A) males (upper graph, gray dots) and B) females (lower graph, black dots). The size of the dots reflects sample size. Dashed lines indicate 1 offspring per year. The fact that data points lie above the dashed line in case of males, but never in case of females, suggests that males have potentially a higher reproductive rate than females.

the harem holder, 45 by other harem males in the colony, 34 by nonharem males, 12 by males resident in a nearby colony, and 12 by unknown males (Voigt et al. 2005b). Despite the high frequency of extraharem young, harem males sire more offspring in larger than in smaller harems (Heckel and von Helversen 2003). Inbreeding avoidance may contribute to the high frequency of extraharem paternities in the mating system of *S. bilineata*. Females with an extraharem offspring were more genetically dissimilar to their extraharem mate than to their harem male (Nagy et al. 2007).

### SEXUAL SELECTION OF THE MALE PHENOTYPE

Sexual selection is influenced most importantly by the divergence of sex-specific potential reproductive rates (Clutton-Brock and Parker 1992). We quantified the reproductive rate of males and females in a colony as an estimate of the sex-specific divergence of this fitness parameter. Only 1 female failed to



produce at least 1 offspring during a 6-year study, whereas 40% of males did not sire any offspring during the same time period (Fig. 3). However, some males were able to produce twice as many offspring as the average female (Fig. 3). In summary, females at most can produce 1 offspring per year, and, therefore, should be choosier than males. Males do not provide any paternal care, are uncertain about the paternity of the young born in their harem territory, but have the capability to produce many more offspring than females. Thus, sexual selection ought to favor male traits that truly reflect a male's quality through means of female choice, or male traits that benefit dominant males during intrasexual competition, or both.

**Morphology.**—In many polygynous mammals, large size of males is beneficial for surveying and defending groups of females, and large, dominant males sire, on average, more offspring than do small, subordinate males (e.g., Anderson and Fedak 1985; Clutton-Brock et al. 1980; also see review in Andersson 1994). *S. bilineata* is sexually dimorphic with males being smaller than females and having a wing sac in the propatagium (Starck 1958). Unlike most polygynous mammals, reproductive success of male *S. bilineata* increases with decreasing size and decreasing fluctuating asymmetry (Voigt et al. 2005b). The correlation between size and reproductive success may be caused by small males being better able to maneuver on the wing at lower energetic costs than large males (Voigt 2000; Voigt et al. 2005b). The correlation between asymmetry and reproductive success may be caused by the fact that symmetric males may have been better able to withstand perturbations of both ecological and genetic nature during juvenile development (Møller and Swaddle 1997). Female *S. bilineata* may then reject asymmetrical mates because symmetry may indicate male quality (Voigt et al. 2005b).

The 2nd obvious morphological feature of male *S. bilineata* is a wing sac with 1 major folding and numerous smaller foldings in each of the antebrachial wing membranes (Scully et al. 2000; Starck 1958; Fig. 4). Males store an odoriferous liquid in their wing sacs and we therefore discuss the function and use of wing sacs in the section about olfactory signals.

**Visual signals.**—Sexually selected visual signals are best described for mammalian species with a lek or polygynous mating system, for example, in ungulates (Clutton-Brock 1982; see review in Andersson 1994). In *S. bilineata*, 2 types of visual signals are obvious, at least to the human observer, that

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**FIG. 4.**—Wing sac in the propatagium of *Saccopteryx bilineata* for A) adult male, showing opened wing sac; B) adult male, showing closed wing sac; C) subadult male, showing opened wing sac; and D) adult female, showing closed wing sac. In males, the opening of the wing sac is formed as 2 lips, a lateral lip adjacent to the forearm and a medial lip at the thoracic side. The interior of the wing sac is whitish in adult males and brownish in subadult males. The interior of the sac is structured by a large fold of the medial lip and 8–14 small folds at each side of the sac. Arrows indicate muscle ligament that attaches to the medial lip (opener of the sac) and to the distal tip of wing sac where both lips touch (closer of the sac).

is, the whitish interior of the wing sacs (Stark 1958) and the frequent hovering displays of males during the mating season (Voigt et al. 2007). The light interior of a male's wing sacs gives short flashes of white when the wing sacs snap open at short time intervals during the hovering display (Voigt and von Helversen 1999). Each time, males lose buoyancy and have to flap their wings a few times to regain their initial position in front of the female. Hovering flight is energetically costly (Voigt and Winter 1999), and it may be particularly exhausting when some wing beats are used to propel air in a vertical direction toward the female instead of providing buoyancy. Accordingly, field metabolic rates of males increase with increasing harem size, that is, with increasing frequency of hovering displays (Voigt et al. 2001). Possibly, females assess the stamina of males by observing the flashes of white when wing sacs open during hovering displays.

