

Chapter 8

Sexually Selected Vocalizations of Neotropical Bats

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Abstract Acoustic signals are by far the best studied component of bats' social communication. Various different vocalization types cover diverse social interactions, which are either under natural selection pressures, such as mother–pup recognition and group cohesion, or under sexual selection pressures, such as male–male aggression, territoriality, and courtship. Here, we summarize the current knowledge about sexually selected vocalizations in Neotropical bats. Specifically, we highlight research findings on sexually selected vocalizations in two species whose social organization and natural history are well understood, namely Seba's Short-tailed Bat *Carollia perspicillata* (Phyllostomidae) and the Greater Sac-winged Bat *Saccopteryx bilineata* (Emballonuridae). Males of both species exhibit resource-defense polygyny and use distinct vocalizations during aggressive male–male interactions and to announce territory ownership. While territorial vocalizations are structurally more complex in *S. bilineata* than in *C. perspicillata*, the latter species uses a more sophisticated, ritualized suite of behavioral displays to mediate male–male aggression than *S. bilineata*. Moreover, males of both species exhibit acoustic courtship which displays with differing degrees of complexity. In *S. bilineata*, courtship vocalizations are long and elaborate, while courtship vocalizations of *C. perspicillata* are comparatively simpler, with one variable syllable repeated in succession. As a synopsis, we discuss whether differences in social organization and behavioral interactions may have implications for the structural complexity and information content of sexually selected vocalizations.

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8.1 Vocalizations of Neotropical Bats Under Different Selection Pressures

Bats' ability to orient and forage by echolocation is enabled by their fine-tuned neural control over their vocal tract (reviewed in Neuweiler 2003). Since echolocation can be a preadaptation for sophisticated vocal communication, bats are an ideal taxon to investigate the interplay of vocal communication and social organization in highly diverse species. Compared to echolocation calls, bats' social vocalizations are still understudied (reviewed in Fenton 1985, Wilkinson 2003). Most investigations focus on selected vocalization types, making studies of species-specific vocal repertoires particularly rare. The few thorough investigations available for Neotropical bats describe the vocal repertoires of only few species, namely Mexican Free-Tailed Bats *Tadarida brasiliensis* (Bohn et al. 2008), Lesser Bulldog Bats, *Noctilio albiventris* (Brown et al. 1983), Pallas's Long-Tongued Bats, *Glossophaga soricina*, and Commissaris's Long-Tongued Bats, *Glossophaga commissarisi* (Knörnschild et al. 2010a), Seba's Short-Tailed Bats, *Carollia perspicillata* (Porter 1979a, b; Straub and Esser 2000; Knörnschild 2014), and Greater Sac-Winged Bats, *Saccopteryx bilineata* (Bradbury and Emmons 1974, Davidson and Wilkinson 2004, Behr and von Helversen 2004).

In contrast to vocal repertoire descriptions, studies focusing on one or a few selected vocalization types are more common; those studies can deepen our understanding of how specific vocalizations are acquired and what selective pressures act on them. Generally speaking, bat vocalizations can either be under natural or sexual selection pressures. Natural selection pressures act on vocalizations produced in the context of mother–pup recognition, e.g., in Greater Spear-Nosed Bats, *Phyllostomus hastatus* (Bohn et al. 2007), Pale Spear-Nosed Bats, *P. discolor* (Esser and Schmidt 1989), *T. brasiliensis* (Balcombe 1990), *C. perspicillata* (Knörnschild et al. 2013), and *S. bilineata* (Knörnschild and von Helversen 2008), or in the context of group cohesion/coordination, e.g., in White-Winged Vampire Bats, *Diaemus youngii* (Carter et al. 2009), Spix's Disc-Winged Bats, *Thyroptera tricolor* (Chaverri et al. 2013), and *P. hastatus* (Wilkinson and Boughman 1998). Sexual selection pressures, on the other hand, act on vocalizations produced in the context of territoriality, male–male aggression, and courtship. Only three Neotropical bat species have been studied thoroughly with regard to their sexually selected vocalizations: Mexican Free-Tailed Bats, *T. brasiliensis* (Bohn et al. 2008, 2009, 2013; see also chap. 6 in this book), Seba's Short-Tailed Bats, *C. perspicillata* (Porter 1979b; Knörnschild et al. 2014, Fernandez et al. 2014), and Greater Sac-Winged Bats, *S. bilineata* (Bradbury and Emmons 1974, Tannenbaum 1975, Davidson and Wilkinson 2004, Behr and von Helversen 2004). The latter two species (Fig. 8.1) shall be used as a case study in this chapter to discuss whether differences in natural history, social organization, and behavioral interactions lead to differences in the structural complexity and information content of sexually selected vocalizations.

