

Chapter 3

Evolution of Echolocation

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Abstract Basic information about echolocation by bats includes aspects of signal design. Specifically the importance of timing, frequencies in the signals and patterns of frequency change over time are considered along with how bats use harmonics in echolocation signals. Also covered are aspects of signal strength and how bats adjust their echolocation behaviour in areas of clutter. The ways in which bats deal with forward masking (self-deafening) are considered along with differences in duty cycle (low duty cycle, separate pulse and echo in time; high duty cycle separate them in frequency). The importance of echolocation signals in communication also is covered. This information about echolocation is then presented in a phylogenetic context including a discussion of the origin of echolocation and its importance in the diversification of bats.

3.1 Introduction

Echolocation is an astonishing behaviour mainly associated with bats, although neither restricted to nor characteristic of them. Echolocation (biosonar) is an active mode of orientation involving animals using echoes of sounds they produce to collect information about their surroundings (Galambos and Griffin 1942; Griffin and Galambos 1941). The data for the echolocator is the difference between what it said and what it hears. For echolocation to work, the animal must register the outgoing signal in its brain for comparison with returning echo(es), and so ideally outgoing signals should not mask returning echoes. Echolocation has been documented in some species of birds (Apodiformes, Caprimulgiformes) and mammals (Afrotheria [Afrosoricida], Laurasiatheria [Lipotyphla, Chiroptera,

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Cetartiodactyla]) (Thomas et al. 2002). Not all bats echolocate; specifically most of those species belonging to the family Pteropodidae and those few pteropodids (*Rousettus* spp.) that do echolocate use tongue clicks as signals. All other bats echolocate and do so using signals produced in the larynx.

Current research on echolocating bats has revealed the complexity and sophistication of the behaviour. First, echolocating bats adjust their calls according to the situation, whether tongue-clicking pteropodids (*Rousettus aegyptiacus*; Yovel et al. 2010) or laryngeal echolocators (e.g. Jakobsen and Surlykke 2010; Surlykke et al. 2009a, b; Ratcliffe et al. 2011). The echolocation behaviour of tongue-clicking pteropodids is not “unsophisticated” as these bats adjust their flight paths and patterns of call production to maximize information return (e.g. Holland et al. 2004; Yovel et al. 2010). Laryngeally echolocating bats adjust their outgoing signals according to clutter (e.g. Brinklov et al. 2010a, b; Hiryu et al. 2010; Stamper et al. 2009), the presence of conspecifics (Chiu et al. 2008, 2009, 2010) and changes that include the use of harmonics (Hiryu et al. 2010; Stamper et al. 2009), as well as adjustments to the sonar beam (Surlykke et al. 2009a, b). Some also adjust call intensities according to the situation which affects both range and strength of echoes (Brinklov et al. 2010a, b). Still others adjust the frequencies that dominate call components apparently affecting range of operation and conspicuousness to hearing-based defences of prey (Goerlitz et al. 2010). The purpose of this chapter is to consider possible origins of echolocation in bats and the role that echolocation may have played in the diversification of bats.

3.2 Echolocation Signals

A sampling of echolocation calls and relevant features (Figs. 3.1 and 3.2) sets the stage for the information that follows. The general topic of echolocation call design and diversification is well covered in several reviews (e.g. Jones and Holderied 2007; Maltby et al. 2009; Schnitzler and Kalko 2001).

3.2.1 Time and Frequency

Durations and inter-call intervals are measured in ms, the frequencies of echolocation calls (and their components) in kHz. Although most bats use echolocation signals with most energy >20 kHz (by definition, ultrasonic=beyond the range of human hearing), their echolocation signals range in frequency from about 8 to over 200 kHz. Echolocation is not synonymous with ultrasonic. Using humans as reference points for frequency (ultrasonic) or signal strength (dB) is ill-advised. In a group of ten people, it is unlikely that any two will have exactly the same hearing sensitivity, whether response to higher frequencies or threshold.