*Acoustic signals.*—In mammals, acoustic signaling in the context of sexual selection has been described in a few species such as red deer (*Cervus elaphus*—Clutton-Brock and Albon 1979), house mice (*Mus musculus*—Holy and Guo 2005), and spotted hyenas (*Crocuta crocuta*—East and Hofer 1991). Among bats, many species use intricate vocalizations to attract mates (e.g., Bradbury 1977b; Russ and Racey 2007; Wilkinson 2003), and *S. bilineata* is probably the most thoroughly studied species of bat with respect to its vocal repertoire.

Bradbury and Emmons (1974) were the 1st to describe the vocal repertoire of male and female *S. bilineata* in combination with the social context, mostly from populations in Trinidad (see also Tannenbaum 1975). One of the vocalizations uttered by males was termed the “song” and it was hypothesized that songs help males to attract or retain females in their territories (Bradbury and Emmons 1974). Davidson and Wilkinson (2002) differentiated the vocal repertoire of *S. bilineata* from Trinidad into 21 simple and 62 composite syllable types. An analysis of vocalizations from males revealed that the number of females roosting in territories of males was positively correlated with the duration and negatively correlated with the number and spectral frequency of a component of the most commonly recorded vocalization type, the screech–inverted-V call (Davidson and Wilkinson 2004). Males differed in peak frequency, duration, and bandwidth of this call type (Davidson and Wilkinson 2002), which might facilitate individual recognition. The screech–inverted-V call resembles the “whistle” described by Behr and von Helversen (2004) that is uttered during the hovering display of males and presumably forms part of the complex multimodal courtship behavior of males. Females respond with screeches to whistles of males, which suggests an antiphonal calling of the sexes.

Males of *S. bilineata* have a complex vocal repertoire with different, often multisyllabic vocalization types used in specific social interactions (Behr and von Helversen 2004; Fig. 5). Courtship songs are used by males during courtship, and territorial songs are used during territorial interactions among males, and therefore both are presumably under the influence of sexual selection. Males utter courtship songs only when they display toward a female; these songs are sometimes uttered over several minutes continuously, and they are complex,

consisting of highly variable syllables. Multivariate analyses of the most common syllable type (“trill”) showed that males could be distinguished by their repertoires. Thus, males showed consistent differences in courtship songs that should facilitate individual recognition and could be used in female mate choice (Behr and von Helversen 2004).

Territorial songs, on the contrary, are short, rather stereotyped, not obviously directed toward certain conspecifics, and uttered in the context of male competition for harem territories (Behr et al. 2006). Males engage in territorial countersinging when reoccupying their day-roost territories in the morning and in the evening before emerging from the colony. Territorial songs are individually distinct. The reproductive success of harem territory holders is higher in individuals that utter more territorial songs per day and that produce long buzz syllables with a lower end frequency (Behr et al. 2006). Long buzzes mostly terminate songs and have a harsh quality due to a pulsation of the fundamental frequency at the syllable onset. They also have the highest sound pressure level of all syllable types in territorial songs. Territorial songs and especially long buzz syllables are likely to advertise the quality and competitive ability of harem territory holders, because high-quality males can bear the supposedly high costs more easily (Behr et al. 2006). Playback experiments that one of us (OB) has performed with territorial songs as stimuli show that low-frequency stimuli elicited a higher countersong rate and longer songs than high-frequency stimuli in the countersong response of territorial males. Thus, males of *S. bilineata* seem to adjust the strength of their territorial signaling response to the fundamental frequency of the stimuli and may perceive low-frequency territorial songs as a more serious threat than high-frequency songs.

Even though courtship and territorial songs are uttered solely by males in adulthood, juveniles of both sexes produce vocalizations resembling elements from courtship and territorial songs during vocal ontogeny. These vocalizations are combined with vocalizations resembling all other known adult vocalization types to form long babbling bouts (Knörnschild et al. 2006). Possibly, infant babbling is necessary during vocal ontogeny of *S. bilineata* to acquire the complex vocal repertoire at adulthood. The fact that juvenile females produce vocalization types that they will not use during adulthood might be explained by the need to create an acoustic template of male songs as a basis for later mate-choice decisions, as shown in birds (Marler and Peters 1982).

