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REVIEW

The origins and diversity of bat songs

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Abstract Singing plays an important role in the social lives of several disparate bat species, but just how significant the behavior may be among bats generally is unknown. Recent discoveries suggest singing by bats might be surprisingly more diverse and widespread than anticipated, but if true then two questions must be addressed: firstly why has singing been so rarely documented among bats, and secondly do bats sing for the same reasons as songbirds? We address the first question by reviewing how sampling bias and technical constraints may have produced a myopic view of bat social communication. To address the second question, we review evidence from 50 years of batsong literature supporting the supposition that bat singing is linked to the same constellation of ecological variables that favored birdsong, including territoriality, polygyny, metabolic constraints, migratory behaviors and especially powered flight. We propose that bats sing like birds because they fly like birds; flight is energetically expensive and singing reduces time spent flying. Factoring in the singular importance of acoustic communication for echolocating bats, it seems likely that singing may prove to be relatively common among certain groups of bats once it becomes clear when and where to look for it.

Keywords Bats · Singing · Communication · Courtship · Territoriality

Introduction

Acoustic communication is central to many social behaviors such as territory defense, mating and group cohesion. For most animals these behaviors are well served by a simple repertoire of calls, but a subset of vertebrates, most notably songbirds and whales, have expanded their vocal repertoire with singing. In the simplest sense, singing is a more elaborate form of calling repeatedly in a stereotyped temporal pattern that is used specifically in support of courtship or territorial defense (Catchpole and Slater 2008). The ecological significance of singing is that it accommodates a broader array of finely tuned behaviors and social interactions than simple calling can support, which makes singing a unique window into the behavioral ecology of the singer. The ecology and evolution of singing has been delineated in birds (Marler and Slabberkoorn 2004; Catchpole and Slater 2008; Bradbury and Vehrencamp 2011) where it is both conspicuous and widespread, but lingering questions remain about why singing is so rare among mammals. Recent studies in bats suggest that singing might not be so rare among this large and diverse order of mammals (Behr and von Helversen 2004; Davidson and Wilkinson 2004; Jahelková et al. 2008; Behr et al. 2009; Bohn et al. 2009), and in light of the central role singing plays in many aspects of bird ecology, the study of bat singing might be a profitable new avenue for expanding our knowledge of bat behavioral ecology. By analyzing which bats sing, why they sing and how their songs compare within the well-established framework of birdsong ecology we intend to show that the selective pressures that uniquely

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favored singing in birds are also widely prevalent in bats and that therefore songs or singing-like behaviors should be expected for many more species.

Bats are not the only mammals that sing. Humpback whales are perhaps the best-known example of a mammal that sings for courtship (Payne and McVay 1971) but singing is not widespread among all cetaceans, having been found only in a few baleen whales (McDonald et al. 2006; Cholewiak et al. 2013). Notably, the echolocating toothed whales (Odontoceti, the sperm whales, beaked whales and dolphins) do not sing, even though they exhibit several other noteworthy vocal behaviors such as the use of signature whistles, vocal learning and codas (Reiss and McCowan 1993; Bradbury and Vehrencamp 2011). Singing has also been documented in some primates and rodents. The common laboratory mouse uses singing for courtship purposes (Holy and Guo 2005), but there is also a genus of neotropical singing mice (*Scotinomys*) (Blondel et al. 2009; Pasch et al. 2013) and a species of singing vole (Batzli and Henttonen 1993). Among primates, singing has been documented among certain species of gibbons (Mitani and Marler 1989; Arnold and Zuberbühler 2006; Clarke et al. 2006). Other primates can produce complex vocal sequences (Ouattara et al. 2009) but these were not labeled songs because the temporal patterns and behavioral contexts in which they were uttered (for example, predator warning calls) are not consistent with singing.

There are at least 1300 species of bats, comprising roughly 20 % of all mammalian species (Kunz and Fenton 2003; Simmons 2005; Fenton and Simmons 2015). Molecular phylogenetics divides bats into two suborders, the Yinpterochiroptera and Yangochiroptera, which together include one family of pteropodids (old world fruit bats and flying foxes) and four superfamilies of laryngeal echolocating bats (Teeling et al. 2005; Jones and Teeling 2006). Songs and singing-like behaviors have been documented in at least 20 different bat species (Fig. 1; Table 1) with representations coming from three of the four superfamilies of echolocating bats (Emballonuroidea, Rhinolophoidea, and Vespertillionoidea). The distinction between echolocating and non-echolocating bats may be relevant in the context of singing because as flying nocturnal animals, the echolocating bats are almost entirely reliant upon acoustic signaling for social communication. The overarching importance of echolocation may have predisposed echolocating bats to enhanced spectrotemporal complexity in their vocal communication behaviors more so than other mammals. Echolocation relies upon a hypertrophied neural architecture for both producing and hearing sonar calls (Altringham and Fenton 2003), giving bats finer control over the timing and acoustic structure of their vocalizations than other mammals (Pollak and Casseday 1989; Smotherman 2007). Though this provides a mechanistic rationale for the capacity to sing, it fails to address the ecological costs and benefits of singing. What do bats have to gain by singing instead of just calling?

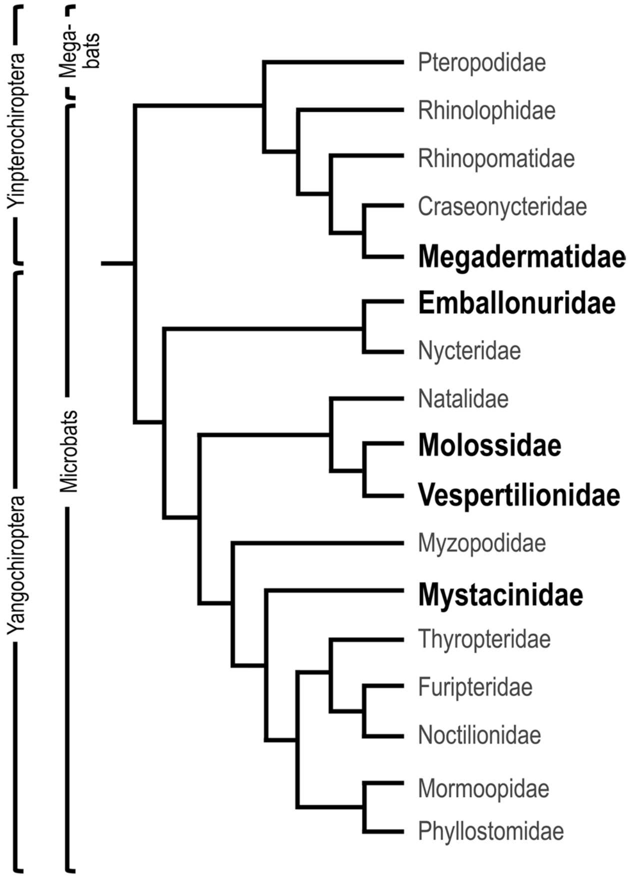


Fig. 1 Evolutionary relationships of chiropteran taxa illustrated by a molecular phylogenetic tree (adapted from Teeling et al. 2005. Reprinted with permission from AAAS and modified with permission from E.C. Teeling). Families that contain singing species (Megadermatidae, Emballonuridae, Molossidae, Vespertilionidae) are *highlighted*

How is singing different from calling?

Songs are an elaborate and specialized form of calling. Ornithology distinguishes between calls and songs by their temporal patterns and behavioral context. Bird vocalizations span a broad spectrum from simple calls to highly complex songs and extensive repertoires. Between these extremes lie many species whose calls/songs fall into a gray area, whereupon the distinction ultimately becomes somewhat arbitrary (Catchpole and Slater 2008). For simplicity and consistency we adhere to the general definitions of calls and songs assigned by Marler and Slabberkoorn (2004), Catchpole and Slater (2008) and Bradbury and Vehrencamp (2011). Calls are short discreet vocalizations

Table 1 Bats for whom singing or singing-like calling behaviors are documented in the literature

Family	Species	Structure	Song vs. call	Posture	References
Molossidae	*Tadarida brasiliensis*	Complex motifs in syntactical order	Song	Sedentary	Bohn et al. (2008, 2009, 2013)
Megadermatidae	*Cardioderma cor*	Different syllable types in basic motif	Song	Sedentary	Vaughan (1976) and McWilliam (1987)
Megadermatidae	*Lavia frons*	Simple syllable types in basic motif	Territorial call (possible courtship function	Sedentary	Wickler and Uhrig (1969) and Vaughan and Vaughan (1986)
Megadermatidae	*Megaderma lyra*	Different syllable types in complex motifs	Song	Flying	Leippert (1994) and Schmidt (2013)
Emballonuridae	*Saccopteryx bilineata*	Different syllable types in gradations and motifs	Song	Sedentary	Bradbury and Emmons (1974), Davidson and Wilkinson (2002, 2004), Behr and von Helversen (2004), Behr et al. (2006, 2009), Knörnschild et al. (2009) and Eckenweber and Knörnschild (2013)
Emballonuridae	*Coleura seychellensis*	Different syllable types in series	Song-like	Sedentary	Gerlach (2009)
Rhinolophidae	*Rhinolophus ferrumequinum*	Different syllable types in series	Song-like	Sedentary	Ma et al. (2006)
Vespertilionidae	*Nyctalus noctula*	Different syllable types in complex motifs	Song	Mainly sedentary, occasionally flying	Weid (1994), Gebhard (1997) and Pfalzer and Kusch (2003)
Vespertilionidae	*Nyctalus leisleri*	Different syllable types in basic motif	Song	Mainly sedentary, occasionally flying	von Helversen and von Helversen (1994) and Pfalzer and Kusch (2003)
Vespertilionidae	*Vespertilio murinus*	Different syllable types in basic motif	Song	Mainly flying, occasionally sedentary	Zagmajster (2003)
Vespertilionidae	*Pipistrellus nathusii*	Different syllable types in complex motifs	Song	Sedentary, flying	Gerell-Lundberg and Gerell (1994), Russ and Racey (2007), Jahelková et al. (2008) and Jahelková and Horáček (2011)
Vespertilionidae	*Pipistrellus hanaki*	Different syllable types in basic motif	Song	Flying	Georgiakakis and Russo (2012)
Vespertilionidae	*Pipistrellus pipistrellus*	Simple syllable type in basic motif	Song-like	Flying	Barlow and Jones (1997a, b), Sachteleben and von Helversen (2006) and Budenz et al. (2009)
Vespertilionidae	*Pipistrelllus pygmaeus*	Simple syllable type in basic motif	Song-like	Flying	Lundberg and Gerell (1986)[a], Gerell-Lundberg and Gerell (1994)[a] and Barlow and Jones (1997a, b)
Vespertilionidae	*Pipistrellus kuhli*	Simple syllable type in basic motif	Song-like	Flying	Barak and Yom-Tov (1991) and Russo and Jones (1999)
Vespertilionidae	*Pipistrellus maderensis*	Simple syllable type in basic motif	Song-like	Flying	Russo et al. (2009)
Vespertilionidae	*Myotis myotis*	Same variable syllable type in series	Courtship call	Sedentary	Zahn and Dippel (1997) and Pfalzer and Kusch (2003)
Vespertilionidae	*Myotis oxygnathus*[b]	Same variable syllable type in series	Courtship call	Sedentary	Hammer (1992) and Dietz et al. (2007)
Vespertilionidae	*Neoromicia nana*[c]	Simple syllable type in series	Territorial call (possible courtship function)	Sedentary, flying	O'Shea (1980)
Phyllostomidae	*Carollia perspicillata*	Same variable syllable type in series	Courtship call, territorial call	Sedentary	Porter (1979) and Knörnschild et al. (2014)
Phyllostomidae	*Erophylla sezekorni*	Simple syllable type in series	Courtship call (likely territorial function)	Sedentary	Murray and Fleming (2008)

Table 1 continued

Family	Species	Structure	Song vs. call	Posture	References
Pteropodidae	*Hypsignathus monstrosus*	Simple syllable type in series	Courtship call (likely territorial function)	Sedentary	Bradbury (1977)
Pteropodidae	*Pteropus alecto*	Simple syllable type in series	Courtship call	Sedentary	Markus (2002)
Mystacinidae	*Mystacina tuberculata*	Different syllable types in series	Song-like	Sedentary	Lloyd 2001 and Toth et al. (2015)

[a] Firstly described as *Pipistrellus pipistrellus*, but actually *P. pygmaeus*

[b] Formerly *Myotis blythii*

[c] Formerly *Pipistrellus nanus*

uttered irregularly or in isolation in support of specific social functions such as alarm calls, contact calls and begging calls, which are typically used within close range of conspecifics to coordinate intraspecific social behaviors. Songs are longer, more complex stereotyped call sequences that are repeated frequently and spontaneously following discrete daily and seasonal emission patterns typically associated with courtship and territorial behaviors (Catchpole and Slater 2008). Singing often involves producing songs in groups called bouts over an extended period of time. Since one of the chief benefits of singing is improved communication over long distances, songs may in part be defined as such if they are acoustically adapted to serve long-range broadcasting. Singing bouts of songs rather than randomly uttering isolated calls enhances the signal efficacy by increasing the likelihood of its detection and expanding the range over which it can be accurately discriminated and localized (Morton 1986; Naguib and Riebel 2006). Singing per se represents an evolutionary optimization of call temporal patterns, balancing the energetic costs of signaling with potential benefits reaped by informing conspecifics of the signaler's identity, location, fitness and motivation state.