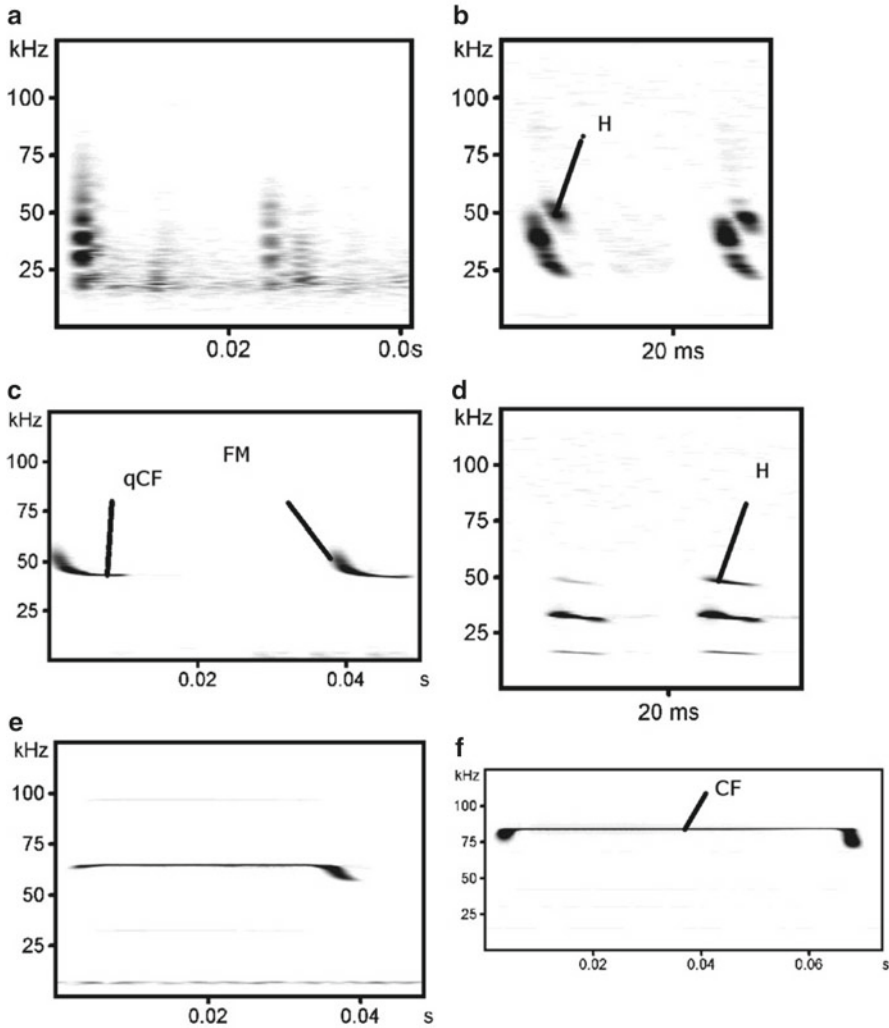


Fig. 3.1 Sampling of echolocation signals, including spectrograms (Part 1) and power spectra (Part 2). Spectrograms include echolocation clicks of *Roussettus aegyptiacus* (a); two search phase calls of *Otonycteris hemprichii* (b), *Lasiurus cinereus* (c) and *Rhinopoma hardwickei* (d); and one each of *Pteronotus parnellii* (e) and *Rhinolophus capensis* (f). Times between pairs of calls have been reduced to show pairs of calls. *H* harmonic, *FM* frequency modulated, *CF* constant frequency, *qCF* quasi-constant frequency. Part 2 shows power spectra, fast Fourier transforms (FFTs) of echolocation calls including *Otonycteris hemprichii* (a), *Lasiurus cinereus* (b), *Rhinopoma hardwickei* (c), *Pteronotus parnellii* (d) and *Rhinolophus capensis* (e). For *O. hemprichii*, *L. cinereus* and *R. hardwickei*, FFTs are of the first of the two calls shown in Fig. 3.1, Part 1. *FM* frequency modulated, *qCF* quasi-constant frequency, *CF* constant frequency, *H* harmonic

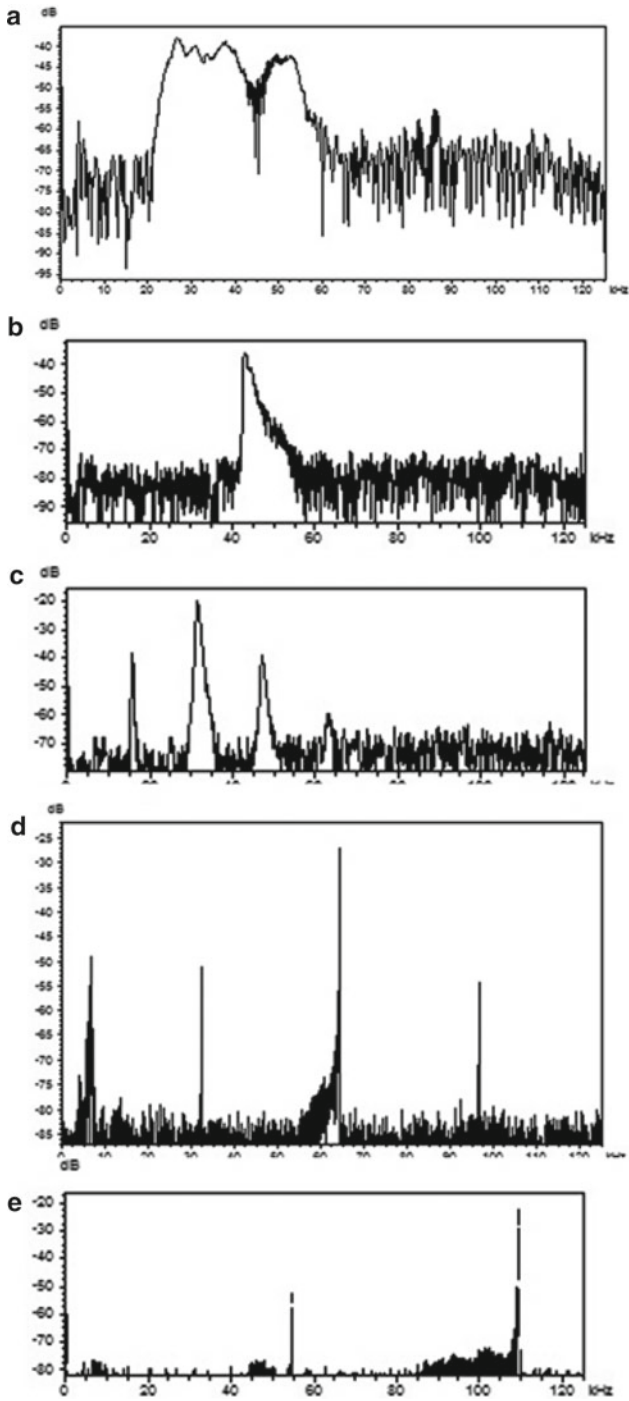


Fig. 3.1 (continued)

3.2.2 Intensity

The strength (intensity) of echolocation calls is usually measured in (dB) sound pressure level (SPL) at a specific distance from the source (e.g. 130 dB SPL at 10 cm; Holderied et al. 2005; Surlykke and Kalko 2008). Intensity (dB) is measured on a log scale where, by definition, 0 dB is the threshold of human hearing at 1 kHz. Griffin (1958) recognized that some bats produced much quieter echolocation calls