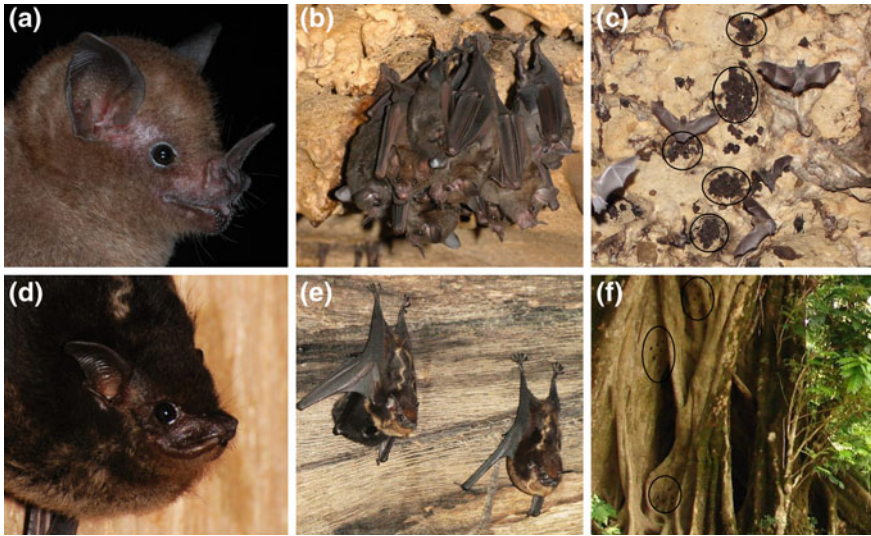


Fig. 8.1 Focal species *C. perspicillata* and *S. bilineata*. *Top panel* (*C. perspicillata*) Lateral view of head (a), harem group (b), and roosting sites of five harem groups in a mixed-species cave (c). *Bottom panel* (*S. bilineata*) Lateral view of head (d), excerpt of harem group depicting the harem male and one female with pup (e), and roosting sites of three harem groups on a tree (f). Harem groups are marked with black circles (c, f). *Photo credits* M. Tschapka (a, b), T. Hiller (c), M. Knörnschild (d, e, f)

8.2 Seba's Short-Tailed Bat *Carollia perspicillata*

Seba's Short-tailed Bat *C. perspicillata* is a common and widely distributed frugivorous generalist in the Neotropics (Cloutier and Thomas 1992). It is a gregarious species that often uses caves or hollow trees as day-roosts (Williams 1986; Fleming 1988; Fig. 8.1).

8.2.1 Social Organization of *C. perspicillata*

Male *C. perspicillata* defend roosting territories against male competitors and allow females to roost there and join their harem; thus, the mating system is a resource defense polygyny (Porter 1979a; Williams 1986; Fleming 1988). Several harem territories as well as bachelor groups, solitary bachelors, and mixed-sex subadult groups can be found in the same day-roost (Porter 1978, 1979a; Williams 1986). Compared to bachelor males, harem males are older and heavier but not always larger (Williams 1986). Harem males abandon their territories only after being displaced or when taking over a competitor's territory that is superior to their current one (i.e. has more females roosting in it; Williams 1986) and male tenure as

harem holders can last up to 2 years (total tenure in all territories averages 277 days; Williams 1986). Displaced harem males sometimes establish a new territory elsewhere in the day-roost (Porter 1979a; Williams 1986). At night, harem males often return to their territories, presumably to defend them against potential intruders, whereas females and bachelor males normally do not return to the day-roost (Williams 1986). Roost site characteristics seem to be more important than male characteristics when females choose a territory to roost in (Williams 1986; Fleming 1988); however, it is unclear what females prefer exactly. Individual females rarely form long-term associations with each other and do not react aggressively toward new females joining their groups (Williams 1986; Fleming 1988). Even though males cannot prevent females from switching freely between harem territories (Porter 1979a, 1978; Williams 1986), females nevertheless spend a lot of their time (62 %) in one primary harem (Williams 1986; Fleming 1988). Harem size can be quite large (up to 18 females plus their current offspring; Williams 1986). Females can bear a single offspring twice per year and have moderately synchronized parturition within the same population (Williams 1986; Fleming 1988). Offspring dispersal from the natal colony seems to be slightly female biased; however, pups of both sexes may also remain in their natal colony, in which case they only leave their natal harem territory (Fleming 1988). Females are intensely courted by the harem males during their postpartum estrus (3–10 days after birth; Badwaik and Rasweiler 2000). Even though harem males have priority access to estrus females roosting in their territories (and thus the potential to father the females' subsequent offspring), they normally have not fathered the females' current offspring because females switched between territories in the past (Porter and McCracken 1983). Since both bachelor and neighboring harem males attempt to gain access to estrus females as well, harem males are regularly engaged in aggressive interactions with competitors (Fernandez et al. 2014).

8.2.2 Sexually Selected Vocalizations of *C. perspicillata*

The vocal repertoire of *C. perspicillata* has been described in considerable depth so far (Porter 1979b; Straub and Esser 2000; Knörnschild et al. 2013, 2014; Fernandez et al. 2014), with observations coming from captive colonies only. *C. perspicillata* produce four different vocalization types in social contexts that are under sexual selection pressure, namely territorial rival deterrence, aggressive male–male interactions, and courtship (Knörnschild 2014, Fig. 8.2, 8.3 and 8.4). These vocalization types are explained in detail below.