Calls and songs fall along a broad spectrum of vocal complexity. To address where bat songs fall along this spectrum, we briefly outline some of the major themes and patterns in birdsong ecology. Among birds, learned song is associated with a unique neural substrate found only in passerines, the "true songbirds" (Jarvis et al. 2005). In passerines vocal learning provides an important avenue for introducing variability in song composition, whereas in non-passerines both calls and songs are genetically hardwired. Increased variability expanded the functionality of singing in support of both intra- and intersexual selection (Catchpole and Slater 2008), but in itself vocal learning and plasticity does not define the behavior. Many non-passerines sing elaborate stereotyped species-specific songs and conversely many passerines sing short, monosyllabic songs (Marler and Slabberkoorn 2004). For some intermediate songbirds, learned songs are built from innate syllable repertoires. Finally, songs and song repertoires can vary in different ways, making direct comparisons of song composition and complexity problematic across species. For example, song repertoires can be expanded either by rearranging a common set of syllables in many different ways or through the addition of song types built from distinct syllable subsets. Our goal is not to redefine the term "song", but rather highlight the fact that bird songs are highly diverse and the bat vocalizations characterized in this review as songs fall somewhere within the broad spectrum of bird vocalizations that have likewise previously been characterized as songs. In the interest of comparing apples to apples, we identify representative examples of songbirds that reflect a similar level of phonological and acoustic complexity for each singing bat species described here.

Why is bat singing so rare? Sampling bias and technical constraints

Until the late 1940s cetaceans were believed to be mute (Cholewiak et al. 2013). In 1952 new tools such as the hydrophone and the spectrograph first revealed a correlation between some underwater sounds and the presence of humpback whales (Schreiber 1952), but it was not for another two decades that the significance of humpback whale song was fully appreciated (Payne and McVay 1971). The spectrogram was also a boon to the study of birdsong in the 1950s (reviewed by Marler and Slabbekoorn 2004), but unlike the situation in mammals, the breadth and diversity of birdsong was already appreciated, predicating key questions about repertoires, dialects, and vocal learning. Spectrographic analyses are constrained by the frequency range of the microphones and sample rate of the recording equipment available: tools and equipment engineered for humans translated readily to the study of birds, insects, amphibians and many mammals, including primates. However, the comparative study of ultrasonic social communications by bats could not really begin until several lingering technical challenges were overcome towards the end of the twentieth century.

Ultrasonic microphones and recording equipment became available shortly after World War II (Griffin 1958), and over the following 50 years revealed an extraordinary diversity of echolocation pulse acoustics and biosonar behaviors displayed by bats. However, as pointed out by Jahelková et al. (2008), acoustic studies of bat social behaviors presented a wholly different set of technical challenges not relevant to echolocation studies. Social calls are more complex, variable and heavily influenced by social and environmental context. Naturalistic social contexts are difficult to reproduce in the lab, and to capture the full repertoire of vocal behaviors in the field many hours of observations and ultrasonic recordings across seasons and behavioral contexts are required. These challenges were not overcome until high-speed, portable ultrasonic data acquisition systems became available at the end of the twentieth century.

Behavioral observations of singing bats were reported as early as 1961 (Goodwin and Greenhall 1961), but these and many subsequent studies (Bradbury and Emmons 1974; Vaughan 1976; Bradbury 1977; Bradbury and Vehrencamp 1977; Vaughan and Vaughan 1986; McWilliam 1987) provided only examples of bats that sang songs audible to humans. The first spectrograms of ultrasonic bat songs did not appear in the literature until the late 1990s when Barlow and Jones (1997b) used a bat detector's time-expansion output to record pipistrelles flightsongs onto a Sony Walkman. However, this method limited them to storing only three of every 33 s of behavior. Zahn and Dippel (1997) obtained spectrograms of the greater mouse-eared bat's courtship songs by placing a Racal Store 4DS high-speed reel-to-reel tape recorder (Racal Records, Southampton, UK) in an urban attic. Davidson and Wilkinson (2002, 2004) were limited to frequencies below 32 kHz by their Sony video camera in their field studies of sac-winged bats in Trinidad. Behr and von Helversen (2004) published the first complete spectrogram of a sac-winged bat's song using a 500 kHz analog-to-digital (A/D) converter on site at the Organization for Tropical Studies La Selva field station in Costa Rica. At La Selva the bats roosted on the walls of the field station's buildings and were accustomed to human observers. Subsequent efforts benefited from newly emerging lightweight portable interfaces such as USB-based high-speed analog-to-digital converters (for example, the Avisoft UltraSoundGate 116 first offered in 2001, Avisoft Bioacoustics, Berlin Germany) or personal computer memory cards (PCMCIA or express cards) which first became available in 2003 (for example, the DAQCard-6062e card, National Instruments, Austin, USA). These new tools allowed investigators to record bat communication sounds across a wide range of habitats, behavioral contexts and time scales.

Since 2003 there have been songs or singing-like behaviors described in 13 different species of bats (Table 1). Each of these examples comes from bats living in urban habitats, on or around artificial structures, and from bats that draw attention to themselves by calling or singing sounds that are at least partially audible to humans. Obviously not all species that live in or around human households sing; for example, extensive lab and field studies of big brown bats (*Eptesicus fuscus*) and little brown bats (*Myotis lucifugus*) revealed no evidence of singing. Considering that the current sampling of bat singing behaviors appears biased towards conspicuous, audible bats, it seems probable that the singing behaviors of many more species of bats may have gone unnoticed and await discovery.

What are the costs and benefits of singing in bats?

Singing is energetically costly, reduces foraging efficiency, and may increase predation risk. For singing to evolve, it must generate benefits that outweigh these costs. The potential benefits of singing include reduced costs associated with territory defense, reduced risk of injury from physical confrontations, and enhanced reproductive success via either intra- or intersexual selection (Read and Weary

1992). Among songbirds these costs and benefits have been linked to several ecological and behavioral factors that correlate with interspecific differences in song output, composition and complexity (Read and Weary 1992; Marler and Slabberkoorn 2004; Catchpole and Slater 2008). Comparative analyses of birdsong revealed that differences in singing parameters may correlate with (1) metabolism (body size and metabolic rate); (2) foraging ecology (habitat, prey type, and territoriality); (3) mating systems (reproductive skew and rate), and (4) migratory behaviors (Read and Weary 1992). This is not an exhaustive list, but highlights variables with the greatest effects. Although it will be a long time before similar analyses become feasible in bats, we can examine current examples of bat singing and ask whether they are consistent with evolutionary patterns evident in songbirds. Below we review the evidence for and against these ecological factors contributing to the evolution of singing in bats as they have in birds and identify the most pressing gaps in knowledge.

Metabolism

Singing is energetically expensive and its costs may impose constraints on who sings, how often they sing, and how elaborate their repertoires may be (Read and Weary 1992). Precise measures of the metabolic cost of singing are hard to pin down, but it is generally accepted that even if the energy required to produce a single song is marginal, the total cost of a typical passerine's long bout is likely to represent a significant part of their daily energy budget (Gil and Gahr 2002). Whether or not singing is energetically favorable depends upon its net effect on an organisms overall daily energy budget. This effect can be positive if it reduces costs elsewhere, for example, by reducing time spent flying to defend a territory. Body size affects daily energy budgets because metabolic rate scales proportionally with body size in birds and mammals (Nagy 1987, 2005): basal metabolic rates increase while mass-specific metabolic rates decrease with body size. Morton (1986) proposed that singing might have originated as a more energy efficient mechanism for maintenance and defense of territories than more costly flight surveillance. He argued that since smaller birds have the tightest energy budgets (highest mass-specific metabolic rate and lowest energy reserves), they would be more likely to benefit from singing than larger birds. However, contrary to Morton's prediction song output increased with body size (Read and Weary 1992), meaning that smaller birds generally spend less time singing than larger birds. Read and Weary (1992) concluded that mass-specific energetic costs may have constrained overall song output (duration and rate) in birds, but other singing parameters (i.e., complexity, repertoire size) were unaffected. Singing roughly doubles the resting metabolic rate for birds (Ophir et al. 2010), but this cost is far less than the 28-fold increase in metabolic rate associated with making short flights (Nudds and Bryant 2000). Several studies have shown that singing is an effective mechanism for deterring competitors (Marler and Slabberkoorn 2004; Catchpole and Slater 2008), which supports Morton's hypothesis that singing originated in birds for territorial defense.

The argument that singing emerged as an energetically favorable mechanism to defend territories also applies to bats. We will look at the evidence in support of territorial behaviors below, but first we address whether a similar set of metabolic parameters are present in singing bats. Bats have a slightly lower basal metabolic rate than similarly sized birds, especially passerines (Nagy 1987), which suggests that singing might be less constrained by overall energy budgets in bats than songbirds of equal size. Flying is energetically expensive for both bats and birds, but there is some evidence that bats are slightly more efficient flyers than birds, and a comparison between nectar-feeding bats and hummingbirds found that bats were surprisingly more efficient at hovering flight (Winter and von Helversen 1998; Voigt and Winter 1999). Still, while bats may face lower energetic constraints than birds they would still receive a significant energetic benefit from singing instead of flying in defense of territories and mates because singing is far less costly than flight.

There is not enough data from bats to infer whether or not body mass correlates positively with song output as observed in birds. In contrast to Read and Weary's (1992) meta-analysis of birdsong, Gillooly and Ophir (2010) examined vocalizations across all animals and concluded that in general larger animals tended to call less often because the cost of calling increases with body mass due to the biomechanical costs affiliated with moving larger body parts (Gillooly and Ophir 2010). However, that model specifically excluded echolocating bats because they have unique physiological adaptations that violate the model's generalized vertebrate assumptions, such as mechanical interactions between flight, vocalizing and energy expenditure (Speakman and Thomas 2003). A difficult challenge lies ahead in evaluating for each species how the costs of calling are balanced against the costs of flying as body mass increases. Although both the costs of calling and flying increase with body mass, the slope of the curve is much steeper for flight, so the net benefits are expected to vary with body mass (Read and Weary 1992). Current examples of singing in bats (Table 1) are mostly confined to relatively small (6–15 g) insectivorous bats, including members of the genus *Pipistrellus*, the genus *Tadarida*, the genus *Myotis*, and the genus *Saccopteryx*, which demonstrates that singing is at least energetically feasible and under circumstances favorable in small bats. Singing has also been reported in two relatively large (30–50 g) carnivorous bats, *Cardioderma cor* and *Megaderma lyra*, both members of the family Megadermatidae (Vaughan 1976; Mcwilliam 1987; Leippert 1994). However, pipistrelles mainly sing in flight, which complicates the issue when comparing them to stationary singers. For bats singing might actually be more economical while flying than while stationary owing to a unique mechanical linkage in bats that efficiently couples the powerful flight muscles to the generation of high subglottic pressures for vocalizing (Speakman and Racey 1991). For *Tadarida* and *Saccopteryx*, songs were produced at the roost and function to control access. In these examples bats do not save time patrolling a territory, although it may save time and energy spent fighting. *C. cor* behaves most like a typical songbird in the way it sings from perches to establish and maintain territory boundaries (Vaughan 1976). Vaughn did not probe the details of when or how often *C. cor* sang, but he did find evidence of seasonal energy constraints influencing song production. To date no studies have directly addressed the relationship between singing and energetics in any bat. Studies targeting how much time bats spend singing, how much energy singing requires, how much energy singing saves, comparisons between flightsong and stationary song, and generally how singing impacts daily energy budgets would be very useful for future analyses of how and why singing evolved in bats.