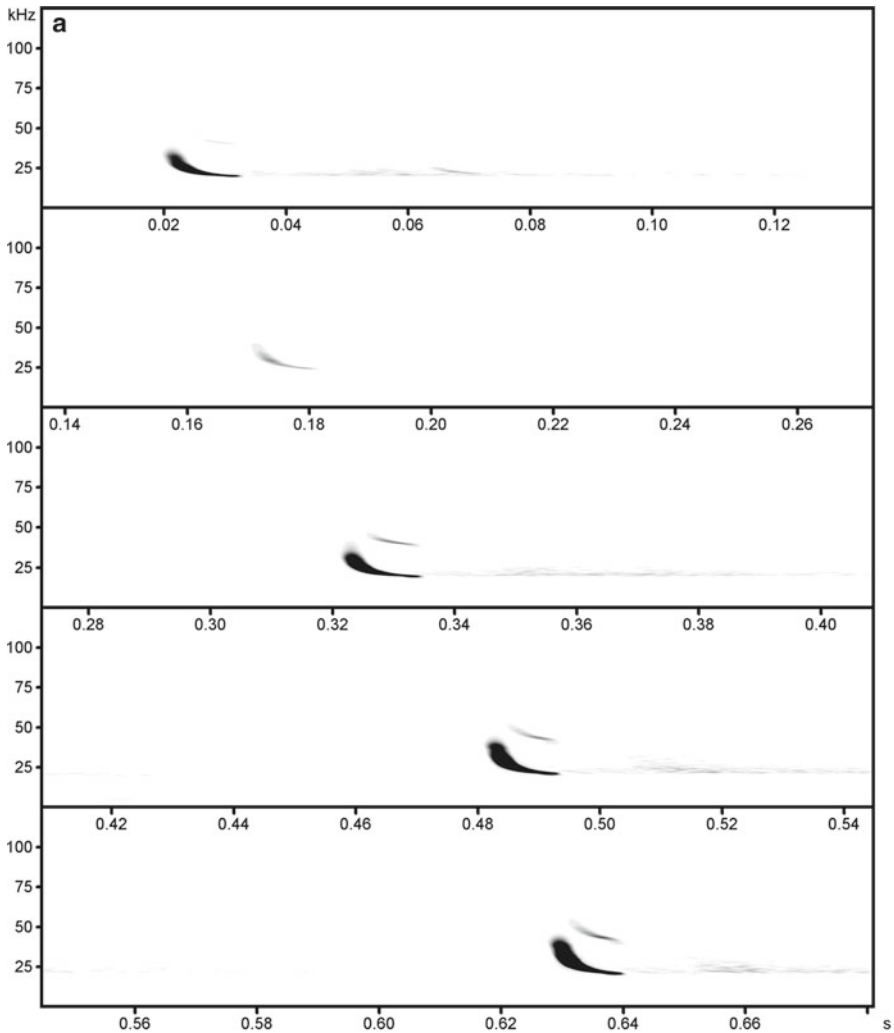


Fig. 3.2 A comparison of low duty cycle (*Lasiurus cinereus*, **a**) and high duty cycle (*Pteronotus parnellii*, **b**) call sequences. Note different patterns of calls, short calls separated by long periods of silence (low duty cycle) versus longer calls separated by short periods of silence (high duty cycle)

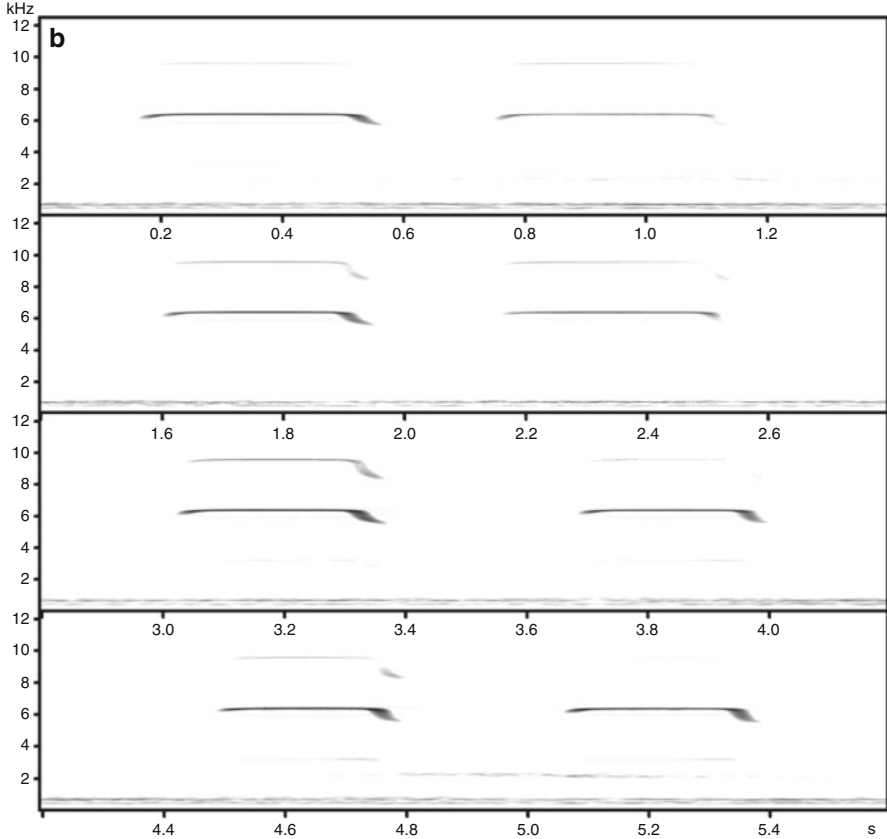


Fig. 3.2 (continued)

than others. He distinguished between whispering bats (e.g. phyllostomids, megadermatids, nycterids) and bats that produced low-intensity echolocation calls (~ 60 dB SPL at 10 cm) and those using higher intensity signals (>110 dB SPL at 10 cm). But we now know that there is a continuum between “whispering” and other bats and that all echolocating species probably use intensities much higher than early estimates suggested. The situation has been best described in phyllostomids.

The echolocation clicks of *R. aegyptiacus* range in intensity from 85 to 96 dB SPL at 1 m (Holland et al. 2004). Mora and Macias (2007) demonstrated that the phyllostomid *Phyllonycteris poeyi* produces more intense echolocation calls than expected, but they did not provide SPL data. Working with arrays of microphones, Surlykke and Kalko (2008) and Brinklov et al. (2009, 2010) showed that, measured at 2 m distant, other phyllostomids produced calls of 99 dB SPL RMS at 10 cm (*Carollia perspicillata*), 105 dB SPL RMS at 10 cm (*Macrophyllum macrophyllum*) or 110 dB RMS at 10 cm (*Artibeus jamaicensis*) (Surlykke and Kalko 2008; Brinklov et al. 2009, 2010a, b).

3.2.3 *Signals and Frequency*

Bandwidth refers to the range of frequencies in an echolocation signal. Some narrowband signals are CF (bandwidth ~0 kHz; Fig. 3.1e, f), but others are broader in bandwidth (quasi-constant frequency—qCF; Fig. 3.1c, d). The echolocation signals of *R. aegyptiacus* (Fig. 3.1a, and presumably other echolocating *Rousettus* spp.) are broadband tongue clicks (Holland et al. 2004). The echolocation signals of all other bats are produced in the larynx and are tonal (Fig. 3.1b–f) showing structured changes in frequency over time. Tonal FM signals can be broadband or narrowband, and some calls include both narrowband and broadband components.