8.2.2.1 Territorial Rival Deterrence

At dusk and dawn, when bats are most active in the day-roost, harem males often hang from a prominent spot at the territory perimeter (e.g. from the outer rim of a

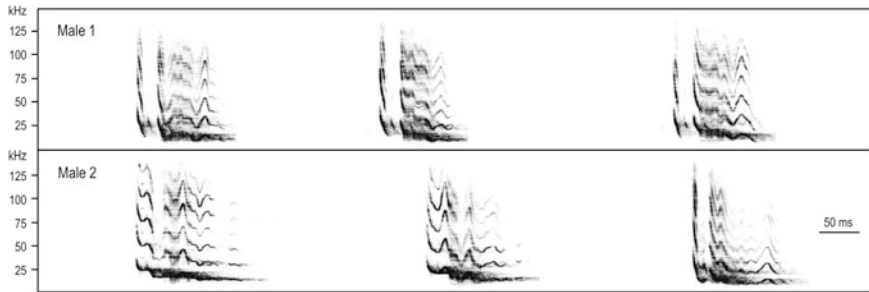


Fig. 8.2 Aggressive trills produced during territorial rival deterrence in male *C. perspicillata*. Three aggressive trills of two harem males are depicted (trills were not produced in succession but came from different recording days). This and all following spectrograms were generated using a 1024-point fast Fourier transform, a frame size of 100 %, and a Hamming window with 87.5 % overlap. All recordings of *C. perspicillata* vocalizations had a sampling rate of 300 kHz and 16 bit depth. *Recording credit* M. Knörnschild

cavity in the cave ceiling, in which the females are huddling together during the day) and produce harsh trills at irregular intervals (Knörnschild et al. 2014). These trills do not seem to be directed at a specific individual; however, trill production rate increases whenever a conspecific is flying by. We named this vocalization type “aggressive trill” (Knörnschild et al. 2014). Males most likely use aggressive trills to announce territory ownership and to deter rivals from approaching their territories. Aggressive trills are exclusively produced by males (Knörnschild et al. 2014). They contain enough interindividual variation to encode an individual signature (Fig. 8.2), and males are able to discriminate between different male rivals based on acoustic information alone (Fernandez et al. 2014). Individual discrimination of rivals likely facilitates adequate behavioral reactions between neighboring territory owners.

8.2.2.2 Aggressive Male–Male Interactions

Whenever rival deterrence based on aggressive trills is insufficient, males engage in physically aggressive interactions with competitors. During these interactions, males produce different vocalization types (Fig. 8.3), namely down-sweeps and warbles (and distress calls if they are in the inferior position). Aggressive trills often precede the actual physical contact between rivaling males, whereas warbles are mainly produced when a conflict escalates into physical contact; down-sweeps, however, are often uttered during comparatively mild disputes that are normally resolved without the opponents exchanging wing blows (Knörnschild et al. 2014). Down-sweeps and warbles are produced by both sexes, aggressive trills only by males (Porter 1979b; Knörnschild et al. 2014). In general, male–male aggressive interactions have a ritualized structure, i.e., they follow a defined succession of behavioral displays with increasing levels of aggression (Porter 1978; Fernandez et al. 2014). Boxing is a highly stereotypic behavior especially noteworthy in this

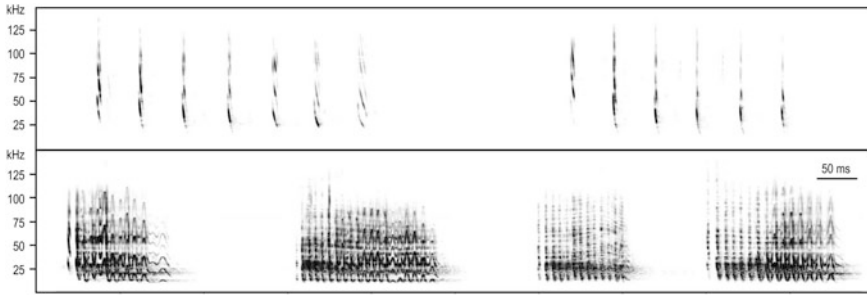


Fig. 8.3 Down-sweeps and warbles produced during aggressive interactions in male *C. perspicillata*. *Top panel* series of down-sweeps produced in succession by one male. *Bottom panel* series of warbles produced in succession by one male. *Recording credit* M. Knörnschild

context because it constitutes the top level of aggression (Fernandez et al. 2014). During boxing bouts, roosting males face one another while hanging from the ceiling of their day-roost and repeatedly distribute blows with their folded wings until one competitor retreats (Porter 1978; Fernandez et al. 2014).