Foraging ecology

Three key parameters, habitat, prey type, and territoriality are closely interrelated, making it difficult to segregate each factor's independent effect on singing. Read and Weary (1992) found no consistent correlation between song parameters and habitat or prey type among songbirds, although in general they concluded that grassland species sang more versatile song repertoires while forest species sang more frequently and continuously. Territory size is heavily influenced by habitat and prey type, and singing increases with territoriality, but deciphering any relationship between singing and territory size for bats is undermined by our poor understanding of territoriality in bats. Until recently it has been essentially impossible to track or observe individual bats during their nightly forays, and while there is ample evidence of roost fidelity virtually nothing is known about foraging site(s) fidelity for most species. Territorial behaviors at the roost have been observed for many species, and not coincidentally most examples of singing have been collected at the roost. However, as new tools emerge for recording and tracking the nightly activity patterns of individuals (Cvikel et al. 2014) evidence is accumulating that bats do compete for food and defend preferred foraging territories, even if only temporarily or seasonally (Corcoran and Conner 2014). To look more closely at this, we next compare representative examples of the interplay between singing and territorial behaviors from four different bat families.

Megadermatidae

If singing first evolved in bats to support territorial defense as has been suggested for birds, then it should figure prominently in the behaviors of bats that are known to establish and defend personal foraging areas. Indeed, the earliest description of bats singing comes from the seminal field studies of the East African heart-nosed bat, *C. cor* by Terry Vaughan (Vaughan 1976). Individuals of this species share a day roost in the cavities of baobab trees (*Adansonia digitata*) with groups of 30–100 conspecifics, but disperse each night to reclaim tightly abutting private foraging areas. *C. cor* is a carnivorous ambush predator that uses passive listening to detect and localize prey, primarily beetles, other terrestrial arthropods and small vertebrates such as frogs (Vaughan 1976; McWilliam 1987; Ryan and Tuttle 1987). These bats prolifically broadcast loud songs every evening from strategically positioned perches while they move around their territory seeking prey, and responded to playback of neighbor's songs from a speaker placed within their territory borders with aggressive responses (Smarsh and Smotherman 2015). *C. cor* navigates by echolocation, uttering low-intensity 1–3 ms broadband (20–100 kHz) pulses for its echolocation (Möhres and Kulzer 1957; Kaňuch et al. 2015). In contrast its loud social calls and songs fall within a much lower bandwidth, with the fundamental frequencies in the range of 6–20 kHz (Smarsh and Smotherman 2015). Their faint, highly directional echolocation pulses are difficult to detect more than 10–15 m away with even the most sensitive microphones, but their territorial songs are readily detected from over 100 m (Vaughan 1976). Figure 2a provides an example of a typical *C. cor* song uttered spontaneously from a perch. These songs are typically composed of 4–15 compound syllables and last 1–3 s. Vaughan suspected that both males and females held exclusive foraging areas, but could not determine whether or not both sexes used song to defend those territories. Based on long-term observations of a single breeding pair McWilliam reported that only the male was ever observed singing (McWilliam 1987), but unlike Vaughan he concluded that males shared their territories with a single female during certain times of the year. Smarsh and Smotherman (2015) also reported that of 12 identified singers captured by mist-netting, all were males. McWilliam's (1987) claim that he was able to distinguish resident males by their "individually distinctive songs" is now supported by quantitative data demonstrating that songs displayed sufficient acoustic variability across

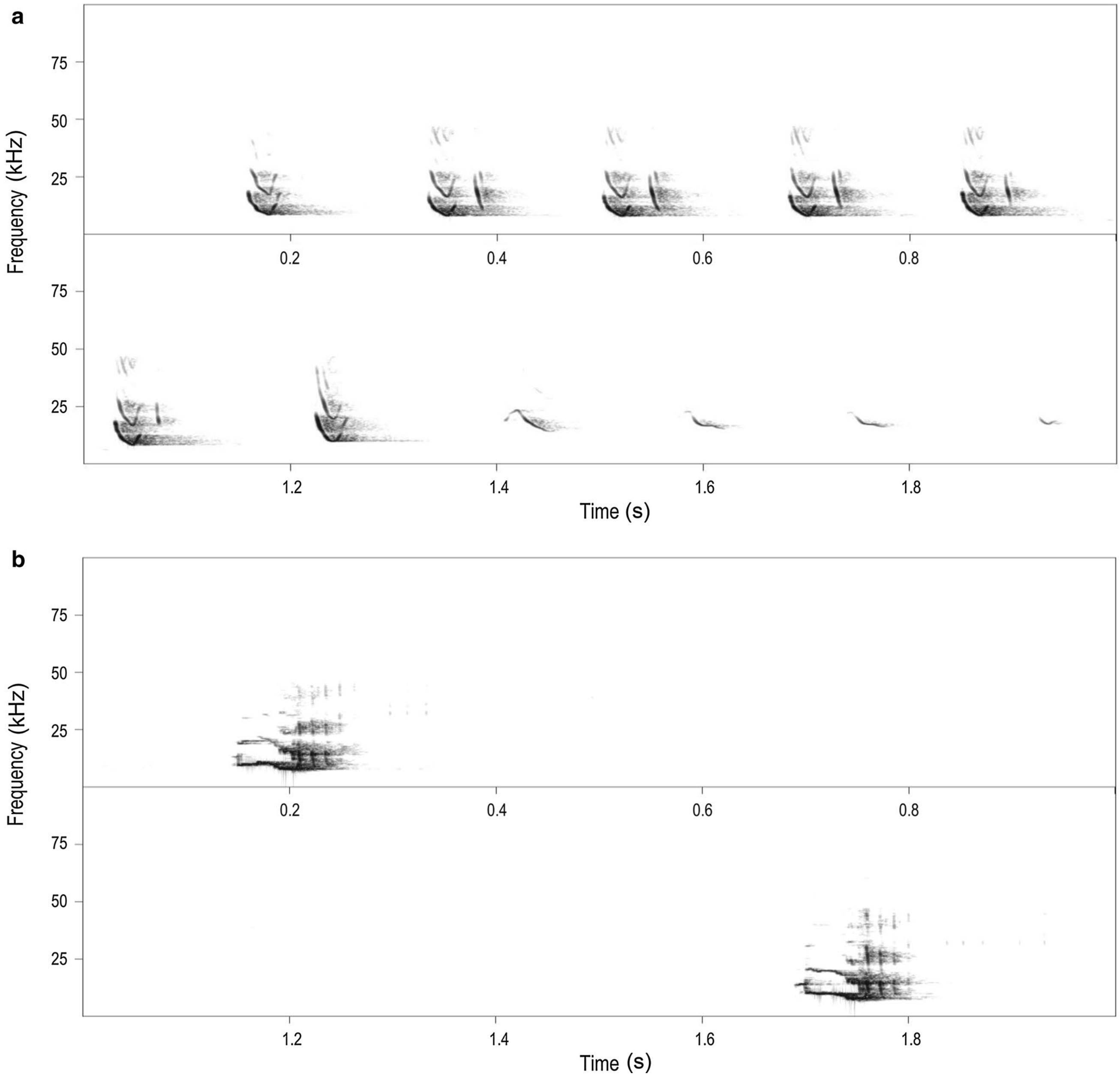


Fig. 2 Megadermatidae songs. **a** *Cardioderma cor* territorial song sung from a perch within the animal's foraging territory. **b** *Lavia frons* territorial calls uttered from perches while patrolling territory borders in the early evening

individuals to support the discrimination of neighbors by their singing (Smarsh and Smotherman 2015). However, whether *C. cor* possesses different song types for different functions, vary their song compositions in different behavioral contexts, or use singing to attract and retain mates are important open questions.

Vaughan also described a similar behavior in the sympatric yellow-winged bat *Lavia frons* (Vaughan and Vaughan 1986*)*. This bat differs from *C. cor* in being an aerial hawking insectivorous bat and exhibits more isolate social behaviors. *L. frons* is unique among the African insectivorous bats in that it forms long-lasting pair bonds. Mated pairs share a tree roost centrally located within their private territory and cooperatively raise pups. Like *C. cor*, the yellow-winged bat moves about its territory at dusk advertising its presence by loud bouts of a singing-like behavior, although *L. frons* utters shorter and simpler vocalizations than those of *C. cor* (Fig. 2b). Male *L. frons* patrol the borders of their territories at sunset, stopping at routine intervals to broadcast their calls from favored perches. Although the behavior resembles singing in the sense that the males move about their territory spontaneously broadcasting an orderly, rhythmic vocal sequence (Vaughan and Vaughan 1986; Smith 1991), the simple acoustic properties are more consistent with what would generally be labeled calls. Vaughan hypothesized that *L. frons* used these vocalizations to defend resource-rich territories that could get them through the long stressful dry season. The territorial calling of *L. frons* is in many ways analogous to singing by the black-capped chickadee (*Poecile atricapillus*), an oscine passerine that supports a sophisticated repertoire with a comparatively simple two-note "fee-bee" call (Christie et al. 2004; Mennill and Ratcliffe 2004), while *C. cor*'s longer, more complex songs are more reminiscent of songbirds such as the swamp sparrow (*Melospiza georgiana*). Why *C. cor* uses elaborate songs while *L. frons* appears to achieve a similar goal with simpler calls is unclear, but may be related to differences in their social systems, preferred prey types, and population densities. Notably *L. frons* never leave their home territories while *C. cor* returns to reestablish boundaries every night, which may underlie the more elaborate singing displayed by the heart-nosed bats.

Vespertilionidae

There are several notable examples of territorial singing during flight (or flightsong), particularly among the European pipistrelles. Most use calls or songs of similar acoustic structure for both territorial and courtship behaviors (Lundberg and Gerell 1986; Barlow and Jones 1997a; Sachteleben and von Helversen 2006; Russ and Racey 2007; Jahelková et al. 2008; Georgiakakis and Russo 2012), but the timing and context in which they are uttered defines their function. Territorial flightsong is produced throughout summer while courtship flightsong appears restricted to the mating season in the fall. A notable exception to this is *Pipistrellus hanaki*, which produces different song types for territorial and courtship purposes (Georgiakakis and Russo 2012). Sachteleben and von Helversen (Sachteleben and von Helversen 2006) reported that Bavarian male *Pipistrellus pipistrellus* arrange their territories in such a way that females must pass through them in search of winter roosting sites (Lundberg and Gerell 1986). The genus *Pipistrellus* contains 30 widely distributed species of relatively small bats. Pipistrelles are common in urban habitats, roosting in buildings and rooftops, and their propensity to use flightsong in defense of both foraging and a courtship territory is well documented (Lundberg and Gerell 1986; Barlow and Jones 1997b; Jahelková et al. 2008; Budenz et al. 2009; Georgiakakis and Russo 2012). Foraging males of the species *P. pipistrellus* patrol densely abutting territories above the city at night and use flightsong to ward off intruders (Sachteleben and von Helversen 2006). Singing while flying may be energetically favorable, but it is also constrained by biomechanical issues not present when perched. These constraints manifest differently in birds and bats owing to major differences in their respiratory physiology and flight mechanics. For bats in flight, breathing and vocalizing are tightly coupled to wingbeat patterns (Suthers et al. 1972; Speakman and Racey 1991), and in small bats the entire wingbeat cycle is often shorter than 100 ms. A single flightsong must therefore be self-contained within the short time frame of a single wingbeat or longer compositions spanning multiple wingbeats would necessarily include longer or irregular silent intervals. For the most part pipistrelles appear to compose their territorial flightsongs of short rapid bursts of special communication calls compressed within a single wingbeat, but some species produce flightsongs that comprised 8–10 different syllables spanning several 100 ms (Georgiakakis and Russo 2012). Again, these shorter songs might be more appropriately labeled calls, but like *L. frons* the context in which these calls are performed, courtship and territorial defense, distinguishes the behavior as singing-like and prompted the many different investigators cited above to label it so. Pipistrelle flightsongs are quite reminiscent of those uttered by passerine birds such as the Dickcissel (*Spiza Americana*), Indigo Bunting (*Passerina cyanea*) and Rose-breasted grosbeak (*Pheucticus ludovicianus*).