3.2.4 *Harmonics*

Harmonics (overtones; Figs. 3.1b, d and 3.2a, c–e) are obvious and a consistent feature of the echolocation calls of some, but not all bats (Fenton et al. 2011). Harmonics effectively broaden the bandwidth of echolocation signals, potentially providing more details to the echolocator (Simmons and Stein 1980). Bats such as *Eptesicus fuscus* use more harmonics when operating in clutter (Stamper et al. 2009). Detecting harmonics in the echolocation calls of free-flying bats in the field often depends upon on the position of the bat relative to the position of the microphone, so only recordings using arrays of microphones where the bat was in (close) proximity may dependably be used in studies of harmonics (Fenton et al. 2011).

3.2.5 *Clutter*

“Clutter” could simply be defined as echoes from anything other than the target of interest, but as Denny (2006) pointed out, the situation can be complicated. The definition of clutter will depend upon several features of the bats involved, such as their size, flight speed and inter-call intervals. For a bat to deal with clutter, it must detect clutter and negotiate a course through it. This means that both echolocation (design of calls and behaviour) and manoeuvrability in flight (wing design) will influence how a bat adjusts to clutter (Aldridge and Rautenbach 1987; Norberg and Rayner 1987). Some bats adjust their echolocation calls (harmonics, Stamper et al. 2009; intensity, Brinklov et al. 2010a, b) when operating in cluttered areas such as thick vegetation. Tactile sensitivity of flight membranes seems to augment flight performance under similar circumstances (Chadha et al. 2011; Miller 2005).

3.2.6 Range

A combination of spherical spreading loss and frequency-dependent atmospheric attenuation (Lawrence and Simmons 1982a) dictates that echolocation in air is a relatively short-range operation. Kick (1982) demonstrated that using echolocation, *E. fuscus* first detected a 19 mm diameter target at 5 m and a 4.8 mm target at 3 m. In the field, Holderied et al. (2005) used videogrammetry to document that *Eptesicus bottae* flew 3–8 m s⁻¹ and first detected large objects at ~40 m. They concluded that the inter-call interval (Fig. 3.3) corresponding to lowest peak in mean wingbeat period provided a useful indicator of maximum range of detection of *E. bottae*-sized targets at about 20 m. Surlykke and Kalko (2008) used an array of microphones and demonstrated that the effective range of detection for insect-sized prey was 20–30 m in many species and more than 60 m in *Cormura brevirostris*. The long detection range in *C. brevirostris* coincides with calls consistently produced in triplets that show consistent changes in frequency as well as prominent harmonics.

Flight speed and effective detection range together have important implications for bats hunting for flying prey. Higher flight speeds mean shorter time from detection to contact and challenge bats accordingly. Several species of bats alternate frequencies between adjacent calls perhaps to thwart insect defences (Goerlitz et al. 2010) or as a means of enhancing the range at which they detect prey (Holderied and von Helversen 2003). Mora et al. (2004) reported neurophysiological specializations in the inferior colliculus of *Molossus molossus* that enhance the effect of alternating frequencies between calls. Ratcliffe et al. (2011) reported that *Saccopteryx bilineata* alternate calls while foraging but not when they are in the vicinity of their roost. They also proposed that *S. bilineata* use call alternation to detect prey at short range in cluttered situations (Ratcliffe et al. 2011).

3.2.7 Self-Deafening (Forward Masking)

Jen and Suga (1977) reported that in *Myotis lucifugus* contraction of the stapedius muscle in the middle ear reduced hearing sensitivity as an echolocation call was produced. Contractions of the muscle significantly reduce the movement of the ossicles, thereby reducing sound transmission to the cochlea (self-dampening), yet allow the outgoing pulse to be registered in the brain. Alternately, separating pulse and echo in time minimizes the chances of loud outgoing pulses masking faint returning echoes, but it also means that most echolocating bats are not expected to be able to effectively broadcast and receive at the same time. Veselka et al. (2010a, b) showed that contact between stylohyal and tympanic bones was a characteristic of laryngeally echolocating bats that may further facilitate registering registration of the outgoing pulse for future comparison with returning echoes.