8.2.2.3 Courtship

When females are estrous, harem males engage in a multimodal courtship display (Porter 1979b; Knörnschild et al. 2013, 2014). Harem males approach estrous females by brachiating or flying toward them and often briefly hover in front of them. Subsequently, they sniff the female with their body arched forward, a distinct posture that is sometimes accompanied by rapid wing beats. After sniffing, harem males repeatedly poke the female with one or both folded wings. Wing poking is the most conspicuous part of the males' courtship display, and sometimes continues for more than a minute. During copulation, males often wrap the female in both

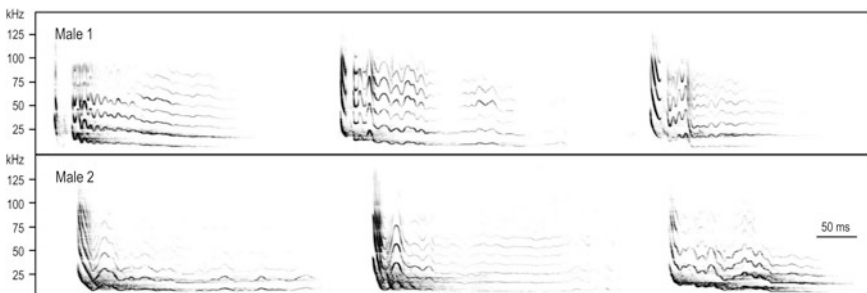


Fig. 8.4 Courtship trills produced during courtship display in male *C. perspicillata*. Three courtship trills of two harem males are depicted (trills came from different recording days). *Recording credit* M. Knörnschild

partially opened wings and apply neck bites display (Porter 1979b; Knörnschild et al. 2013, 2014). Throughout courtship (but not during copulation), males produce highly variable tonal trills at irregular intervals, which we named “courtship trills” (Fig. 8.4; Knörnschild et al. 2014). Acoustic measurements of courtship trills suggest a strong individual signature which has the potential to facilitate mate recognition or female choice (Knörnschild et al. 2014); however, a playback experiment confirming this is still lacking. A courtship trill is sometimes preceded by one or two down-sweeps (which are normally used during mild aggressive interactions; see above), especially when females elude the wing poking of males. Therefore, producing down-sweeps in addition to courtship trills might encode the extent of male agitation (Knörnschild et al. 2014).

8.3 Greater Sac-Winged Bat *Saccopteryx bilineata*

The Greater Sac-Winged Bat *S. bilineata* is a common and widespread insectivorous bat in the lowlands of Central America (Yancey et al. 1998). It is one of the best-studied bat species worldwide with regard to its natural history, social structure, and communication system (reviewed in Voigt et al. 2008). *S. bilineata* is a very light-tolerant species that roosts on the outside of large trees, the mouths of caves, in well-lit hollow trees, or on/in man-made structures such as buildings and bridges (Fig. 8.1; Bradbury and Emmons 1974). This choice of day-roost and the fact that these bats maintain a distance of at least one body length to adult conspecifics makes it possible to observe and record individual bats with relative ease in the wild. *S. bilineata* is sexually dimorphic; males are smaller than females and have a wing-sac in each of their antebrachial membranes (Yancey et al. 1998).

8.3.1 Social Organization of *S. bilineata*

The mating system of *S. bilineata* is a resource-defense polygyny with single-male/multifemale groups (‘harems’). Each harem male defends a small roosting territory (approx. 1–2 m²) in the colony’s day-roost. Neighboring territories can be directly adjacent to one another (Bradbury and Emmons 1974; Tannenbaum 1975). Normally, 2–3 adult females roost in each territory, but large harems can include up to 8 females. Average sized colonies contain 2–3 harems, but large colonies can consist of more than 10 harems (Bradbury and Vehrencamp 1976, 1977). Adult nonharem males that are queuing for territory access are also present (Heckel and von Helversen 2002; Voigt and Streich 2003), especially in large and average-sized colonies (normally 1–2 queuing males per harem). The reproductive success of harem males is much higher than that of nonharem males (Heckel and von Helversen 2002), which queue for up to 3 years to take over a newly vacant territory (Nagy et al. 2012). This normally happens when the territory

owner fails to return from foraging in the morning, likely because it was predated upon. The nonharem male with the longest tenure is the first to fill in such a vacancy (Voigt and Streich 2003). However, highly aggressive territory takeovers (or attempts thereof) also occur. In this case, an intruding immigrant male (or, very rarely, a queuing non-harem male) fights with the harem male until one competitor is defeated. These fights can be severe, consisting of areal chases and collisions, biting, clawing, and hitting each other with folded wings (Tannenbaum 1975). Displaced harem males have never been observed to establish a new territory elsewhere or to remain in their colony (Tannenbaum 1975; own observations). Established harem males do not attempt to take over competitors' territories. At night, adult individuals from the same colony forage separately and do not use communal night roosts (Hoffmann et al. 2007).