Emballonuridae

The most thoroughly studied example of bat singing behavior comes from the family Emballonuridae, or sac-winged bats, and in particular the greater sac-winged bat *Saccopteryx bilineata*. Colonies of *S. bilineata* inhabit a roost that is centrally located within a foraging home range covering averaging approximately 6 hectares (Bradbury and Vehrencamp 1976), wherein individuals were described as foraging opportunistically across a series of preferred foraging sites. *S. bilineata* and other Emballonuridae have been reported to aggressively defend preferred foraging sites, particularly those immediately surrounding their day roost; however, singing has not been described during foraging (Bradbury and Vehrencamp 1976). Like the pipistrelles examples, *S. bilineata's* singing serves both territorial and a courtship function, but the singing has only been observed at the roost. *S. bilineata* exhibit resource-defense polygyny; males defend harems on small day roost territories usually located on tree buttresses or on man-made structures. Colonies of up to 60 animals have been reported but harems typically include less than 10 females (Nagy et al. 2012). Resident colony males are descended from few patrilines (Nagy et al. 2007). Males use stereotyped territorial songs to defend their roosting territories from other males year round, and they use complex courtship songs to attract and retain females to their harem (Behr and von Helversen 2004). Courtship songs are by comparison much longer,

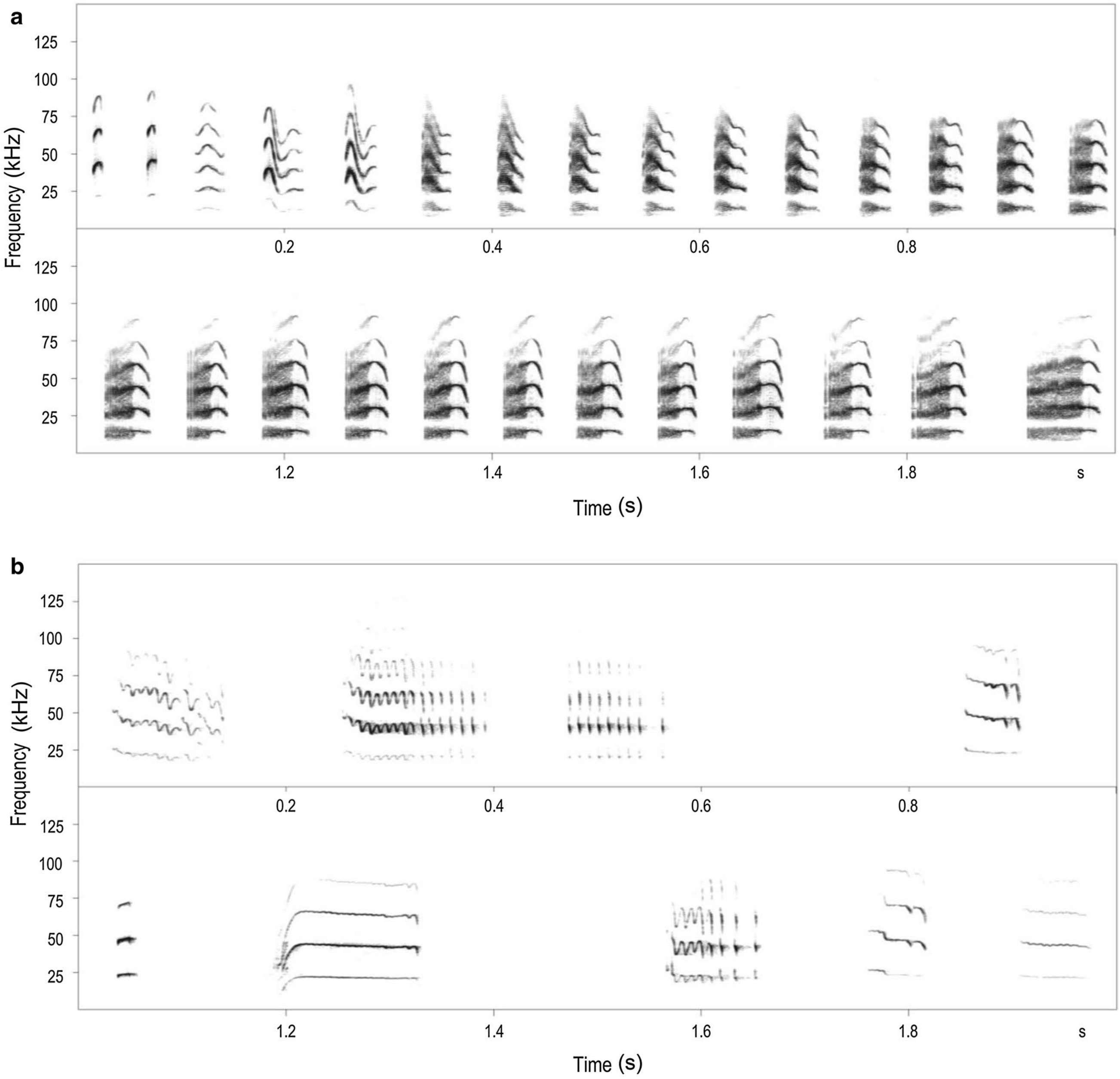


Fig. 3 *Saccopteryx bilineata* songs. **a** Territorial song produced by reproductive males during dusk and dawn to defend their day-roost territory against male competitors. **b** Male courtship song excerpt produced during a multimodal courtship display

generally lasting more than 40 s, and they are composed of more variable, higher frequency syllables including a high proportion of trills (Fig. 3b). Despite a high degree of intra-individual variability in song composition, each bat's courtship songs possess unique acoustic features permitting individual identification (Behr and von Helversen 2004). Different males display different repertoires, and males with more elaborate repertoires have more females in their harem (Behr and von Helversen 2004; Davidson and Wilkinson 2004). Harem males are able to discriminate the sex of approaching conspecifics by the acoustic properties of their echolocation pulses and thereby selectively broadcast the appropriate song type (Knörnschild et al. 2013), directing territorial songs at approaching males and courtship songs at approaching females.

Territorial songs are characterized as lasting roughly 1.5 s and composed of 10–50 mostly tonal syllables that merge into low-frequency end syllables with a distinctly pulsed buzz (Fig. 3a) (Behr and von Helversen 2004). Territorial songs encode both individual and group signatures (Eckenweber and Knörnschild 2013) and low-frequency songs elicit stronger countersinging in playback experiments than high-frequency songs (Behr et al. 2009). Singing is observed most frequently at sunset and sunrise and is primarily triggered by the singer hearing the pulses of a conspecific approaching or leaving the roost. The behavioral trigger is significant because it assures that bat only expends energy singing in the appropriate context, influencing who enters and leaves the roost and when.

Molossidae

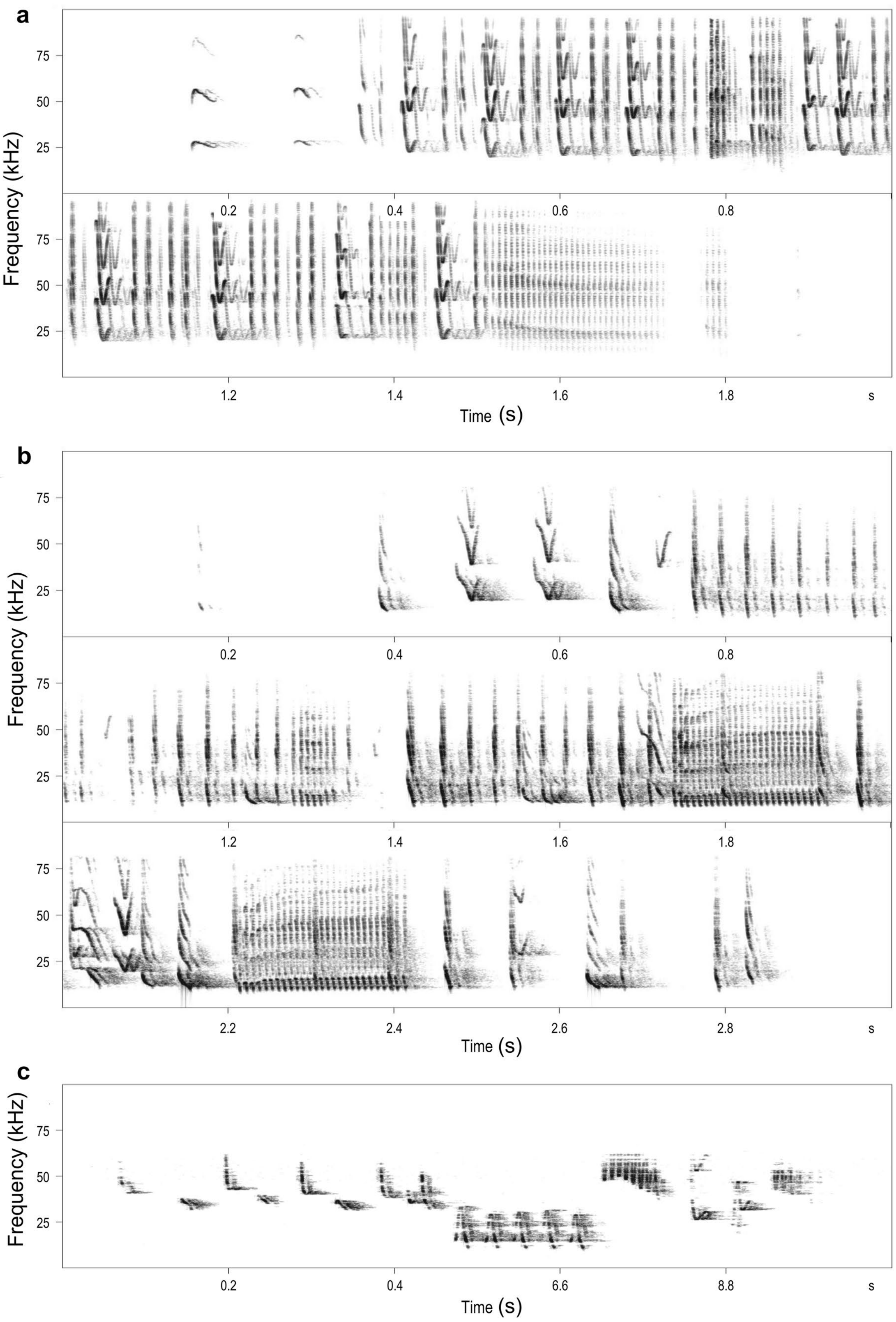
The family Molossidae is large, diverse (16 genera, 86 species) and widely distributed (Novak 1994). Some species are notably gregarious, forming dense colonies of millions in a single cave while others form small colonies in caves, trees and man-made structures. The Brazilian or Mexican free-tailed bat, *Tadarida brasiliensis* is flexible in its roosting and foraging behaviors, is widely distributed throughout North and South America, and is perhaps best distinguished by its biannual migrations spanning thousands of miles, traveling south in the fall to avoid freezing temperatures and returning north each spring to take advantage of fruitful temperate foraging grounds (Davis et al. 1962). Mating occurs during early spring before or during the northward migration. Males form small colonies along the migratory routes wherever they can find a suitable day roost, but may travel more than 100 km each night in search of prey (Best and Geluso 2003; Horn and Kunz 2008). Territorial defense of such large foraging areas is impractical and unlikely, but reliable day roosts, even temporary ones, are a limited resource and male *T. brasiliensis* aggressively defend these (Bohn et al. 2009; Schwartz et al. 2007). From within their day roosts male *T. brasiliensis* are prolific singers, using song particularly during the early spring to repel males and alert passing females to the presence and location of their roost (Bohn et al. 2013).

Like the sac-winged bats, the free-tailed bat sings mostly at sunset and sunrise, a pattern that arises because songs are evoked by hearing the echolocation pulses of bats entering and exiting neighboring roosts (Bohn et al. 2013). Male *T. brasiliensis* sit poised just within the entrance to their roost alertly listening for the echolocation sounds of an approaching bat, and upon hearing the pulses begin to loudly and repeatedly broadcast their songs (Bohn et al., 2013). Unlike the sac-winged bats, however, male free-tailed bats cannot discriminate the sex of a passing conspecific based solely on their pulse acoustics (Gillam and McCracken 2007; Tressler and Smotherman 2009; Tressler et al. 2011). Perhaps it is because they do not know the gender of a passing bat that these composite songs must carry more than one message.