*Olfactory signals.*—The importance of chemical signals as an honest signal in mate choice has been demonstrated in many animal taxa (reviewed in Wyatt 2003). Individual odors allow potential mates to discriminate individuals of lower social status (Gosling and Roberts 2001) or poor health (Kavaliers et al. 2003; Zala et al. 2004), and they allow individuals to gain information about group affiliation, sex (Hayes et al. 2002; Hofer et al. 2001; Safi and Kerth 2003), or compatible genotypes (Penn and Potts 1998). Chemical signals seem particularly suitable for mate choice, because chemical signals are inevitable by-products of everyday life, and, therefore, difficult to cheat with. They may reflect the momentary health

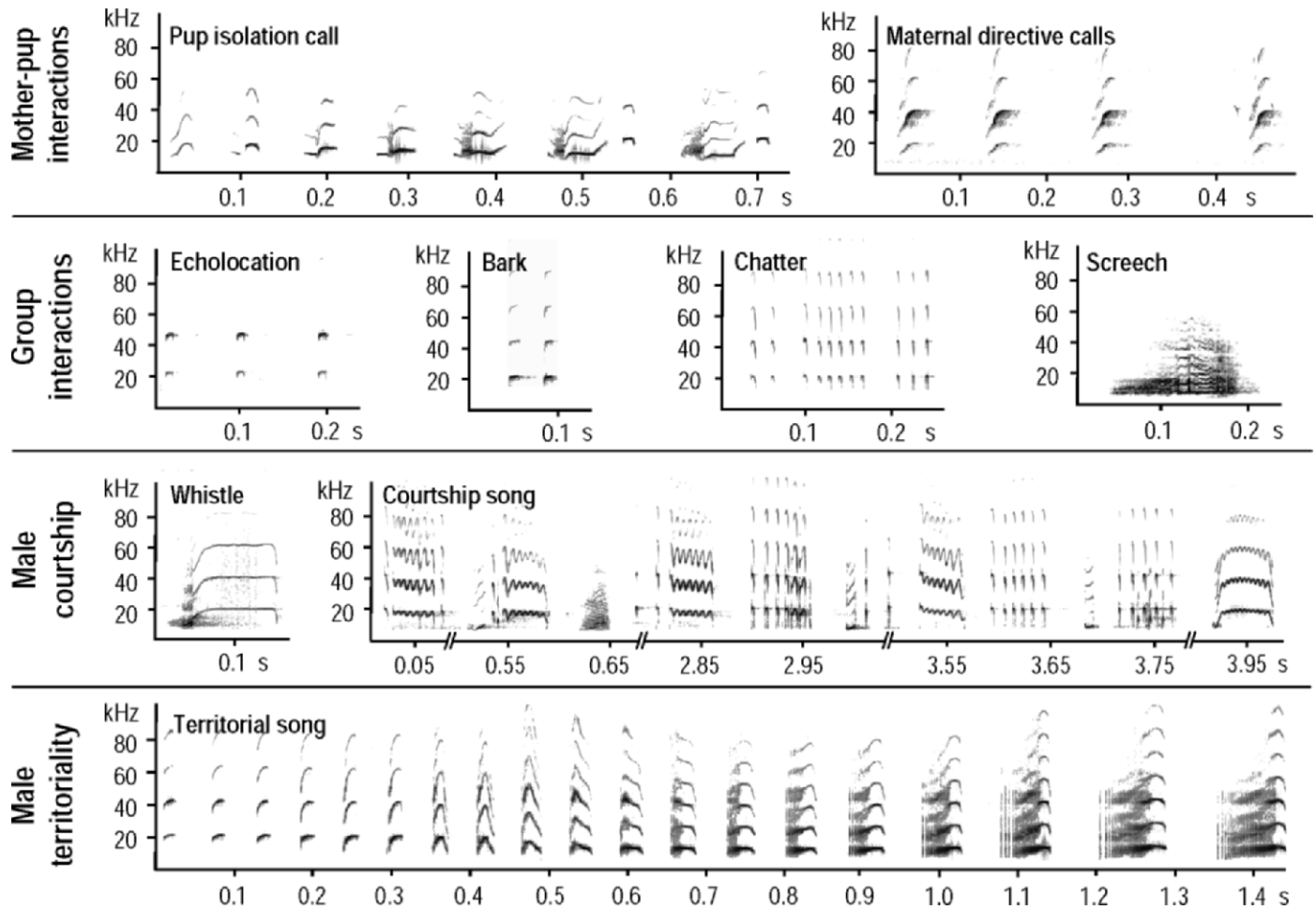


FIG. 5.—The most common vocalization types in the acoustic repertoire of adult and juvenile *Saccopteryx bilineata*. The sonogram plots frequency in kilo-Hertz as a function of time in seconds (1,024-point fast Fourier transform, Hamming window with 75% overlap). After a figure by Behr and von Helversen originally published in *Behavioral Ecology and Sociobiology* 56(2):106–115, June 2004. Reprinted with kind permission of Springer Science + Business Media.