Male *S. bilineata* are philopatric; thus, resident males belong to only a few patrines (Nagy et al. 2007). Despite the high costs of local mate competition, male *S. bilineata* receive both direct and indirect fitness benefits when roosting with close kin (Nagy et al. 2012). Harem males often lose paternities to neighboring competitors (in large colonies, up to 70 % of pups are not fathered by the respective harem male; Heckel et al. 1999; Heckel and von Helversen 2003), but since resident males are normally related to many of their male neighbors, they may still gain inclusive fitness benefits. More importantly, harem male tenure (which is the best predictor of male lifetime reproductive success) is strongly and positively influenced by colony size (Nagy et al. 2012), probably because the risk of harem-takeovers by alien immigrant males is drastically reduced in colonies in which several resident males (harem and non-harem males alike) harass and may fend off the intruder simultaneously (Nagy et al. 2012).

Female choice is extremely pronounced in *S. bilineata* (Heckel and von Helversen 2003; Voigt et al. 2008). All subadult females disperse from their natal colony to avoid inbreeding with their fathers (Nagy et al. 2007) and once they are established in a new colony, they preferentially mate with genetically dissimilar males therein, and one reason for this is to avoid inbreeding with male descendants (Nagy et al. 2007). Moreover, females prefer mating partners that have a dissimilar major histocompatibility complex class I (which harbors immune genes responsible for intracellular parasite resistance; Santos et al. under review). Resident females, which often spend their entire life roosting in the same harem territory, regularly behave aggressively to each other and to dispersal females, for reasons that are currently unclear (Tannenbaum 1975, own observations). Females bear a single offspring per year and parturition is fairly synchronized (Tannenbaum 1975). Since females are larger than and physically superior to males, harem males cannot prevent females from visiting other territories in the day-roost and mating with a competitor (Heckel et al. 1999). From a female's perspective, the core social unit is likely not "harem" (as it is for the males) but "colony," because mating partners are almost always selected among the resident colony males (Heckel and von Helversen 2003). Females are in estrus for only a few days each year (Voigt and Schwarzenberger 2008), but are courted by males throughout the whole year (Behr

and von Helversen 2004), which most likely reflects the large influence of female choice in this species.

8.3.2 Sexually Selected Vocalizations of *S. bilineata*

The rich vocal repertoire of *S. bilineata* has been described in great detail in the wild (Bradbury and Emmons 1974; Tannenbaum 1975; Bradbury and Vehrencamp 1976; Davidson and Wilkinson 2004; Behr and von Helversen 2004; Knörnschild et al. 2006; Knörnschild and von Helversen 2008), making it one of the best-studied bat species with regard to its social vocalizations. *S. bilineata* produce five different vocalization types in social contexts that are under sexual selection pressure (Behr and von Helversen 2004), namely territorial rival deterrence, aggressive male–male interactions, and courtship (Fig. 8.5, 8.6, 8.7). Two of these vocalizations are complex, multisyllabic songs (Behr and von Helversen 2004; Davidson and Wilkinson 2004; Behr et al. 2009). Olfactory communication plays an important role in territorial maintenance and in mate choice as well (reviewed in Voigt et al. 2008); however, only sexually selected vocalizations of *S. bilineata* are described in detail below.

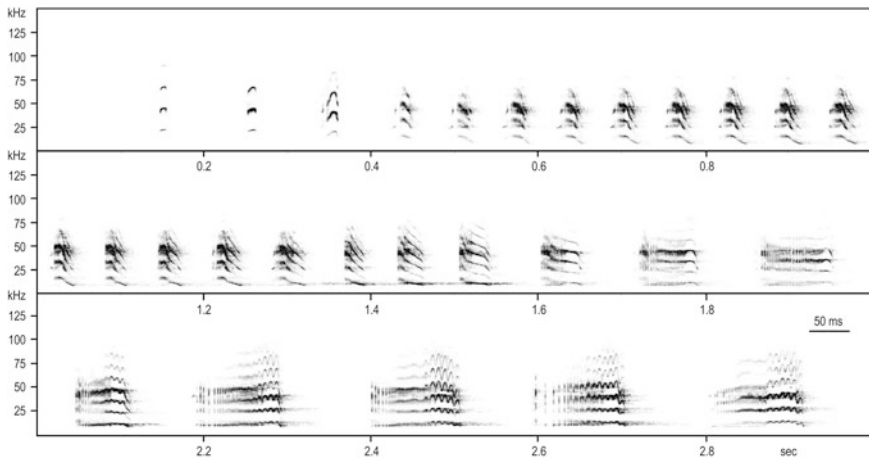


Fig. 8.5 Territorial song produced by male *S. bilineata*. This multisyllabic song starts with simple tonal syllables that gradually merge into composite end syllables (buzz syllables), which consist of a pulsed, noisy part, and a tonal part. When territorial songs precede aggressive male–male interactions, the modestly modulated tonal part of buzz syllables changes to a highly modulated trill (starting at 2.0 s). All recordings of *S. bilineata* vocalizations had a sampling rate of 500 kHz and 16 bit depth. *Recording credit* M. Knörnschild