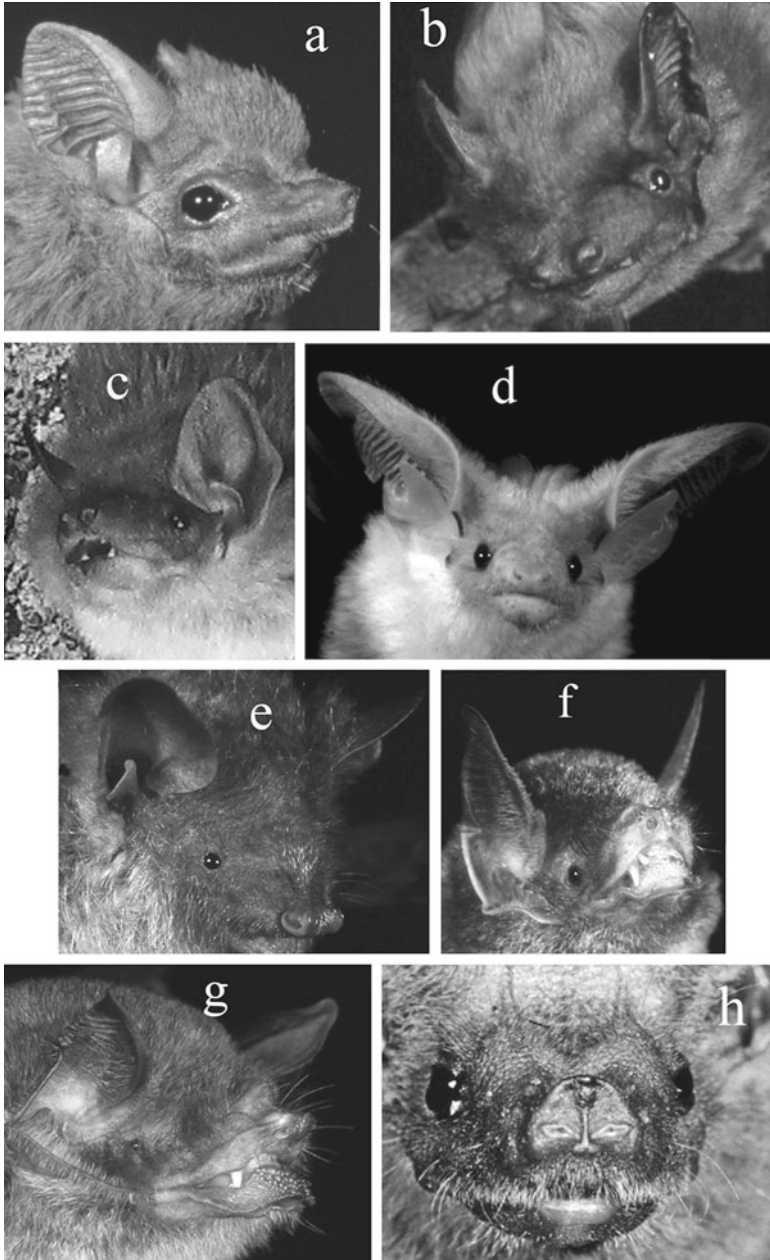


Fig. 3.3 A comparison of the faces of bats with special reference to ears, tragi, noseleaves and related structures. Included are *Balantiopteryx io* (a), *Nyctalus noctula* (b), *Eptesicus fuscus* (c), *Otonycteris hemprichii* (d), *Murina leucogaster* (e), *Pteronotus personatus* (f), *Pteronotus parnellii* (g), *Rhinopoma hardwickei* (h), *Asellia tridens* (i), *Rhinolophus clivosus* (j), *Megaderma lyra* (k), *Nycteris grandis* (l), *Phyllostomus discolor* (m), *Anoura caudifer* (n), *Desmodus rotundus* (o), *Chrotopterus auritus* (p) and *Macrotus waterhousii*

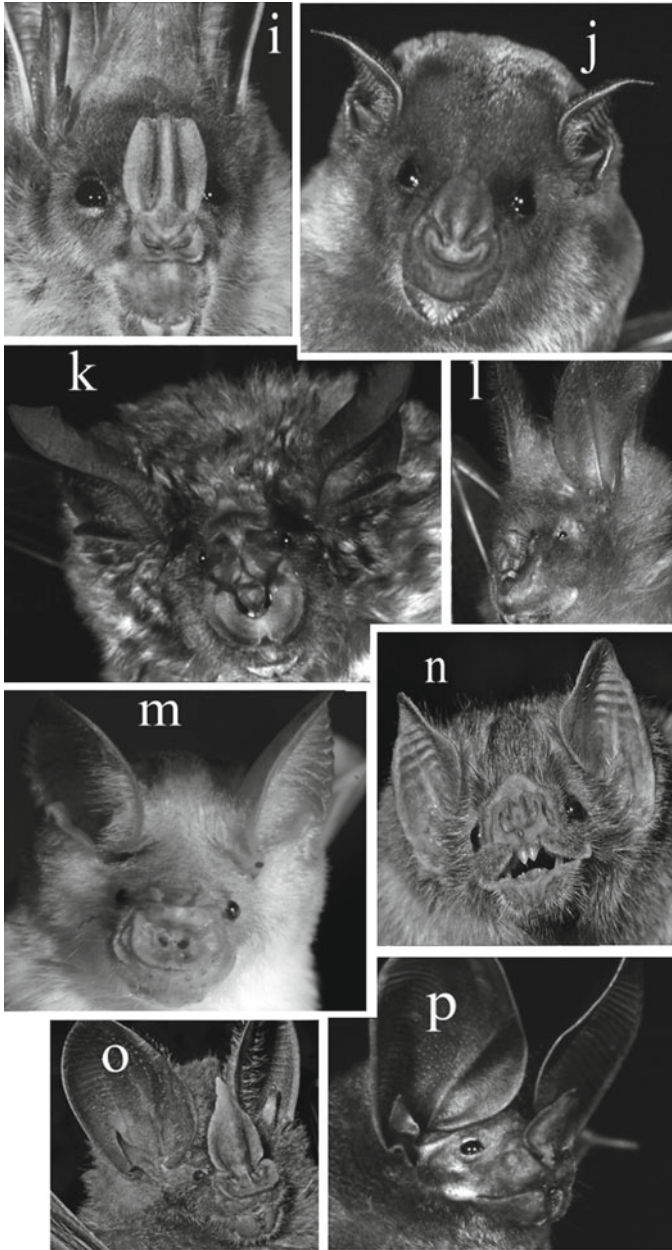


Fig. 3.3 (continued)

Bats in the families Rhinolophidae and Hipposideridae and the mormoopid *Pteronotus parnellii* use Doppler-shifted echolocation calls so as to separate pulse and returning echoes in frequency. These bats can broadcast and receive at the same time.

3.2.8 Duty Cycle

Bats that separate pulse and echo in time produce short echolocation calls separated by long periods of silence (Fig. 3.3a), producing a signal about 5 % of the time they are echolocating—a low duty cycle. Species that separate pulse and echo in frequency produce long calls separated by short periods of silence (Fig. 3.3b). These bats broadcast at a high duty cycle, producing a signal >40 % of the time they are echolocating.

Each echolocation call of a high duty cycle bat is dominated by a single frequency (CF), but most calls begin and end with an FM sweep. Echolocation calls of low duty cycle bats are more variable, being FM signals with a range of bandwidths. Even low duty cycle echolocators producing long, narrowband signals (qCF) echolocate at low duty cycle. The advantage of narrowband signals is that for every ten times reduction in bandwidth, signal strength increases by 10 dB with no additional cost of sound production (Oppenheim et al. 1999).

3.3 Signal Production

With the exception of *Rousettus* species that use tongue clicks, echolocating bats produce their signals in the larynx. Earlier work provided details of pulse production and anatomy of the larynx and associated structures (e.g. Fattu and Suthers 1981; Griffiths 1978). Tracheal chambers and nasal cavities may further modify signals after they leave the larynx (Suthers et al. 1989). In *Rhinolophus hildebrandtii*, emitted echolocation calls have most energy in the second harmonic, and three tracheal cavities are involved in suppressing the fundamental frequency of sounds leaving the larynx (Suthers et al. 1989).