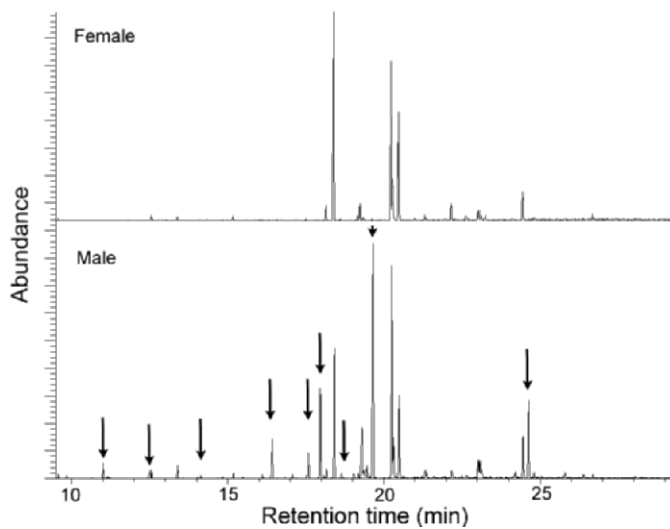


FIG. 6.—Volatile compounds of wing sacs in adult a) female and b) male *Saccopteryx bilineata*, measured by gas chromatography. Abundance is indicated as the intensity of the detector signal, which is plotted against retention time of the compounds (min). Male-specific compounds are marked with arrows (modified from Caspers 2008).

status or parasite load of the carrier, or they may carry information about the immune system, such as the major histocompatibility complex (Penn and Potts 1998, 1999).

Males of *S. bilineata* use various chemical signals for social communication (Voigt et al. 2007; Voigt and von Helversen 1999). Males are best known for their antebrachial wing sacs, which contain an odoriferous liquid. Each day, males refill the content of these sacs during a time-consuming 2-stage process called perfume-blending. First, males clean their wing sacs with urine and then transfer secretions from various body regions, such as mouth and genital area, into the wing sacs (Voigt 2002; Voigt and von Helversen 1999). Males possibly control microbial growth in the wing sacs by cleaning them daily, thus preventing an uncontrolled degradation of their sequestered volatiles (Voigt et al. 2005a).

Wing sac odors of males consist mainly of terpenoids, aromatic compounds, and fatty acids, of which 9 are specific to males (Caspers et al. 2008; Fig. 6). Three of the 9 male-specific substances occur only in wing sacs of adult males and are therefore most likely influenced by hormonal changes during puberty (Caspers 2008). Apart from information about sexual

maturity, wing sac odors encode information about species, sex, and individual identity as well as reproductive status (Caspers et al. 2008), all being important when females assess potential mates and, hence, all probably shaped by female choice to varying extents. In odor choice experiments, females preferred the odor of male conspecifics over that of males from the sister taxon *S. leptura*. In addition to interspecific communication, males of *S. bilineata* use chemicals in intraspecific communication, such as territorial scent-marking (Voigt and von Helversen 1999). Males of *S. bilineata* scent-mark the borders of their harem territory almost daily by pressing their submandibular region onto the substrate they are hanging on and by turning their head alternately left and right, each time releasing a droplet of secretion (Caspers 2008; Voigt and von Helversen 1999). Males scent-mark more often before and during the mating season than afterward (Caspers 2008). Scent-marking of male *S. bilineata* fits well with the assessment or scent-matching hypothesis, which states that males may provide competitors the possibility for an olfactory association between the scent-mark and the harem territory owner (Gosling 1982, 1990). Scent-matching also may be relevant during salting, a behavior in which harem territory owners fan the scent of their wing sacs toward a male in a neighboring harem territory (Caspers 2008).

*Open questions.*—This review describes the social organization and mating behavior involving sexually selected visual, acoustic, and olfactory cues in *S. bilineata*. Some important questions regarding sexually selected signals in *S. bilineata* are still unanswered. Most importantly, we lack information about the causal mechanisms underlying sexual selection in *S. bilineata*, because our current knowledge is based purely on correlational data. Despite the evidence for multiple characters correlating with reproductive success of males, we currently know nothing about their relative importance in female choice. Meanwhile, we have begun behavioral experiments involving acoustic and olfactory cues, which provide a promising approach for disentangling the causal factors for mate-choice decisions. Furthermore, it is unclear whether females choose their mating partner based on the quantity of certain odor compounds, that is, specific sexual pheromones, or whether they choose a chemical profile, or blend, that correlates with male traits such as the major histocompatibility complex (Mayer and Brunner 2007). Lastly, we do not know whether *S. bilineata* exhibits a typical mating system of a bat species in the tropics or, rather, whether this species is an exception. A comparative approach of closely and more distantly related species could help to reconstruct the evolution of the highly derived behavior of *S. bilineata*, and to understand underlying evolutionary mechanisms.