8.3.2.1 Territorial Rival Deterrence

Harem males leave the day-roost last in the evening and return first in the morning. During these periods, they also produce the most territorial songs, both when they are alone and in reaction to conspecifics (Bradbury and Emmons 1974; Tannenbaum 1975; Behr and von Helversen 2004). Harem males utter territorial songs when male conspecifics approach the day-roost and courtship songs (see below) when females approach the day-roost (Knörnschild et al. 2012). Territorial songs are multisyllabic vocalizations. They start with simple tonal syllables that gradually merge into composite end syllables ('buzz syllables') consisting of a harsh, pulsed part, and a tonal part (Fig. 8.5). Territorial songs are comparatively long (on average 1.6 s, maximum 4 s) and low in frequency (on average 14.5 kHz, minimum 7 kHz; peak frequency of buzz syllables was measured), making them unusual bat vocalizations (Behr et al. 2006, 2009). Adult females do not produce territorial songs (Behr and von Helversen 2004). Male reproductive success is positively correlated with song rate and negatively correlated with song peak frequency (Behr et al. 2006). Harem males respond more aggressively to broadcast territorial songs with a lower peak frequency than to songs with a higher peak frequency (Behr et al. 2009), indicating that the former are perceived as a greater threat. Male song rate is positively correlated with the number of male competitors and the number of harem females (Davidson and Wilkinson 2004; Behr et al. 2009; Eckenweber and Knörnschild 2013), suggesting that male singing augments with increasing male–male competition. The buzz syllables of territorial songs (which are equivalent to the screech-inverted-V call type described in Davidson and Wilkinson 2002; 2004; pers. comm. G. Wilkinson) contain enough interindividual information to encode an individual signature (Davidson and Wilkinson 2002, Eckenweber and Knörnschild 2003). Moreover, buzz syllables from colonies within hearing range of each other encode a group signature (Eckenweber and Knörnschild 2003) and, over a larger geographic scale, buzz syllables show regional variation (Davidson and Wilkinson 2002). However, playback experiments confirming that *S. bilineata* actually uses those signatures are still lacking. Since territorial songs are not innate but learned by imitating tutor males during ontogeny (Knörnschild et al. 2010b; Knörnschild 2014), it is currently unclear whether group signatures and regional differences are caused by learning processes or genetic effects (i.e. because philopatric, related males sing similarly). Despite the fact that territorial songs are used to mediate territorial claims among males, it is conceivable that they can also be directed at females. The above-mentioned correlation between male reproductive success on the one hand and song rate and peak frequency on the other hand (Behr et al. 2006) does not allow us to infer whether territorial songs advertise the competitive ability of males (a signal directed at other males) or the quality of territory holders (a signal directed at females); of course, both options are not mutually exclusive.

8.3.2.2 Aggressive Male–Male Interactions

Aggressive interactions between males involving physical contact are rare in *S. bilineata*, but when they occur they are severe (Tannenbaum 1975; Behr and von Helversen 2004; own observations). Territorial songs (and scent-marking at territory borders; Voigt and von Helversen 1999; Caspers and Voigt 2009) are normally sufficient to keep male rivals at bay, but once territory ownership is challenged, harem males react most aggressively. Territorial songs often precede aggressive male–male interactions (Tannenbaum 1975; Behr and von Helversen 2004; own observations); in this case, the tonal part of buzz syllables changes from its normal modest frequency modulation to a highly modulated trill, while the pulsed part remains unchanged or decreases in length (Eckenweber and Knörnschild 2013, own observations; see also Fig. 8.5). During physically aggressive interactions, males produce three different vocalization types (Fig. 8.6), namely barks, screeches, and pulsed trains (and, if they are inferior, also distress calls; Behr and von Helversen 2004; own observations). Pulsed trains are somewhat similar to buzz syllables of territorial songs, but the former are produced singly, not in succession and their harsh, pulsed part is greatly enhanced when compared to buzz syllables (however, a short tonal part is sometimes present at the end of pulsed trains as well). Screeches and pulsed trains are mainly produced when a conflict escalates; barks, however, are often uttered during comparatively mild disputes, or, like territorial songs, before the onset of a dispute (Behr and von Helversen 2004; own observations). Screeches, barks, and pulsed trains can be produced by both sexes, but males utter much more barks and pulsed trains than females (own observations).

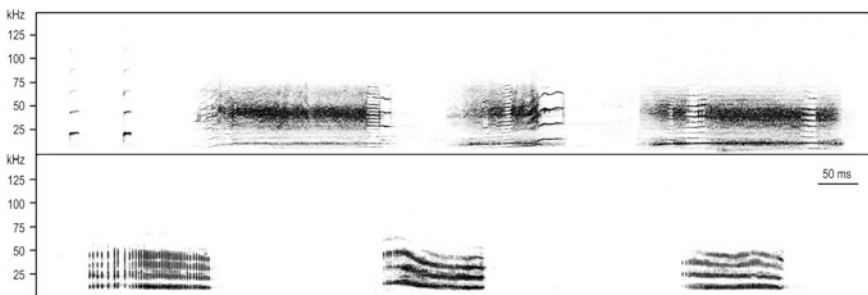


Fig. 8.6 Barks, screeches, and pulsed trains produced during aggressive interactions in male *S. bilineata*. *Top panel* two barks produced in succession by one male and three screeches (from different males; not produced in succession). *Bottom panel* Three pulsed trains, reminiscent of buzz syllables in territorial songs, from different males (not produced in succession) *Recording credit* M. Knörnschild