Most bats emit their echolocation calls through their open mouths, but some (rhinolophids, hipposiderids, nycterids, megadermatids and phyllostomids) emit them through their nostrils (Pedersen 1995, 1996, 1998). The difference in call emission influences cranial anatomy, but the role that other cranial features, such as concavities in the basisphenoid and/or basioccipital bones, play in echolocation remains unclear (DeBaeremaeker and Fenton 2003).

Noseleafs and related structures (Fig. 3.4) can further influence the signal leaving the bat. Hartley and Suthers (1987) demonstrated that the dorsal lancet of the

noseleaf of *C. perspicillata* directed echolocation signals (short, broadband FM pulses) vertically. Microcomputed tomography reveals that lancet furrows in the noseleaf complex of *Rhinolophus* affect the FM sweep that terminates each echolocation call (Zhuang and Mueller 2006). Vanderelst et al. (2010) used a comparison of *Micronycteris microtis* and *Phyllostomus discolor* to demonstrate that in phyllostomid bats noseleaves can focus energy and help the bats distinguish between echoes from the periphery from those of objects in the area of focus.

Flying bats tend to produce echolocation calls during the expiration phase of the wingbeat cycle (Suthers et al. 1972), so that they do not incur additional costs associated with sound production during echolocation (Speakman and Racey 1991, but see Parsons et al. 2010). Contractions of abdominal wall muscles further assist call production in flying *P. parnellii* (Lancaster et al. 1995; Lancaster and Speakman 2001). Of particular note is the striking difference between high duty cycle *P. parnellii* and low duty cycle *Eptesicus*, *Pipistrellus* and *Myotis* (Lancaster and Speakman 2001) in terms of how the diaphragm contributes to vocalization.

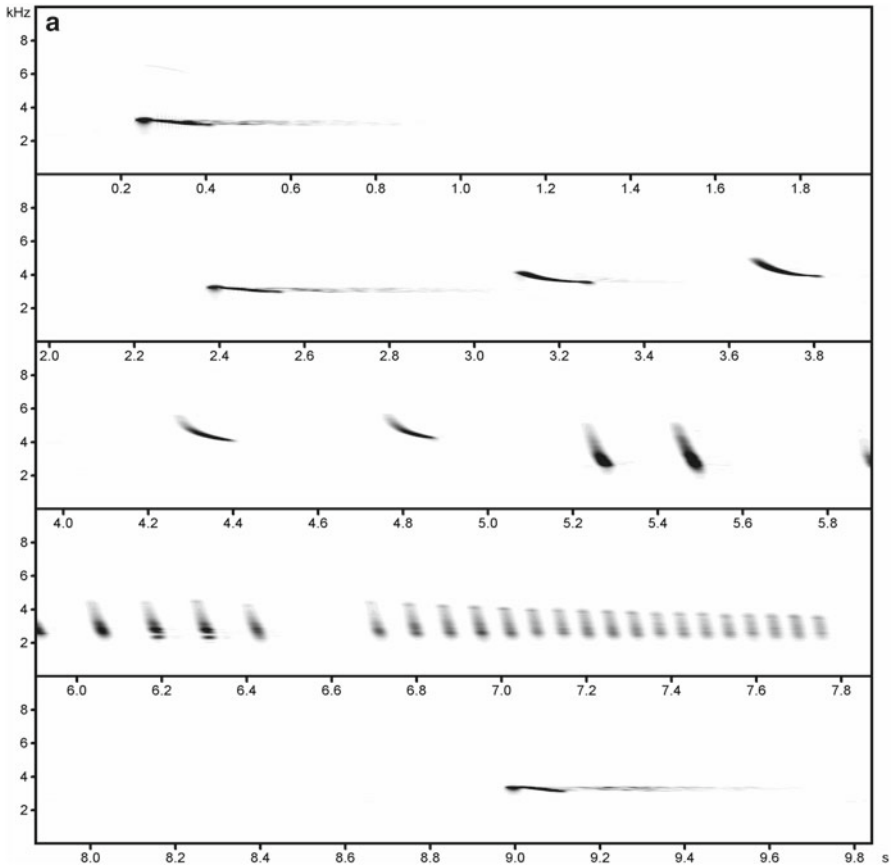


Fig. 3.4 A comparison of a feeding buzz (*Molossus ater*, **a**) and a social buzz (*Tadarida teniotis*, **b**)