Free-tailed bat songs are composed of several syllables and three stereotyped phrases that follow a hierarchically organized composition (Fig. 4a) (Bohn et al. 2008, 2009). Songs often begin with a tonal introductory note, and are then composed of chirp, trill and buzz phrases whose number and order vary greatly from one song rendition to the next, resulting in a rich repertoire of unique combinations (Bohn et al. 2009). Chirp phrases are in turn composed of two types of syllables, downward FM sweeps that are no different than echolocation pulses (type A syllable) and a more complex frequently modulated upper-harmonic tonal call (type B syllable) that is similar in design to the begging calls used by pups to attract the attention of their mothers (Gelfand and McCracken 1986; Balcombe and McCracken 1992). Conversely, sometimes males produce trill phrases to herd females within their territories (Bohn et al. 2008), and males also use the terminal buzz at the end of the song as a stand-alone syllable during bouts of fighting and intrasexual aggression (Schwartz et al. 2007). Thus, the song appears to contain both an affiliate component directed at females and a threat component warding off approaching males, a pattern of song composition also seen in *M. lyra* (Leippert 1994) and some pipistrelles (Jahelková et al. 2008) (described below). These observations provide an important clue to understanding the evolution of compound song architecture: multiple distinct syllables and phrases are required when songs serve multiple functions. In the greater sac-winged bat, small, stable group sizes and echolocation pulse structure facilitates individual identification and therefore more personalized vocal responses, while in the free-tailed bats (at least among *Tadarida*), massive colony sizes, expansive migratory patterns and plastic echolocation pulse design may drive the use of dualistic song compositions.

Mating systems

Sexual selection played a significant role in the evolution of birdsongs (Collins 2004). Songs may directly or indirectly carry honest information about the singer's fitness, and consequently sexual selection is expected to promote more complex and elaborate song repertoires in birds where female preference is a driving factor (Collins 2004). Most birds are socially monogamous, whereas most mammals exhibit some form of polygynous mating system (Wink and Dyrcz 1999; McCracken and Wilkinson 2000). Monogamy is rare among mammals, but may be unusually common among bats where it has been reported for roughly 25 % of the species for which the mating system is known (Wittenberger and Tilson 1980; McCracken and Wilkinson 2000). Among songbirds polygyny was negatively correlated with song rate but positively correlated with song complexity and repertoire size (Read and Weary 1992), indicating that song output is strongly affiliated with the formation of lasting social bonds and song complexity arises conditionally


a
Frequency (kHz)
75
50
25
0.2
0.4
0.6
0.8
1.2
1.4
1.6
1.8
s
Time (s)
b
Frequency (kHz)
75
50
25
0.2
0.4
0.6
0.8
1.2
1.4
1.6
1.8
2.2
2.4
2.6
2.8
s
Time (s)
c
Frequency (kHz)
75
50
25
0.2
0.4
6.6
8.8
s
Time (s)

◀ **Fig. 4** Courtship/territorial songs of three different members of the Tadarida genus (Molossidae): **a** *Tadarida brasiliensis* recorded in Texas, USA; **b** *Tadarida teniotis* recorded in Portugal; **c** *Tadarida pumila* recorded in northern Tanzania

under more intense sexual selection such as in polygynous mating systems. Another aspect of mating that has been shown to influence singing in birds is fecundity; males tend to sing more frequently and continuously among species with higher annual fecundities (clutch sizes) (Read and Weary 1992). Bats almost exclusively give birth to one or two offspring per year. Since there are no species with unusually high reproductive rates, fecundity is unlikely to influence singing behaviors in bats. Based on the evolutionary patterns identified in birds, the central questions in bats are (1) whether or not lasting social bonds are positively correlated with song production and (2) whether sexual selection has promoted more complex song repertoires. The limited evidence available suggests that singing is correlated with resource-defense polygyny (*S. bilineata*, several species of *Tadarida*, several species of *Pipistrellus*, and *M. lyra)* with varying levels of group cohesion. *L. frons* and *C. cor* have both been labeled monogamous (Vaughan 1976; Mcwilliam 1987; Vaughan and Vaughan 1986), but this needs to be confirmed for *C. cor* and both species seem to sing for territorial more so than courtship purposes. Clearly we will need many more species examples before a comparative analysis is justified. However, it must first be demonstrated that singing influences mating choice and reproductive success in bats, and this has been done in several species.

Courtship songs and sexual selection

The Indian false vampire bat *M. lyra,* so named for its *lyrical* behaviors, has been reported to use "melodious" courtship songs to attract mates (Leippert 1994; Schmidt 2013). In colonies of *M. lyra,* only the dominant male in a group sings around the roost at night and singing usually precedes mating (Leippert 1994). The compound song contains both aversive and affiliative syllables, and there is sufficient variability in syllable acoustics to support individual recognition and female assessment of male fitness (Schmidt 2013). Leippert hypothesized that males sang throughout the year to sustain long-term relationships with females and defend their positions in a social hierarchy. *M. lyra* uses song for maintaining a social dominance hierarchy while *C. cor* appears to sing principally in defense of a foraging territory. The increased variability of *M. lyra's* songs relative to *C. cor* is consistent with hypotheses that sexual selection exerts a positive influence on song complexity and repertoire size.

The best evidence for sexual selection comes from the long-term acoustic analyses and paternity studies of *S. bilineata's* harems. Microsatellite DNA analyses confirmed that male song provided an honest signal of territory holder quality that influenced competitiveness, mating opportunities and ultimately the number of offspring sired by the singer (Behr et al. 2006). Correspondingly it was shown that males produce more territorial songs with increasing male–male competition (Behr et al. 2009; Eckenweber and Knörnschild 2013).

Among Vespertilionidae, *Pipistrellus pygmaeus* in Sweden exhibits a resource-defense polygyny mating system in which the males use flightsong to protect and maintain a day roost located within their territory that housed multiple females (Lundberg and Gerell 1986). In that study more females visited males that spent the most time uttering flightsong. Other members of the family, including the northern European bats *Vespertilio murinus* (Zagmajster 2003), *Nyctalus leisleri (*von Helversen and von Helversen 1994; Weid 1994*)* and *Nyctalus noctula* (Ruczynski et al. 2007) have also been reported to use flightsong in the late fall to capture the attention of passing females searching for roosts to overwinter. These observations demonstrate that females respond to the courtship songs, but precisely which song parameters influence their decision-making and whether or not it actually enhances reproductive success remain to be determined.

Migratory behaviors

In songbirds, migratory species have larger syllable and song repertoires than their congeners (Read and Weary 1992). It was hypothesized that migratory species have less time to establish a territory and attract a mate than continuous resident species, leading to more intense sexual selection favoring greater song complexity (Catchpole 1980; Catchpole and Slater 2008). Among singing bats, the tropical species (*Saccopteryx*, *Cardioderma, Lavia*) do not migrate, although *C. cor* may make seasonally movements to follow prey (Vaughan 1976). Several examples of singing do derive from migratory temperate species. Among the European species of pipistrelles the males are believed to arrange their foraging territories along migration paths, but the species with the most substantial seasonal migration (*P. nathusii*) displays the most complex songs within the genus (Gerell-Lundberg and Gerell 1994; Zahn and Dippel 1997; Jarzembowski 2003; Jahelková et al. 2008; Jahelková and Horáček 2011). The songs of pipistrelles are typically very simple; however, so while sexual selection may have encouraged singing it has not promoted complex repertoires. *T. brasiliensis* has a very complex and flexible song composition (Bohn et al. 2009; Bohn et al. 2013) and migration plays a very big role in its mating strategy. Male *T. brasiliensis* use singing to lure females into their roosts during the long spring migrations (Davis et al. 1962), and its often the case that many nearby males can all be heard to sing intensely in response to a single passing bat, with all possessing equally suitable day roosts (Smotherman, personal observation). However, neither the European species *T. teniotis* or the African species *T. pumila* undergo expansive annual migrations like *T. brasiliensis*, although short seasonal migrations are possible. This might reflect phylogenetic history if the *Tadarida* song composition evolved very early in this genus. Likewise, the fact that pipistrelles songs are fairly simple may reflect phylogenetic constraints arising from the fact that this genus commonly sings in flight, which limits phrase lengths and song composition. Overall there is convincing evidence that migratory behaviors are positively correlated with singing behaviors in bats, but there is not a strong connection between migration and vocal complexity as suggested for songbirds.

Repertoire size, complexity and vocal learning

Phonological syntax refers to the specific temporal patterns of composite syllable types used to create distinctive songs. Different song types serve different behaviors in distinct contexts. Songbirds may broaden their song repertoires either by adding distinct song types for different functions or by flexibly modifying the phonological syntax of a primary song with changing context. *S. bilineata* provides an example of increased repertoire size through the addition of distinct song types (Behr and von Helversen 2004). *T. brasiliensis* provides evidence that bats can also increase repertoire size via flexible phonological syntax (Bohn et al. 2013).

Vocal learning in birds is hypothesized to have evolved in support of more elaborate song repertoires. Bats are one of the few mammalian taxa for which the capacity for both social modification of innate vocalizations and learned acquisition of new vocalizations has been demonstrated (Knörnschild 2014). There are several lines of evidence of a capacity for vocal learning in bats (Esser 1994; Boughman 1998; Knörnschild et al. 2006, 2009; Knörnschild 2014), but definitive evidence of song learning is elusive, largely because of technical challenges associated with rearing singing bats in isolation. The question is significant because among birds vocal learning is only found among three clades, the oscine songbirds (Passiformes), parrots (Psittaciformes) and hummingbirds (Apodiformes), where it provided a powerful mechanism for more rapid diversification among sympatric species by creating regional dialects and promoting cultural evolution (Farries 2004; Catchpole and Slater 2008). Many of the suboscine non-vocal-learning birds also sing but do not learn song and develop their species-specific song even in the absence of hearing (Kroodsma 2004). Although the suboscines vary widely in song composition and repertoire size, some evidence exists for vocal matching, regional dialects and vocal learning (Trainer et al. 2002; Kroodsma 2004; Seddon 2005). Whether or not vocal learning contributes significantly to any bats singing behavior remains largely unanswered, but vocal learning of songs has been examined in *S. bilineata*. There, Knörnschild and colleagues demonstrated that infant sac-winged bats use babbling behaviors similar to primates and songbirds to experiment with novel vocalization patterns during a critical period of development (Knörnschild et al. 2006) and that pups of both sexes imitate territorial songs from their parental tutor during babbling bouts (Knörnschild et al. 2006, 2009).

Until more details emerge about the proximate and ultimate mechanisms of vocal learning in bats, it is impossible to know whether there exists a similar subdivision among bats separating vocal learners and non-learners or whether this capacity is functionally linked to song complexity as it is in birds. In the meantime, the diverse singing behaviors so far described in bats appear most analogous to the range displayed by the suboscine songbirds.