## RESUMEN

Como en otros mamíferos, *Saccopteryx bilineata* presenta un sistema de apareamiento poligínico, en el cual el macho defiende un grupo de hembras llamado harén. Las colonias están formadas por algunos grupos de harenes, y los machos solitarios perchan junto a éstos. Al contrario que en la mayoría

de los mamíferos, las hembras se dispersan de su colonia natal y los machos jóvenes permanecen en éstas. De este modo, las colonias constituyen patrilineas las cuales promueven la competencia local entre machos. Las hembras entran en estro durante algunas semanas al final de la época de lluvia. El apareamiento suele ser iniciado por las hembras y es precedido por un intenso cortejo desplegado por los machos. Cuarenta por ciento de los machos de la colonia no son responsables de la paternidad de ninguna cría durante su permanencia en la colonia, mientras que algunos machos pueden ser padres de hasta 6 crías en un solo año. Los machos usan señales olfativas, visuales y acústicas para el cortejo, y delimitan el territorio con marcas olfativas, llamadas de baja frecuencia, y despliegues visuales. Los machos asociados a los harenes son padres de más crías que los machos solitarios, pero únicamente tienen la paternidad del 30% de las crías de su harén, mientras que el 70% de la paternidad es adjudicada a machos de otro harén o a machos solitarios. El éxito reproductivo de los machos se incrementó con la reducción en tamaño, la asimetría fluctuante y la frecuencia básica de las llamadas territoriales. Además, las hembras que presentaban parentesco cercano con el macho del harén tendían a reproducirse con machos ajenos al harén. La selección sexual en *S. bilineata* está muy probablemente influenciada por la intensa competencia local causada por los escasos refugios y por la organización patrilineal de las colonias.

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## LITERATURE CITED

- ANDERSON, S. S., AND M. A. FEDAK. 1985. Grey seal males: energetic and behavioural links between size and sexual success. *Animal Behaviour* 33:928–938.
- ANDERSSON, M. A. 1994. *Sexual selection*. Princeton University Press, Princeton, New Jersey.
- BARCLAY, R. M. R. 1983. Echolocation calls of emballonurid bats from Panama. *Journal of Comparative Physiology, A. Sensory, Neural, and Behavioral Physiology* 151:515–520.
- BEHR, O., AND O. VON HELVERSEN. 2004. Bat serenades—complex courtship songs of the sac-winged bat (*Saccopteryx bilineata*). *Behavioral Ecology and Sociobiology* 56:106–115.
- BEHR, O., O. VON HELVERSEN, G. HECKEL, M. NAGY, C. C. VOIGT, AND F. MAYER. 2006. Territorial songs indicate male quality in the sac-winged bat *Saccopteryx bilineata* (Chiroptera, Emballonuridae). *Behavioral Ecology* 17:810–817.
- BRADBURY, J. W. 1977a. Social organization and communication. Pp. 1–72 in *Biology of bats* (W. A. Wimsatt, ed.). Vol. III. Academic Press, London, United Kingdom.