8.3.2.3 Courtship

Males court females everyday throughout the whole year with conspicuous and multimodal courtship displays that consist of visual, olfactory, and acoustical components (Bradbury and Emmons 1974; Tannenbaum 1975; Bradbury and Vehrencamp 1976; Voigt and von Helversen 1999; Behr and von Helversen 2004; Davidson and Wilkinson 2004). Males court females mostly when they return to their harem territory at dawn, and, to a lesser extent, before they leave it at dusk (Behr and von Helversen 2004). Male courtship is most intense during the mating season and continues at lower levels through the rest of the year (Tannenbaum 1975; Behr and von Helversen 2004). The most conspicuous aspect of male courtship is a hover display during which a male hovers in front of a roosting female while presenting olfactory signals from the wing-sacs (Voigt and von Helversen 1999) and vocalizations (Behr and von Helversen 2004; Davidson and Wilkinson 2004). Hovering males produce long whistles to which females often respond with screeches in a

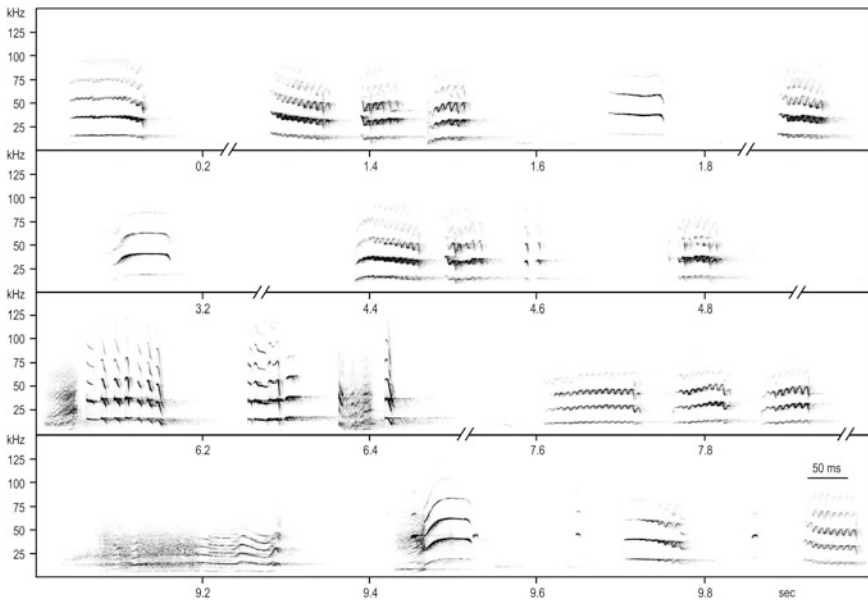


Fig. 8.7 Courtship song produced by male *S. bilineata*. Courtship song excerpt from one harem male, depicting different trill types, long tonal calls, noise bursts, and a whistle. The excerpt ends with a hover display: the female's screech (9.0–9.3 s) is followed by the male's whistle (9.4–9.5 s) and two trills (9.7–10.0 s). The screech (9.0–9.3 s) and four echolocation calls (9.4–9.9 s) were produced by the female, all other vocalizations by the male. Please note that several silent parts (of approx. 1 s each) are not depicted in the spectrogram. *Recording credit* M. Eckenweber

duet-like way (Behr and von Helversen 2004; own observations). Copulations are normally preceded by male hover displays (Tannenbaum 1975; own observations), so they seem to be crucial for females to assess male quality. Male hover displays are embedded in long courtship songs during which the male approaches a roosting female from different angles by short flights and crawling (Behr and von Helversen 2004). This male approach behavior, accompanied by conspicuous head turns toward the courted female, is always associated with the production of courtship songs; when it ends, song production ceases as well (Behr and von Helversen 2004). In the mating season, courtship attempts (and thus courtship songs) directed at one particular female that can last for up to one hour, but most courtship songs are much shorter (on average 42 s; Behr and von Helversen 2004). Courtship songs consist of different syllables types, with purely tonal trills being the most common one (Fig. 8.7). Trills are highly variable, and males differ in their trill repertoire (Behr and von Helversen 2004), suggesting that females might use trills for mate choice decisions; however, a playback experiment confirming this is still lacking. When not interested in male courtship attempts, females do not evade them but terminate them aggressively (Tannenbaum 1975; Behr and von Helversen 2004).

8.4 Synopsis

Despite the fact that both *S. bilineata* and *C. perspicillata* exhibit resource-defense polygyny and live in single-male/multifemale groups, their social organizations seem to differ remarkably in certain aspects, e.g., the way resident harem males interact with each other or the amount of female choice involved in mating (see Table 8.1 for an overview of key differences between both species). It is conceivable that these differences have implications for the structural complexity and information content of sexually selected vocalizations.