Phylogenetic constraints and evolutionary patterns

Echolocation might constrain singing

The evolution of bats is approaching a consensus with regards to the phylogenetic definition of the larger monophyletic groups (Jones et al. 2002), but attempts to reconstruct the evolution of echolocation are confounded by the extensive adaptive radiation patterns overriding phylogenetic constraints (Jones and Teeling 2006). The finely tuned bat auditory system has necessarily evolved in concert with echolocation behaviors and consequently imposed a constraint on social communication that would not have been present in birds or other mammals (Bohn et al. 2006). In most instances the optimal acoustics for echolocation pulses would not be optimal for long-range communication behaviors. The bat larynx had to undergo substantial specializations to produce ultrasonic pulses (Suthers 1988), and because the rate of atmospheric attenuation increases with frequency, the ultrasonic pulses produced by bats are poorly suited for communication over the ranges that birds typically use singing for. Additionally, there is an inverse relationship between pulse frequency and body size in echolocating bats; smaller bats emit higher frequency pulses (Schnitzler and Kalko 2001) which have the potential to constrain singing in very small bats. A meta-analysis by Bohn et al. (2006) found evidence that the pitch of a species' biosonar pulses co-varied with the pitch of their social calls, the two presumably linked by upward shifts in the most sensitive bandwidth of the auditory system. There is no evidence that this has constrained singing however, since several examples of singing already come from relatively small bats. Those bats appear to have escaped any constraints emerging from their biosonar by either (a) employing a biosonar system with harmonic components that accommodate both high-frequency pulse emissions and low-frequency calls and singing (for example, long quasi- or constant-frequency multi-harmonic pulses); (b) relying upon a broadly tuned auditory system (for example, bats that utilize flexible broadband FM pulses), or (c) having segregated physiological adaptions for producing and processing their biosonar and social vocalizations. There is evidence that for many bats, social calls and echolocation pulses are produced by distinct neuromotor pathways (although both are produced by a common larynx) and that these sounds may be processed separately in the auditory system (Pollak and Casseday 1989; Metzner and Schuller 2007), and indeed some bats exhibit separate low-threshold auditory sensitivities for biosonar and social sounds (Bohn et al. 2006). There is evidence of all three possibilities in the examples outlined above. Megadermatidae emit short, high-frequency broad-band sonar pulses but use low-frequency tonal calls and songs, consistent with a separate social and sonar vocal motor systems and a broadly tuned auditory systems (Möhres and Kulzer 1957). The greater sac-winged bat uses quasi-constant frequency multi-harmonic sonar pulses and songs that overlap with the lower bandwidth of their sonar range. *T. brasiliensis* uses highly flexible broadband multi-harmonic sonar pulses and has songs that overlap with the lower range of its pulse emission bandwidth. Notably, *Tadarida* incorporates sonar pulses into its song composition, and both *T. brasiliensis* and *S. bilineata* use broadband buzzes in their songs. Songs from the genus *Pipistrellus* are of a comparatively high frequency (30–50 kHz), but fall within the lower bandwidth as their sonar pulses. Some of the highest frequency echolocation pulses are found among Rhinolophidae, so it is notable that a high-frequency (≈80 kHz) "song" was described in the horseshoe bat, *Rhinolophus ferrumequinum* (Ma et al. 2006). Thus, while there are many reasons why echolocation might constrain singing, it cannot be concluded that echolocation precludes singing even for bats that emit very high frequency ultrasonic pulses.

How often has singing evolved in bats?

Even if singing turns out to be widespread in bats, current evidence supports the hypothesis that singing or singing-like calling behaviors have emerged independently several times. Singing has been reported most often among the superfamily Vespertilonoidea, which includes members of the Vespertilionidae (*Myotis, Pipistrellus, Vespertilio, Neoromicia, and Nyctalus* species) and Molossidae (*Tadarida* species). Singing appears to be common to the *Tadarida* genus, but other Molossidae species appear restricted to using simple territorial calls (*Molossus rufus and M. molossus* (Bohn personal observation). *Tadarida* songs are readily distinguished by common song architecture. Songs recorded from three different species of *Tadarida* on three different continents illustrate the characteristic features of the genus (Fig. 4a–c), including the two-note repeating syllable pattern in the body of the song and the incorporation of buzzes. However, some species-specific variations in song features are also recognizable. Figure 4b illustrates a song recorded from *T. teniotis* in Europe (recorded by Bohn), and Fig. 4c a song from *T. pumila* in East Africa (recorded by Smarsh). The unmistakable similarities between the songs of these three species suggest that the basic song structure of *Tadarida* was already established when these species diverged roughly 21 million years ago (Ammerman et al. 2012). The songs of these *Tadarida* species are very different from the songs and singing behaviors displayed by the Vespertilionidae, which also share some similarities in the phonological syntax and acoustics, including quasi- frequency-modulated pulse-like vocal sequences often including warble-type syllables. Thus, we would hypothesize that singing-like behaviors associated with foraging and roosting territories probably evolved fairly early among the Vespertilionidae, likely originating with the use of simple species-specific calls for courtship and territorial defense that were later elaborated into compound sequences in some lineages. Since singing in *Tadarida* seems closely linked with migration, which may be a derived trait among Molossidae, singing may have evolved fairly recently in that genus alone.

Phylogenetic analyses place Megadermatidae as one of the earliest offshoots of the Yinpterochiroptera, and singing-like behaviors along with other complex vocalizations are common to this group. Only *M. lyra* and *C. cor* display true songs, but *L. frons* use of spontaneous call sequences as they patrols territory borders is reminiscent of the simple singing behaviors exhibited by many birds. The common theme in this family may be their stable social groups and foraging territories. While singing may have emerged independently in *M. lyra* and *C. cor*, its ecological roots are apparent in the foraging ecology and mating behaviors of the entire family.

S. bilineata is not the only member of Emballonuridae that sings. There are 16 genera and 62 species (Lim and Dunlop 2008), far more than Megadermatidae, and other species of sac-winged bats are prolific singers, such as *Peropteryx kappleri* (Smotherman, personal observations) and *Rhynchonycteris naso* (Knörnschild, Nagy, personal observations). Many of these utilize a polygynous-harem style mating system similar to *Saccopteryx*, but there is also a broad diversity of roosting ecology and social systems within the family (Bradbury and Vehrencamp 1977). Lacking evidence of singing in their closest relatives, the Nycteridae, it must be concluded that singing may have emerged fairly recently among a subgroup of Emballonuridae. Thus the comparative study of singing among the sac-winged bats has the potential to be a profitable path for elucidating the relationship between sociality and singing in bats.

The neural substrate for singing in bats

Despite substantial efforts to elucidate the neural control of echolocation (Neuweiler 2000; Metzner and Schuller 2007; Smotherman 2007) there are few clues about where to look for the neural substrate for song production in bats, and major differences in avian and mammalian brain architecture allow for only tenuous predictions based on hypothetical neuroanatomical analogies (Jarvis et al. 2005). Male oscine songbirds possess a dedicated network of forebrain nuclei for vocal learning and song production that does not exist in mammals. The mammalian brain architecture differs from that of birds and reptiles in that its functional organization was fundamentally redefined by the addition of a layered cortex, which is believed to have enhanced the efficiency and capacity of brains to integrate and transfer information across sensory, motor and cognitive systems (Butler and Hodos 2005). The behavioral significance of this is controversial, but appreciating how this fundamental change in neural hardware impacted the evolution of communication may prove central to understanding how human speech and language evolved. Typical mammalian syllables are encoded by endogenous central pattern generators selectively triggered by descending motivational inputs (Metzner and Schuller 2007; Hage 2010). Nothing is currently known about how flexible combinations of syllables might be orchestrated in the mammalian brain. Some of the more specialized midbrain neurocircuits supporting the echolocating bats' abilities to rapidly manipulate their pulse acoustics have been identified (Gooler and O'Neill 1987; Smotherman 2007), but critical details about how even a simple echolocation pulse is produced are elusive. There is experimental evidence that free-tailed bats incorporate a basal ganglia circuitry into their sensorimotor control of the vocalizations (Schwartz and Smotherman 2011; Tressler et al. 2011), which is important because both humans and songbirds were previously shown to rely upon basal ganglia circuits to learn and produce normal vocalizations. The basal ganglia play an important role in motor learning and sensorimotor integration in both songbirds and mammals (Doupe and Kuhl 1999; Doupe et al. 2005), and although their precise role in speech is poorly understood their pathological disruption is linked to some of the most common speech disorders (Vargha-Khadem et al. 1998; Duffy 2005). Characterizing the neural substrate for bat songs has the potential to shed new light on the mechanisms with which the mammalian brain rhythmically links syllables together to more efficiently tailor communication to social and environmental context. However, these neurobiological questions will be better served by more detailed behavioral analyses of the breadth and capacity of singing in more bats, especially those that can be bred in captivity. For the intrepid young scientist interested in animal communication, the study of bat song may afford novel opportunities at many levels of inquiry.

Synthesis and future directions

Most species of bats that sing appear to do so in defense of foraging or roosting territory, but there are also many examples where song repertoires appear expanded or tailored to support courtship behaviors, which is consistent with the general pattern of song evolution proposed for birds (Morton 1986; Read and Weary 1992; Marler and Slabberkoorn 2004; Catchpole and Slater 2008). We have presented evidence that batsong repertoires can be expanded either through the addition of discrete song types, by varying song composition, or through a combination of the two mechanisms. Expanding repertoire size may further support added functions such as individual recognition, group affiliation, social status, and fitness. These functions might be related to some standardized measures of social complexity, and the observations summarized here warrant the hypothesis that there may exist a correlation between vocal and social complexity across bat species. This is a central theme for interpreting the evolution of acoustic communication, including human speech, and may be an area where bats can contribute novel insight. Moving forward it will be profitable to characterize singing behaviors among new species reflecting the full diversity of social structures and mating systems in bats (McCracken and Wilkinson 2000).

The bat singing behaviors so far include relatively simple calls used in singing-like behaviors for territorial defense (*L. frons* and some *Pipistrellus* species) to highly complex and flexible song repertoires used for combinations of courtship and territorial purposes (e.g., *T. brasiliensis, S. bilineata, M. lyra*, *Pipstrellus nathusii*). These examples overlap with a significant spectrum of bird singing behaviors, reinforcing the hypotheses that bats receive the same benefits as birds when they sing and are subject to many of the same costs that have shaped birdsong. Importantly, one of the key benefits, energy savings associated with powered flight, is unique to birds and bats, which may be why singing is otherwise rare among mammals. The singing examples reported for mice and voles are for courtship purposes and are used in close encounters, and the ecological significance of singing in gibbons is unknown but probably associated with group cohesion, as many arboreal primates use long calls for this purpose. Interpreting bat songs within the context of birdsong ecology leads to predictions that (1) simple, highly stereotyped songs should be relatively common among species in which males regularly compete for private roosts and foraging territories (i.e., intrasexual selection), and (2) more elaborate repertoires and complex songs should be anticipated wherever intense intersexual selective pressures exist (i.e., polygyny).

Obviously more data are needed, but there are reliable indications that many more bat species might sing and the tools are now available to investigate these possibilities. There are several major taxonomic groups of small bats whose vocal repertoires and social behaviors deserve greater attention. Chief among these are the widely distributed old world horseshoe bats (Rhinolophidae), which are sister taxa to the Megadermatidae and many of which are territorial ambush predators with high foraging site fidelity (Neuweiler et al. 1987). Many species of horseshoe bats are socially gregarious in the roost, but may return nightly to private foraging territories, much like *C. cor*, and there is evidence from the lab of an underappreciated repertoire of social vocalizations that includes songs (Ma et al. 2006). Likewise, the new-world mustached bat *Pteronotus parnellii* uses complex vocal syntax and displays an elaborate vocal repertoire in captivity (Kanwal et al. 1994), but little is known about the functional significance of these vocalizations or their social behaviors in the wild. These and other species offer profitable avenues for investigating the evolutionary interactions between the social and vocal behaviors of mammals.

The influence of sexual selection on the elaboration of vocal complexity continues to be a hotly debated question. In this context lekking bats become especially intriguing. A lek is an aggregation of males during the breeding season that compete for the attention of females through exaggerated visual and acoustic displays. Under these conditions sexual selection can have profound influences on the elaboration of signal traits. The hammer-headed bat *Hypsignathus monstrosus* is a lek breeder that conspicuously uses courtship calls along with wing-flapping displays during lekking (Bradbury 1977). *H. monstrosus* is a large yinpterochiroteran, and a group of the loudly croaking males were likened to "a pond full of noisy American wood frogs" (Lang and Chapin 1917). These acoustically simple courtship calls fall outside the range of what we characterize as singing. However, lekking is also found in a small yangochiropteran, the New Zealand lesser short-tailed bat, *Mystacina tuberculata*, which is also known to sing highly variable vocal sequences while lekking (Toth et al. 2015). During the mating season males gather together in small groups to sing in small clusters around tree cavities (Lloyd 2001; Carter and Riskin 2006; Toth et al. 2015), but a detailed analysis of the acoustic properties of these vocalizations is lacking. Reduced interspecific competition, the absence of major predators and ample roosting sites (Sedgeley 2003) may have created a unique set of conditions in New Zealand wherein sexual selection rather than territoriality per se has played a larger role in shaping the singing behavior of this bat.

In conclusion, it is proposed that singing may be an important and widespread phenomenon among bats. The small but rapidly expanding list of singing bats reflects technical constraints that have only recently been breached, which leads to the prediction that over the next few decades many more examples of bat song can be expected. The combination of powered flight, territorial behaviors, sexual selection and a unique dependence upon acoustic communication makes singing advantageous to bats for the same reasons singing became a hugely successful adaptation in birds. Singing appears most beneficial when it mitigates the high costs of flying, which is likely why singing is otherwise very rare among mammals. Studying singing in bats will be important because it provides a new window into the behavioral ecology of one of the most diverse groups of animals on earth.