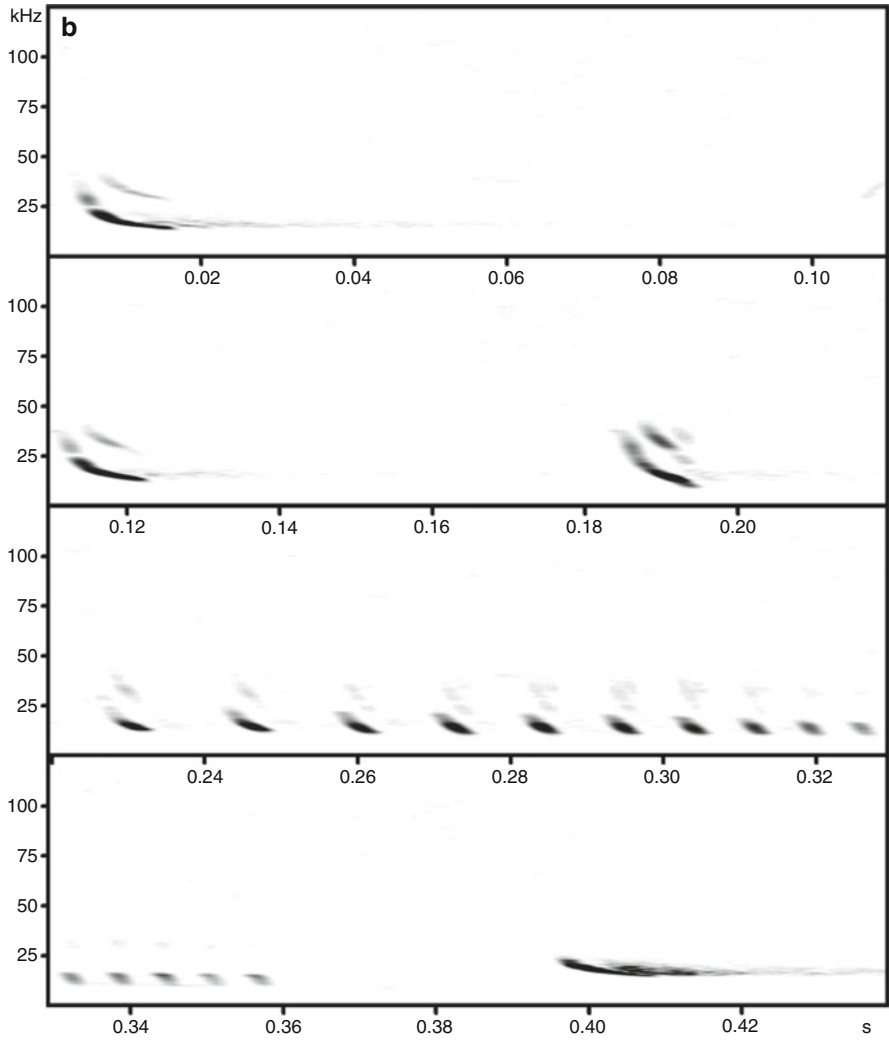


Fig. 3.4 (continued)

3.4 Signal Reception

The pinnae of bats (Fig. 3.4) generally increase the sensitivity of hearing, notably so in high duty cycle species where the pinnae are mechanically tuned to the dominant frequencies of their echolocation calls (Obrist et al. 1993). The degree of specialization of pinnae varies across taxa, and in some species, the ears are better tuned to detecting the sounds of prey than to echolocation signals (Obrist et al. 1993).

Gleaning bats, such as *Megaderma lyra*, detect very low-intensity rustling sounds (Hubner and Weigrebe 2003). Sensitivity arising from tuning of the pinnae is further enhanced by neurological tuning in the inferior colliculus (e.g. Mora et al. 2004).

Some parts of the ear, such as the thickened lower edge of the pinnae in *Nyctalus* spp. combined with the tragus (Fig. 3.4b), reduce extra side lobes in the echoes reaching the bat (Mueller et al. 2006). Early evidence suggested that the tragus affected vertical localization of targets by *E. fuscus* (Lawrence and Simmons 1982a, b). More recent work with microcomputed tomography indicates that the tragus in *E. fuscus* reduces extra side lobes from echoes (Mueller 2004). The variety of tragi and ear structures in bats promises new insights from this emerging area of research.

3.5 Uses for Echolocation

Some species of *Rousettus* may use echolocation only to gain access to dark roosts and little more (Holland et al. 2004); however, many other species of bats use echolocation to detect, assess and track prey, a process that is particularly clear during feeding buzzes produced during attacks on prey (Fig. 3.5a) (e.g. Kalko and Schnitzler 1989; Schnitzler and Kalko 2001). Echolocation calls of foraging insectivorous bats have received considerable attention, providing a rich array of examples of specific behaviour and call design (e.g. Chiu et al. 2010; Goerlitz et al. 2010; Stamper et al. 2009). The role of echolocation in foraging of fruit eaters and blood feeders remains unclear; however, some New World flowers use nectar guides that reflect ultrasonic signals in order to attract flower-visiting bats and thereby increase rates of pollination (Von Helversen and von Helversen 1999, 2003; Yovel et al. 2008).

Möhres (1966) noted that the signals one bat uses in echolocation may also affect the behaviour of other bats, and Barclay (1982) used playback experiments to further explore this aspect of echolocation. More recently, more evidence of the role of echolocation signals in communication has expanded our knowledge (e.g. Bayefsky-Anand et al. 2008; Gillam et al. 2007; Schuchmann and Siemers 2010; Swartz et al. 2007; Ulanovsky et al. 2004; Voight-Heucke et al. 2010). Kingston and Rossiter (2004) proposed that enhanced communication may underlie the taxonomic diversification of some high duty cycle echolocating bats. When several bats fly in the same airspace, they may shift the dominant frequencies in their echolocation calls which suggests jamming avoidance and/or enhanced communication (Ulanovsky et al. 2004; Voight-Heucke et al. 2010). In many situations, foraging bats produce social buzzes (Fig. 3.5b) apparently directed at nearby conspecifics. In some situations *E. fuscus* stop producing echolocation calls apparently to avoid jamming (Chiu et al. 2008).

Information leakage and short operational range are two important drawbacks to using echolocation as a pursuit strategy. Bat-detecting ears have attracted considerable attention (e.g. Pye 1968; Roeder 1967), and their widespread occurrence among insects (Ratcliffe 2009) testifies to the importance of bats as predators. The