- BRADBURY, J. W. 1977b. Lek mating behavior in the hammer-headed bat. *Zeitschrift für Tierpsychologie* 45:225–255.
- BRADBURY, J. W., AND L. EMMONS. 1974. Social organization of some Trinidad bats. I: Emballonuridae. *Zeitschrift für Tierpsychologie* 36:137–183.
- BRADBURY, J. W., AND S. L. VEHRENCAMP. 1976. Social organization and foraging in emballonurid bats. I: field studies. *Behavioral Ecology and Sociobiology* 1:337–381.
- BRADBURY, J. W., AND S. L. VEHRENCAMP. 1977. Social organization and foraging in emballonurid bats. III: mating systems. *Behavioral Ecology and Sociobiology* 2:1–17.
- CASPERS, B. 2008. Olfactory communication in the greater sac-winged bat, *Saccopteryx bilineata*. Ph.D. dissertation, Humboldt University, Berlin, Germany.
- CASPERS, B., S. FRANKE, AND C. C. VOIGT. 2008. The wing sac odour of male greater sac-winged bats *Saccopteryx bilineata* (Emballonuridae) as a composite trait: seasonal and individual differences. Pp. 151–160 in *Chemical signals in vertebrates XI* (J. Hurst, R. J. Beynon, S. C. Roberts, and T. D. Wyatt, eds.). Springer-Verlag, Berlin, Germany.
- CLUTTON-BROCK, T. H. 1982. The functions of antlers. *Behaviour* 79:108–125
- CLUTTON-BROCK, T. H. 1989a. Review lecture: mammalian mating systems. *Proceedings of the Royal Society of London, B. Biological Sciences* 236:339–372.
- CLUTTON-BROCK, T. H. 1989b. Female transfer and inbreeding avoidance in social mammals. *Nature* 337:70–72.
- CLUTTON-BROCK, T. H. 1991. *The evolution of parental care*. Princeton University Press, Princeton, New Jersey.
- CLUTTON-BROCK, T. H., AND S. D. ALBON. 1979. The roaring of red deer and the evolution of honest advertisement. *Behaviour* 69:145–170.
- CLUTTON-BROCK, T. H., S. D. ALBON, AND P. H. HARVEY. 1980. Antlers, body size and breeding group size in the Cervidae. *Nature* 285:565–567.
- CLUTTON-BROCK, T. H., AND P. H. HARVEY. 1978. Mammals, resources and reproductive strategies. *Nature* 273:191–195.
- CLUTTON-BROCK, T. H., AND K. ISVARAN. 2006. Paternity loss in contrasting mammalian societies. *Biology Letters* 2:513–516.
- CLUTTON-BROCK, T. H., AND G. A. PARKER. 1992. Potential reproductive rates and the operation of sexual selection. *Quarterly Review of Biology* 67:437–456.
- DAVIDSON, S. M., AND G. S. WILKINSON. 2002. Geographic and individual variation in vocalizations by male *Saccopteryx bilineata* (Chiroptera: Emballonuridae). *Journal of Mammalogy* 83:526–535.
- DAVIDSON, S. M., AND G. S. WILKINSON. 2004. Function of male song in the greater white-lined bat, *Saccopteryx bilineata*. *Animal Behaviour* 67:883–891.
- DECHMANN, D. K. N., E. K. V. KALKO, AND G. KERTH. 2007. All-offspring dispersal in a tropical mammal with resource defence polygyny. *Behavioral Ecology and Sociobiology* 61:1219–1228.
- EAST, M. L., AND H. HOFER. 1991. Loud-calling in a female-dominated society: II. Behavioural contexts and functions of whooping of spotted hyaenas, *Crocuta crocuta*. *Animal Behaviour* 42:651–669.
- GANNON, W. L., R. S. SIKES, AND THE ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMALOGISTS. 2007. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy* 88:809–823.
- GOSLING, L. M. 1982. A reassessment of the function of scent marking in territories. *Zeitschrift für Tierpsychologie* 60:89–118.
- GOSLING, L. M. 1990. Scent marking by resource holders: alternative mechanisms for advertising the costs of competition. Pp. 315–328 in *Chemical signals in vertebrates V* (D. W. Macdonald, D. Mueller-Schwarze, and S. E. Natynczuk, eds.). Oxford University Press, Oxford, United Kingdom.