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References

Altringham JD, Fenton MB (2003) Sensory ecology and communication in the Chiroptera. In: Kunz TH, Fenton MB (eds) Bat ecology. University of Chicago Press, Chicago, pp 90–127

Ammerman LK, Lee DN, Tipps TM (2012) First molecular phylogenetic insights into the evolution of free-tailed bats in the subfamily Molossidae (Molossidae, Chiroptera). J Mammal 93:12–28

Arnold K, Zuberbühler K (2006) Semantic combinations in primate calls. Nature 441:303

Balcombe JP, McCracken GF (1992) Vocal recognition in Mexican free-tailed bats—do pups recognize mothers? Anim Behav 43:79–87

Barak Y, Yom-Tov Y (1991) The mating system of *Pipistrellus kuhli* (Microchiroptera) in Israel. Mammalia 55:285–292

Barlow KE, Jones G (1997a) Differences in songflight calls and social calls between two phonic types of the vespertilionid bat *Pipistrellus pipistrellus*. J Zool 241:315–324

Barlow KE, Jones G (1997b) Function of pipistrelle social calls: field data and a playback experiment. Anim Behav 53:991–999

Batzli GO, Henttonen J (1993) Home range and social organization of the singing vole (*Microtus miurus*). J Mammal 74:868–878

Behr O, von Helversen O (2004) Bat serenades-complex courtship songs of the sac-winged bat (*Saccopteryx bilineata*). Behav Ecol Sociobiol 56:106–115

Behr O, von Helversen O, Heckel G, Nagy M, Voigt C, Mayer F (2006) Territorial songs indicate male quality in the sac-winged bat *Saccopteryx bilineata* (Chiroptera, Emballonuridae). Behav Ecol 17:810–817

Behr O, Knörnschild M, von Helversen O (2009) Territorial counter-singing in male sac-winged bats (Saccopteryx bilineata): low-frequency songs trigger a stronger response. Behav Ecol Sociobiol 63:433–442

Best TL, Geluso KN (2003) Summer foraging range of mexican free-tailed bats (*Tadarida brasiliensis* mexicana) from Carlsbad cavern, New Mexico. Southwest Nat 48:590–596

Blondel DV, Pino J, Phelps SM (2009) Space use and social structure of the long-tailed singing mice (*Scotinomys xerampelinus*). J Mammal 90:715–723

Bohn KM, Moss CF, Wilkinson GS (2006) Correlated evolution between hearing sensitivity and social calls in bats. Biol Lett 2:561–564

Bohn KM, Schmidt-French B, Ma ST, Pollak GD (2008) Syllable acoustics, temporal patterns, and call composition vary with behavioral context in mexican free-tailed bats. JASA 124:1838–1848

Bohn KM, Schmidt-French B, Schwartz C, Smotherman M, Pollak GD (2009) Versatility and stereotypy of free-tailed bat songs. PLoS One 4:e6746

Bohn KM, Smarsh GC, Smotherman M (2013) Social context evokes rapid changes in bat song syntax. Anim Behav 85:1485–1491

Boughman JW (1998) Vocal learning by greater spear-nosed bats. Proc R Soc B 265:227–233

Bradbury JW (1977) Lek mating behavior in the hammer-headed bat. Z Tierpsychol 45:225–255

Bradbury JW, Emmons LH (1974) Social organization of some Trinidad bats. Z Tierpsychol 36:337–381

Bradbury JW, Vehrencamp SL (1976) Social organization and foraging in Emballonurid bats. I. Field Studies. Behav Ecol Sociobiol 1:337–381

Bradbury JW, Vehrencamp SL (1977) Social organization and foraging in Emballonurid bats. III. Mating systems. Behav Ecol Sociobiol 2:1–17

Bradbury JW, Vehrencamp SL (2011) Principles of animal communication, 2nd edn. Sinauer Associates Inc, Sunderland

Budenz T, Heib S, Kusch J (2009) Functions of bat social calls: the influence of local abundance, interspecific interactions and season on the production of pipistrelle (*Pipistrellus pipistrellus*) type D social calls. Acta Chiropterol 11:173–182

Butler AB, Hodos W (2005) Comparative vertebrate neuroanatomy: evolution and adaption, 2nd edn. Wiley, Hoboken

Carter GC, Riskin DK (2006) Mystacina tuberculata. Mammalian Species 790:1–8

Catchpole C (1980) Sexual selection and the evolution of complex songs among European warblers in the genus Acrocephalus. Behaviour 74:149–166

Catchpole C, Slater PJB (2008) Bird song: biological themes and variations. Cambridge University Press, Cambridge

Cholewiak DM, Sousa-Lima RA, Cerchio S (2013) Humpback whale song hierarchical structure: historical context and discussion of current classification issues. Mar Mammal Sci 29:E312–E332

Christie PJ, Mennill DJ, Ratcliffe LM (2004) Pitch shifts and song structure indicate male quality in the dawn chorus of black-capped chickadees. Behav Ecol Sociobiol 55:341–348

Clarke E, Reichard UH, Zuberbühler K (2006) The syntax and meaning of wild gibbon songs. PLoS One 1:e73

Collins S (2004) Vocal fighting and flirting: the functions of birdsong. In: Marler P, Slabberkoorn H (eds) Nature's music: the science of birdsong. Elsevier Academic Press, Amsterdam, pp 39–70

Corcoran AJ, Conner WE (2014) Bats jamming bats: food competition through sonar interference. Science 346:745–747

Cvikel N, Berg KE, Levin E, Hurme E, Borissov I, Boonman A, Armichai E, Yovel Y (2014) Bats aggregate to improve prey search but might be impaired when their density becomes too high. Curr Biol 25:206–211

Davidson SM, Wilkinson GS (2002) Geographic and individual variation in vocalizations by male *Saccopteryx bilineata* (Chiroptera: Emballonuridae). J Mammal 83:526–535

Davidson SM, Wilkinson GS (2004) Function of male song in the greater white-lined bat, *Saccopteryx bilineata*. Anim Behav 67:883–891

Davis RB, Herreid CF, Short HL (1962) Mexican free-tailed bats in Texas. Ecol Monogr 32:311–346

Dietz C, von Helversen O, Nill D (2007) Handbuch der Fledermäuse Europas. Franckh Kosmos Verlags GmbH, Germany

Doupe AJ, Kuhl PK (1999) Birdsong and human speech: common themes and mechanisms. Ann Rev Neurosci 22:567–631

Doupe AJ, Perkel DJ, Reiner A, Stern EA (2005) Birdbrains could teach basal ganglia research a new song. Trends Neurosci 28:353–363

Duffy JR (2005) Motor speech disorders. Elsevier Mosby, St. Louis

Eckenweber M, Knörnschild M (2013) Social influences on territorial singing in male greater sac-winged bats. Behav Ecol Sociobiol 67:639–648

Esser KH (1994) Audio-vocal learning in a non-human mammal: the lesser spear-nosed bat, *Phyllostomus discolor*. Neuroreport 5:1718–1720

Farries MA (2004) The avian song system in comparative perspective. Ann N Y Acad Sci 1016:61–76

Fenton MB, Simmons NB (2015) Bats, a world of science and mystery. University of Chicago Press, Chicago, p 303

Gebhard J (1997) Fledermäuse. Birkhäuser Verlag, Germany

Gelfand DL, McCracken GF (1986) Individual variation in the isolation calls of Mexican free-tailed bat pups (*Tadarida brasiliensis mexicana*). Anim Behav 34:1078–1086

Georgiakakis P, Russo D (2012) The distinctive structure of social calls by Hanak's dwarf bat Pipistrellus hanaki. Acta Chiropterol 14:167–174

Gerell-Lundberg K, Gerell R (1994) The mating behaviour of the pipistrelle and the Nathusius' pipistrelle (Chiroptera)-a comparison. Folia Zool 43:315–324

Gerlach J (2009) Social vocalisations in the Seychelles sheath-tailed bat *Coleura seychellensis*. Le Rhinolophe 18:25–30

Gil D, Gahr M (2002) The honesty of bird song: multiple constraints for multiple traits. TREE 17:133–141

Gillam EH, McCracken GF (2007) Variability in the echolocation of *Tadarida brasiliensis*: effects of geography and local acoustic environment. Anim Behav 74:277–286

Gillooly JF, Ophir AG (2010) The energetic basis of acoustic communication. Proc R Soc B 277:1325–1331

Goodwin GG, Greenhall AM (1961) A review of the bats of Trinidad and Tobago. Bull Am Mus Nat Hist 122:195–301

Gooler DM, O'Neill WE (1987) Topographic representation of vocal frequency demonstrated by microstimulation of anterior cingulate cortex in the echolocating bat, *Pteronotus parnelli parnelli*. J Comp Physiol A 161:283–294

Griffin DR (1958) Listening in the dark: the acoustic orientation of bats and men. Yale University Press, New Haven

Hage SR (2010) Neuronal networks involved in the generation of vocalization. In: Brudzynski SM (ed) Handbook of mammalian vocalization. Elsevier, Amsterdam, pp 339–349

Hammer M (1992) Untersuchungen zum Paarungssystem des Kleinen Mausohrs (*Myotis blythi*) an individuell markierten Tieven eines Balzverbandes in Nordgriechenland. Julius Maximilians Universität

Holy TE, Guo Z (2005) Ultrasonic songs of male mice. PLoS Biol 3:e386

Horn JW, Kunz TH (2008) Analyzing NEXRAD doppler radar images to assess nightly dispersal patterns and population trends in Brazilian free-tailed bats (*Tadarida brasiliensis)*. Integr Comp Biol 48:24–39

Jahelková H, Horáček I (2011) Mating system of a migratory bat, Nathusius' pipistrelle (*Pipistrellus nathusii*): different male strategies. Acta Chiropterol 13:123–127

Jahelková H, Horáček I, Bartonička T (2008) The advertisement song of *Pipistrellus nathusii* (Chiroptera, Vespertilionidae): a complex message containing acoustic signatures of individuals. Acta Chiropterol 10:103–126

Jarvis ED, Gunturkun O, Bruce L, Csillag A, Karten H, Kuenzel W, Medina L, Paxinos G, Perkel DJ, Shimizu T, Striedter G, Wild JM, Ball GF, Dugas-Ford J, Durand SE, Hough GE, Husband S, Kubikova L, Lee DW, Mello CV, Powers A, Siang C, Smulders TV, Wada K, White SA, Yamamoto K, Yu J, Reiner A, Butler AB (2005) Avian brains and a new understanding of vertebrate brain evolution. Nat Rev Neurosci 6:151–159

Jarzembowski T (2003) Migration of Nathusius' pipistrelle *Pipistrellus nathusii* (Vespertilionidae) along the Vistula Split. Acta Theriol 48:301–308

Jones G, Teeling EC (2006) The evolution of echolocation in bats. TREE 21:149–156

Jones KE, Purvis A, MacLarnon A, Bininda-Emonds ORP, Simmons NB (2002) A phylogenetic supertree of the bats (Mammalia: Chiroptera). Biol Rev 77:223–259

Kaňuch P, Agová T, Meheretu Y, Šumbera R, Bryja J (2015) New discoveries on the ecology and echolocation of the heart-nosed bat *Cardioderma cor* with a contribution to the phylogeny of Megadermatidae. Afr Zool 50:53–57

Kanwal JS, Matsumura S, Ohlemiller K, Suga N (1994) Analysis of acoustic elements and syntax in communication sounds emitted by mustached bats. JASA 96:1229–1254

Knörnschild M (2014) Vocal production learning in bats. Curr Opin Neurobiol 28:80–85

Knörnschild M, Behr O, von Helversen O (2006) Babbling behavior in the sac-winged bat (*Saccopteryx bilineata*). Naturwissenschaften 93:451–454

Knörnschild M, Nagy M, Metz M, Mayer F, von Helversen O (2009) Complex vocal imitation during ontogeny in a bat. Biol Lett 6:156–159

Knörnschild M, Jung K, Nagy M, Metz M, Kalko E (2013) Bat echolocation calls facilitate social communication. Proc R Soc B 279:4827–4835

Knörnschild M, Feifel M, Kalko E (2014) Male courtship displays and vocal communication in the polygynous bat *Carolia perspicillata*. Behaviour 151:781–798