When considering vocalizations used in the context of territoriality or aggression, we find obvious differences in vocal complexity and associated behaviors between both species. Male *S. bilineata* produce long, structured territorial songs encoding information about male quality, identity, and group membership (Davidson and Wilkinson 2002, 2004; Behr et al. 2006, 2009; Eckenweber and Knörnschild 2013) which, together with scent marking (Voigt and von Helversen 1999; Caspers and Voigt 2009), is often enough to keep male rivals at bay. When disputes cannot be solved from a distance by singing and scenting, the resulting physically aggressive conflicts are severe and do not follow a ritualized structure (Tannenbaum 1975, own observations). This contrasts sharply with the ritualized aggressive interactions between male *C. perspicillata*, in which a defined succession of behavioral displays with increasing levels of aggression mediates conflicts (Porter 1978; Fernandez et al. 2014). Physically aggressive interactions between males are much more common in *C. perspicillata* than in *S. bilineata* throughout the year. This is probably caused by the fact that *C. perspicillata* bachelor males do not queue for territory access and that resident harem males fight among each other

Table 8.1 Key characteristics of social organization and behavioral interactions in *S. bilineata* and *C. perspicillata*

Characteristics	<i>Scopteryx bilineata</i>	<i>Carollia perspicillata</i>
Mating system	Resource-defense polygyny	Resource-defense polygyny
Social structure	One-male/multifemale groups (harems) with bachelor males (single)	One-male/multifemale groups (harems) with bachelor males (single or in groups)
Colony structure	Often several harems (up to 12)	Often several harems (up to 18)
Roosting behavior	Adults roost at least one body length away from conspecifics	Adults roost with body contact
Sexual dimorphism	Males are approximately 15 % smaller than females; only males have wing-sacs	In most areas, males are heavier but not larger than females
Harem size	Up to 8 females	Up to 18 females
Average tenure as harem male	On average 1.9 years (up to 9 years)	On average 0.8 years (up to 2 years)
Territorial scent marking by males	Yes	No
Superior sex in aggressive interactions	Females	Males
Male-male aggression	Acoustical and olfactory rival deterrence is very common, physical conflicts are rare but severe	Acoustical rival deterrence is very common, physical conflicts are common but normally not severe
Female-female aggression	Prominent	Rare
Multimodality of male courtship display	Acoustical, olfactory, visual	Acoustical, tactile, olfactory (?)
Vocal response of females to male courtship	Yes	No
Female estrus	One seasonal estrus	One postpartum estrus and one seasonal estrus
Parturition	Fairly synchronized (within 2–3 weeks)	Moderately synchronized (within 6–8 weeks)

for the territories most preferred by females (Williams 1986; Fleming 1988). Thus, it is not surprising that male *C. perspicillata* use comparatively simple vocalizations, aggressive trills, to announce territory ownership but resort to a comparatively more advanced suite of ritualized behavioral displays to resolve the numerous physically aggressive conflicts than *S. bilineata* males.

We also find strong differences in vocal complexity and accompanying behaviors between both species when considering vocalizations used in the context of courtship. Male *S. bilineata* produce extremely long courtship songs, which

incorporate sophisticated hover displays in which males and females often interact with each other in a duet-like fashion (Behr and von Helversen 2004). In contrast to the elaborate, year-round courtship of *S. bilineata* males (which also has an important olfactory component; reviewed in Voigt et al. 2008), male *C. perspicillata* produce single courtship trills in succession while following an estrous female on foot in their harem territory until the female consents to mating (Porter 1979a; Knörnschild 2014). This obvious difference in male courtship behavior may be caused by two factors: First, female choice might be more pronounced in *S. bilineata* than in *C. perspicillata* because, in the former species, females are larger and thus physically superior to males (Yancey et al. 1998). Second, ownership of a territory that is particularly preferred by females (and thus heavily fought for among males) is already a strong indicator of male quality in *C. perspicillata*, which may explain why courtship in *C. perspicillata* is less elaborate than in *S. bilineata*. Female *S. bilineata* do not obviously prefer a specific male territory, probably because their roosting associations within a colony are not automatically determining their mating partners (Heckel et al. 1999; Heckel and von Helversen 2003). Instead, female *S. bilineata* can evaluate all resident males in a colony throughout the whole year and make their yearly mate choice decisions accordingly, which may have led to the complex courtship displays of male *S. bilineata*.

In conclusion, *S. bilineata* seem to have more complex territorial and courtship vocalizations than *C. perspicillata* because male *S. bilineata* try to resolve territorial disputes without physical aggression and because female choice is extremely pronounced, driving males to court females year-round. Thus, not only the strength of sexual selection pressures (which can be hard to assess), but the details of a species' social organization and behavioral interactions can influence the structural complexity and information content of sexually selected vocalizations in bats.

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