- GOSLING, L. M., AND S. C. ROBERTS. 2001. Scent-marking by male mammals: cheat-proof signals to competitors and mates. *Advances in the Study of Behavior* 30:169–217.
- GREENWOOD, P. J. 1980. Mating systems philopatry and dispersal in birds and mammals. *Animal Behaviour* 28:1140–1162.
- HAYES, R. A., B. J. RICHARDSON, S. C. CLAUS, AND S. G. WYLLIE. 2002. Semiochemicals and social signalling in the wild European rabbit in Australia: II. Variations in chemical composition of chin gland secretion across sampling sites. *Journal of Chemical Ecology* 28:2613–2625.
- HECKEL, G., C. C. VOIGT, F. MAYER, AND O. VON HELVERSEN. 1999. Extra-harem paternity in the white-lined bat *Saccopteryx bilineata*. *Behaviour* 136:1173–1185.
- HECKEL, G., AND O. VON HELVERSEN. 2002. Male tactics and reproductive success in the harem polygynous bat *Saccopteryx bilineata*. *Behavioral Ecology* 12:219–227.
- HECKEL, G., AND O. VON HELVERSEN. 2003. Genetic mating system and the significance of harem associations in the bat *Saccopteryx bilineata*. *Molecular Ecology* 12:219–227.
- HOFER, H., M. EAST, I. SÄMMANG, AND M. DEHNHARD. 2001. Analysis of volatile compounds in scent-marks of spotted hyenas (*Crocuta crocuta*) and their possible function in olfactory communication. Pp. 141–148 in *Chemical signals in vertebrates IX* (A. Marchlewski-Koj, J. J. Lepri, and D. Müller-Schwarze). Kluwer Academic/Plenum Publishers, New York.
- HOFFMANN, F. F., J. HEJDUK, B. CASPERS, B. M. SIEMERS, AND C. C. VOIGT. 2007. In bat mating systems auditory constraints prevent efficient female surveillance by eavesdropping male bats. *Canadian Journal of Zoology* 85:863–872.
- HOLY, T. E., AND Z. GUO. 2005. Ultrasonic songs of male mice. *PLoS Biology* 3:2177–2186.
- JUNG, K., E. K. V. KALKO, AND O. VON HELVERSEN. 2007. Echolocation calls in Central American emballonurid bats: signal design and call frequency alternation. *Journal of Zoology (London)* 272:125–137.
- KAVALIERS, M., D. D. COLWELL, W. J. BRAUN, AND E. CHOLERIS. 2003. Brief exposure to the odour of a parasitized male alters the subsequent mate odour responses of female mice. *Animal Behaviour* 65:59–68.
- KNÖRNCHILD, M., O. BEHR, AND O. VON HELVERSEN. 2006. Babbling behavior in the sac-winged bat (*Saccopteryx bilineata*). *Naturwissenschaften* 93:451–454.
- KUNZ, T. H., AND W. HOOD. 2000. Parental care and postnatal growth in the Chiroptera. Pp. 415–468 in *Reproductive biology of bats* (G. Crichton and P. H. Krutzsch, eds.). Academic Press, New York.
- LAWSON HANDLEY, J. L., AND N. PERRIN. 2007. Advances in our understanding of mammalian sex-biased dispersal. *Molecular Ecology* 16:1559–1578.
- LIM, B. H., M. D. ENGSTROM, J. W. BICKHAM, AND J. C. PATTON. 2008. Molecular phylogeny of New World sheath-tailed bats (Emballonuridae: Diclidurini) based on loci from the four genetic transmission systems in mammals. *Biological Journal of the Linnean Society* 93:189–209.
- MARLER, P., AND S. PETERS. 1982. Subsong and plastic song: their role in the vocal learning process. Pp. 25–50 in *Acoustic communication in birds* (D. E. Kroodsma, E. H. Miller, and O. Ouellet Henri, eds.). Academic Press, New York.
- MAYER, F., AND A. BRUNNER. 2007. Non-neutral evolution of the major histocompatibility complex class II gene *DRB1* in the sac-winged bat *Saccopteryx bilineata*. *Heredity* 99:257–264.