Kroodsma DE (2004) The diversity and plasticity of birdsong. In: Marler PSH, Slabberkoorn H (eds) Nature's Music: the science of birdsong. Elsevier Academic Press, San Diego, pp 108–131

Kunz TH, Fenton MB (2003) Bat ecology. The University of Chicago Press, Chicago

Lang H, Chapin JP (1917) Notes on the distribution and ecology of central African Chiroptera. Bull Am Mus Nat Hist 37:479–563

Leippert D (1994) Social-behavior on the wing in the False Vampire, *Megaderma lyra*. Ethology 98:111–127

Lim BK, Dunlop JM (2008) Evolutionary patterns of morphology and behavior as inferred from a molecular phylogeny of new world Emballonurid bats (Tribe Diclidurini). J Mammal Evol 15:79–121

Lloyd BD (2001) Advances in New Zealand mammalogy 1990–2000: short talied bats. J R Soc N Zeal 31:59–81

Lundberg K, Gerell R (1986) Territorial advertisement and mate attraction in the bat *Pipistrellus pipistrellus*. Ethology 71:115–124

Ma J, Kobayasi K, Zhang S, Metzner W (2006) Vocal communication in adult greater horseshoe bats, *Rhinolophus ferrumequinum*. J Comp Physiol A 192:535–550

Markus N (2002) Behaviour of the black flying fox Pteropus alecto: 2. Territoriality and courtship. Acta Chiropterol 4(2):153–166

Marler P, Slabberkoorn H (2004) Nature's music: the science of birdsong. Elsevier Academic Press, Amsterdam

McCracken GF, Wilkinson GS (2000) Bat mating systems. In: Crichton EG, Krutszch PH (eds) Reproductive biology of bats. Academic Press, New York, pp 321–362

McDonald DB, Mesnick SL, Hildebrand JA (2006) Biogeographic characterisation of blue whale song worldwide: using song to identify populations. J Cetacean Res Manag 8:55–65

Mcwilliam AN (1987) Territorial and pair behavior of the African False Vampire Bat, *Cardioderma cor* (Chiroptera, Megadermatidae), in Coastal Kenya. J Zool 213:243–252

Mennill DJ, Ratcliffe LM (2004) Overlapping and matching in the song contests of black-capped chickadees. Anim Behav 67:441–450

Metzner W, Schuller G (2007) Vocal control in echolocating bats. In: Brudzynski SM (ed) Handbook of mammalian vocalizations. Elsevier, Amsterdam, pp 403–415

Mitani JC, Marler P (1989) A phonological analysis of male gibbon singing behavior. Behaviour 109:20–45

Möhres FP, Kulzer E (1957) Megaderma-ein konvergenter Zwischentyp der Ultraschallpeilung bei Fledermaüsen. Naturwissenschaften 44:21–22

Morton ES (1986) Predictions from the ranging hypothesis for the evolution of long distance signals in birds. Behaviour 99:65–86

Murray KL, Fleming TH (2008) Social structure and mating system of the buffy flower bat, *Erophylla sezekorni* (Chiroptera, Phyllostomidae). J Mammal 89:1391–1400

Naguib M, Riebel K (2006) Birdsong: a key model in animal communication. Encycl Lang Linguist 2:40–53

Nagy KA (1987) Field metabolic rate and food requirement scaling in mammals and birds. Ecol Monogr 57:111–128

Nagy KA (2005) Field metabolic rate and body size. J Exp Biol 208:1621–1625

Nagy M, Heckel G, Voigt C, Mayer F (2007) Female-biased dispersal and patrilocal kin groups in a mammal with resource-defense polygyny. Proc R Soc B 274:3019–3025

Nagy M, Knörnschild M, Voigt C, Mayer F (2012) Male greater sac-winged bats gain direct fitness benefits when roosting in multimale colonies. Behav Ecol 23:597–606

Neuweiler G (2000) The biology of bats. Oxford University Press, New York

Neuweiler G, Metzner W, Heilmann U, Rubsamen R, Eckrich M, Costa HH (1987) Foraging behaviour and echolocation in the rufous horseshoe bats, *Rhinolophus rouxi*, of Sri Lanka. Behav Ecol Sociobiol 20:53–67

Novak RM (1994) Bat's of the world. John Hopkins University Press, Baltimore

Nudds RL, Bryant DM (2000) The energetic cost of short flights in birds. J Exp Biol 203:1561–1572

Ophir AG, Schrader SB, Gillooly JF (2010) Energetic cost of calling: general constraints and species-specific differences. J Evol Biol 23:1564–1569

O'Shea TJ (1980) Roosting, social organization and the annual cycle in a Kenya population of the bat *Pipistrellus nanus*. Z Tierpsychol 53:171–195

Ouattara K, Lemasson A, Zuberbühler K (2009) Campbell's monkeys concatenate vocalizations into context-specific call sequences. PNAS 106:22026–22031

Pasch B, Bolker BM, Phelps SM (2013) Interspecific dominance via vocal interactions mediates altitudinal zonation in neotropical singing mice. Am Nat 182:E161–E173

Payne RS, McVay S (1971) Songs of humpback whales. Science 173:585–597

Pfalzer G, Kusch J (2003) Structure and variability of bat social calls: implications for specificity and individual recognition. J Zool (Lond) 261:21–33

Pollak GD, Casseday JH (1989) The neural basis of echolocation in bats. Springer, Berlin, New York

Porter FL (1979) Social behavior in the leaf-nosed bat, *Carolia perspicillata.* II Social communication. Z Tierpsychol 50:1–8

Read AF, Weary DM (1992) The evolution of birdsong: comparative analyses. Philos Trans R Soc B 338:165–187

Reiss D, McCowan B (1993) Spontaneous vocal mimicry and production by bottlenose dolphins (*Tursiops truncatus*): evidence for vocal learning. J Comp Psychol 107:301–312

Ruczynski I, Kalko EKE, Siemers BM (2007) The sensory basis of roost finding in a forest bat, *Nyctalus noctula*. J Exp Biol 210:3607–3615

Russ JM, Racey PA (2007) Species-specificity and individual variation in the song of male Nathusius' pipistrelles (*Pipistrellus pipistrelles*). Behav Ecol Sociobiol 61:669–677

Russo D, Jones G (1999) The social calls of Kuhl's pipistrelles *Pipistrellus kuhlii* (Kuhl, 1819): structure and variation (Chiroptera: Vespertilionidae). J Zool 249:476–481

Russo D, Teixeira S, Cistrone L, Jesus J, Teixeira D, Freitas T, Jones G (2009) Social calls are subject to stabilizing selection in insular bats. J Biogeogr 36:2212–2221

Ryan MJ, Tuttle MD (1987) The role of prey-generated sounds, vision, and echolocation in prey localization by the African bat *Cardioderma cor* (Megadermatidae). J Comp Physiol A 161:59–66

Sachteleben J, von Helversen O (2006) Songflight behaviour and mating system of the pipistrelle bat (*Pipistrellus pipistrellus*) in an urban habitat. Acta Chiropterol 8:391–401

Schmidt S (2013) Beyond echolocation: emotional acoustic communication in bats. In: Altenmuller E, Schmidt S, Zimmermann E (eds) Evolution of emotional communication: from sounds in nonhuman mammals to speech and music in man. Oxford University Press, Oxford

Schnitzler H-U, Kalko EKV (2001) Echolocation by insect-eating bats. Biosciences 51:557–569

Schreiber OW (1952) Some sounds from marine life in the Hawaiian area (abstract). JASA 24:116

Schwartz C, Smotherman M (2011) Mapping vocalization-related immediate early gene expression in echolocating bats. Behav Brain Res 224:358–368

Schwartz C, Tressler J, Keller H, Vanzant M, Ezell S, Smotherman M (2007) The tiny difference between foraging and communication buzzes uttered by the Mexican free-tailed bat, *Tadarida brasiliensis*. J Comp Physiol A 193:853–863

Sedgeley JA (2003) Roost site selection and roosting behavior in lesser short-tailed bats (*Mystacina tuberculata*) in comparison with long-tailed bats (*Chalinolobus tuberculatus*) in Nothofagus forest, Fiordland. N Zeal J Zool 30:227–241

Seddon N (2005) Ecological adaptation and species recognition drives vocal evolution in neotropical suboscine songbirds. Evol 59(1):200–215

Simmons NB (2005) Order Chiroptera. In: Wilson DE, Reeder DM (eds) Mammalian species of the world: a taxonomic and geographic reference. Johns Hopkins University Press, Baltimore

Smarsh GC, Smotherman MS (2015) Singing away from home: songs are used on foraging territories in the African megadermatid bat, *Cardioderma cor*. POMA 25(1):1–11

Smith WJ (1991) Singing is based on two markedly different kinds of signalling. J Theor Biol 152:241–253

Smotherman MS (2007) Sensory feedback control of mammalian vocalizations. Behav Brain Res 182:315–326

Speakman JR, Racey PA (1991) No cost of echolocation for bats in flight. Nature 350:421–423

Speakman JR, Thomas D (2003) Physiological ecology and energetics of bats. In: Kunz TH, Fenton MB (eds) Bat ecology. University of Chicago Press, Chicago, pp 430–490

Suthers RA (1988) The production of echolocation signals by birds and bats. In: Nachtigall PE, Moore PWB (eds) Animal sonar: processes and performance. Plenum Press, New York, pp 23–45

Suthers RA, Thomas SP, Suthers BJ (1972) Respiration, wing-beat and ultrasonic pulse emission in an echo-locating bat. J Exp Biol 56:37–48

Teeling EC, Springer MS, Madsen O, Bates P, O'Brien SJ, Murphy WJ (2005) A molecular phylogeny for bats illuminates biogeography and the fossil record. Science 307:580–584

Toth CA, Dennis TE, Pattemore DE, Parsons S (2015) Females as mobile resources: communal roosts promote the adoption of lek breeding in a temperate bat. Behav Ecol 26:1156–1163

Trainer JM, McDonald DB, Learn WB (2002) The development of coordinated singing in cooperatively displaying long-tailed manakins. Behav Ecol 13:65–69

Tressler J, Smotherman MS (2009) Context-dependent effects of noise on echolocation pulse characteristics in free-tailed bats. J Comp Physiol A 195:923–934

Tressler J, Schwartz C, Wellman P, Hughes S, Smotherman M (2011) Regulation of bat echolocation pulse acoustics by striatal dopamine. J Exp Biol 214:3238–3247

Vargha-Khadem F, Watkins KE, Price CJ, Ashburner J, Alcock KJ, Connelly A, Frackowiak RS, Friston KJ, Pembrey ME, Mishkin M, Gadian DG, Passingham RE (1998) Neural basis of an inherited speech and language disorder. PNAS 95:12695–12700

Vaughan TA (1976) Nocturnal behavior or the african false vampire bat (*Cardioderma cor*). J Mammal 57:227–248

Vaughan TA, Vaughan RP (1986) Seasonality and the behavior of the african yellow-winged bat. J Mammal 67:91–102

Voigt C, Winter R (1999) Energetic cost of hovering flight in nectar-feeding bats (Phyllostomidae: Glossophaginae) and its scaling in moths, birds and bats. J Comp Physiol A 169:38–48

von Helversen O, von Helversen D (1994) The advertisement song of the lesser noctule bat (*Nyctalus leisleri*). Folia Zool 43:331–338

Weid R (1994) Social calls of male noctule bats (Nyctalus noctula). Bonner Zoologische Beitraege 45:33–38

Whittenberger JF, Tilson RL (1980) The evolution of monogamy: hypothesis and evidence. Ann Rev Ecol Syst 11:197–232

Wickler W, Uhrig D (1969) Behavioral and ecological niche of the Yellow-winged bat, *Lavia frons* (Geoffroy) (Chiroptera, Megadermatidae). Zur Tierpsychologie 26:726–736

Wink M, Dyrcz A (1999) Mating systems in birds: a review of molecular studies. Acta Ornithol 34(2):91–101

Winter R, von Helversen D (1998) The energy cost of flight: do small bats fly more cheaply than birds? J Comp Physiol A 168:105–111

Zagmajster M (2003) Display song of parti-coloured bat *Vespertilio murinus* Linnaeus, 1758 (Chiroptera, Mammalia) in southern Slovenia and preliminary study of its variability. Natura Sloveniae 5:27–41

Zahn A, Dippel B (1997) Male roosting habits and mating behaviour of *Myotis myotis*. J Zool 243:659–674