- McCracken, G. F. 1984. Social dispersion and genetic variation in two species of emballonurid bats. *Zeitschrift für Tierpsychologie* 66:55–69.
- McCracken, G. F., and G. S. Wilkinson. 2002. Bat mating systems. Pp. 321–362 in *Reproductive biology of bats* (E. G. Crichton and P. H. Krutzsch, eds.). Academic Press, San Diego, California.
- Møller, A. P., and J. P. Swaddle. 1997. Asymmetry, developmental stability, and evolution. Oxford University Press, Oxford, United Kingdom.
- Muñoz, J., and C. A. Cuartas. 2001. *Saccopteryx antiquiensis* n. s. (Chiroptera: Emballonuridae) del noroeste de Colombia. *Actualidades Biológicas* 23:53–61.
- Nagy, M., G. Heckel, C. C. Voigt, and F. Mayer. 2007. Female-biased dispersal and patrilocal kin groups in a mammal with resource-defence polygyny. *Proceedings of the Royal Society of London, B. Biological Sciences* 274:3019–3025.
- Penn, D., and W. J. Potts. 1998. Chemical signals and parasite mediated sexual selection. *Trends in Ecology and Evolution* 13: 391–396.
- Penn, D., and W. J. Potts. 1999. The evolution of mating preferences and major histocompatibility complex genes. *American Naturalist* 153:145–164.
- Russ, J. M., and P. A. Racey. 2007. Species-specificity and individual variation in the song of male Nathusius' pipistrelles (*Pipistrellus nathusii*). *Behavioral Ecology and Sociobiology* 61: 669–677.
- Safi, K., and G. Kertth. 2003. Secretions of the interaural gland contain information about individuality and colony membership in the Bechstein's bat. *Animal Behaviour* 65:363–369.
- Scully, W. M., M. B. Fenton, and A. S. M. Saleuddin. 2000. A histological examination of holding sacs and scent glandular organs of some bats (Emballonuridae, Hipposideridae, Phyllostomidae, Vespertilionidae and Molossidae). *Canadian Journal of Zoology* 78:613–623.
- Starck, D. 1958. Beitrag zur Kenntnis der Armtaschen und anderer Hautdrüsenorgane von *Saccopteryx bilineata* Temminck 1838 (Chiroptera Emballonuridae). *Gegenbaur Morphologisches Jahrbuch* 99:3–25.
- Tannenbaum, R. 1975. Reproductive strategies in the white-lined bat. Ph.D. dissertation, Cornell University, Ithaca, New York.
- Trivers, R. L. 1972. Parental investment and sexual selection. Pp. 136–176 in *Sexual selection and the descent of man, 1871–1971* (B. Campbell, ed.). Heinemann, London, United Kingdom.
- Voigt, C. C. 2000. Intraspecific scaling of flight costs in the bat *Glossophaga soricina* (Phyllostomidae). *Journal of Comparative Physiology, B. Biochemical, Systemic, and Environmental Physiology* 170:403–410.
- Voigt, C. C. 2002. Individual variation of perfume-blending in male sac-winged bats. *Animal Behaviour* 63:907–913.
- Voigt, C. C. 2003. Sac-winged bats, sheath-tailed bats, and ghosts bats (Emballonuridae). Pp. 355–365 in *Grizmek's life encyclopedia: mammals II* (D. G. Kleiman, V. Geist, M. Hutchins, and M. C. McDade, eds.). Vol. 13. Gale Group, Farmington Hills, Michigan.
- Voigt, C. C., B. Caspers, and S. Speck. 2005a. Bats, bacteria and bat smell: sex-specific diversity of microbes in a sexually selected scent organ. *Journal of Mammalogy* 86:745–749.
- Voigt, C. C., G. Heckel, and F. Mayer. 2005b. Sexual selection favours small and symmetric males in the polygynous greater sac-winged bat *Saccopteryx bilineata* (Emballonuridae, Chiroptera). *Behavioral Ecology and Sociobiology* 57:457–464.
- Voigt, C. C., G. Heckel, and O. von Helversen. 2006. Conflicts and strategies in the harem-polygynous mating system of the sac-winged bat *Saccopteryx bilineata*. Pp. 269–278 in *Functional and evolutionary ecology of bats* (G. McCracken, A. Zubaid, and T. H. Kunz, eds.). Oxford University Press, Oxford, United Kingdom.
- Voigt, C. C., and F. Schwarzenberger. 2008. Reproductive endocrinology of a small tropical bat (female *Saccopteryx bilineata*; Emballonuridae) monitored by fecal hormone metabolites. *Journal of Mammalogy* 89:50–57.
- Voigt, C. C., and W. J. Streich. 2003. Queuing for harem access in colonies of the sac-winged bat. *Animal Behaviour* 65:149–156.
- Voigt, C. C., W. J. Streich, and M. Dehnhard. 2007. Assessment of fecal testosterone metabolite analysis in free-ranging *Saccopteryx bilineata* (Chiroptera; Emballonuridae). *Acta Chiropterologica* 9:463–476.
- Voigt, C. C., and O. von Helversen. 1999. Storage and display of odor by male *Saccopteryx bilineata* (Chiroptera; Emballonuridae). *Behavioral Ecology and Sociobiology* 47:29–40.
- Voigt, C. C., O. von Helversen, R. Michener, and T. H. Kunz. 2001. The economics of harem maintenance in the sac-winged bat, *Saccopteryx bilineata*. *Behavioral Ecology and Sociobiology* 50:31–36.
- Voigt, C. C., and Y. Winter. 1999. The energetic costs of hovering flight in nectar-feeding bats (Phyllostomidae, Glossophaginae) and its scaling in sphingid moths, hummingbirds and bats. *Journal of Comparative Physiology, B. Biochemical, Systemic, and Environmental Physiology* 169:38–48.
- Wilkinson, G. S. 2003. Social and vocal complexity in bats. Pp. 322–341 in *Animal social complexity: intelligence, culture and individualized societies* (F. B. M. de Waal and P. L. Tyack, eds.). Harvard University Press, Cambridge, Massachusetts.
- Wyatt, T. D. 2003. Pheromones and animal behaviour. Cambridge University Press, Cambridge, United Kingdom.
- Zala, S. M., W. K. Potts, and D. J. Penn. 2004. Scent-marking displays provide honest signals of health and infection. *Behavioral Ecology* 15:338–344.

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