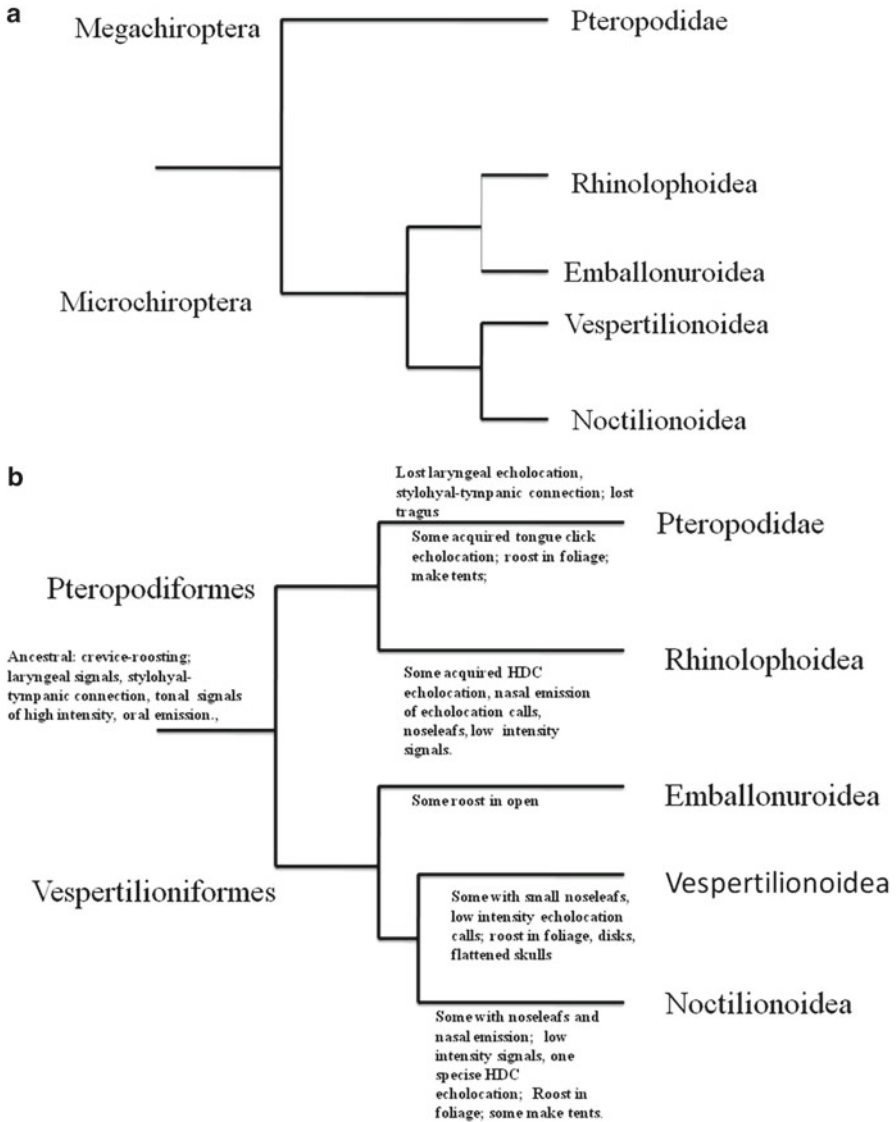


Fig. 3.5 The “old” (a) and “new” (b) phylogenies of bats

success of hearing-based defences in many insects reflects the problem of information leakage. Bats use various strategies to circumvent insect defences; behaviours ranging from an allotonic approach (broadcast outside the frequencies to which insect ears are most sensitive; Fenton and Fullard 1979), to stealth, are producing calls of lower intensity (Goerlitz et al. 2010). Bats such as *Lasiurus borealis* use echolocation calls that are detected by moths with ears, many of which successfully

evade the bats (Acharya and Fenton 1992, 1999); however, *L. borealis* still preys heavily on these moths (Clare et al. 2009).

Laryngeally echolocating bats use morphological specializations of their pinnae that include tuning to a particular frequency or better sound collection (Obrist et al. 1993) combined with neurological adaptations to increase their hearing sensitivity and, thus, their effective target detection range (Neuweiler 1989, 1990). The echolocation-based hunting strategies of many bats are most impressive (Neuweiler 1989), ranging from those detecting, pursuing and attacking flying insects (e.g. Goerlitz et al. 2010; Lazure and Fenton 2011) to those taking prey from the water's surface (e.g. Hartley et al. 1989; Kalko and Schnitzler 1989; Schnitzler et al. 1994). Other bats may or may not use echolocation when gleaning prey from surfaces (Faure and Barclay 1994; Hubner and Weigrebe 2003; Siemers and Schnitzler 2004), while others may use vision (Bell 1985). The tactile sensitivity of small sensory hairs located on the bats' wings has also been shown to augment flight performance during pursuit or gleaning activities (Chadha et al. 2011; Miller 2005).

3.6 Echolocation and the Phylogeny of Bats

Teeling (2009) and Jones and Teeling (2006) have provided excellent overviews of the three hypotheses concerning the origin of echolocation in bats. Simmons and Geisler (1998) proposed that flight was ancestral, providing the ancestors of bats with mobility, and that echolocation evolved later. Simmons et al. (2008) proposed that the Eocene *Onychonycteris finneyi* could fly but not echolocate, also supporting the flight-first hypothesis (Simmons 2008). Fenton et al. (1995) proposed that echolocation was ancestral in bats and was the key innovation that provided the ancestors of bats access to flying nocturnal insects as food. Speakman and Racey (1991) proposed that flight and echolocation evolved simultaneously in the ancestors of bats allowing them to produce intense signals on the downstroke, covering the cost of signal production with the costs of flight. It appears that this coincidence may not apply to all bats, for example, *Mystacina tuberculata* (Parsons et al. 2010) and *S. bilineata* (Ratcliffe et al. 2011).

Morphology, particularly of the shoulder girdle, supports the view that *Onychonycteris* and other Eocene bats could fly (Simmons and Geisler 1998; Simmons et al. 2008). In bats, connections between stylohyal and tympanic bones are unambiguous morphological indicators of laryngeal echolocation (Veselka et al. 2010a). Simmons and Geisler (1998) used features of the proximal end of the stylohyal bone and the relative size of the cochlea to argue that other Eocene bats (e.g. *Icaronycteris*, *Hassianycteris*, *Palaeochiropteryx*) could echolocate. The two specimens of *O. finneyi* are not well enough preserved to assess possible contact between tympanic and stylohyal bones, leaving open the question of whether or not the bat had the capacity for laryngeal echolocation (Simmons et al. 2010; Veselka et al. 2010b).

If laryngeal echolocation is ancestral, then it evolved once in the ancestors of Chiroptera but was lost in the lineage leading to Pteropodidae. Within the

pteropodids, echolocation by tongue clicking appears to have evolved secondarily once. If laryngeal echolocation was not ancestral, then it could have evolved twice, once in each suborder of Chiroptera (Yinpterochiroptera and Yangochiroptera, Fig. 3.6). As noted by Teeling (2009), the emergence of the new phylogeny and classification of bats has implications for the evolution of echolocation. In the “old” classification, separation of Pteropodidae as Megachiroptera from all other bats presented a different situation than the “new” classification in which both suborders include laryngeal echolocators. High duty cycle echolocation has evolved independently in both Yinpterochiroptera and Yangochiroptera, along with other features such as low-intensity echolocation calls and the use of prey-generated sounds for finding food (Fenton et al. in press). As of 2012 it appears that only the discovery of additional fossil material would resolve the question of the origin of echolocation among Chiroptera. Data on the incidence of genes associated with hearing and vocalizing (*Prestin* and *FoxP2*—Li et al. 2007, 2008, respectively) does not resolve the situation or provide unambiguous support for either the traditional (Megachiroptera, Microchiroptera) or “new” (Yinpterochiroptera, Yangochiroptera) phylogeny.

Most data about the phylogeny of bats suggest that Chiroptera is monophyletic (Eick et al. 2005; Simmons 1994; Simmons et al. 1991; Simmons and Geisler 1998), but this view is not unanimous (Pettigrew 1991; Dell et al. 2010; Kruger et al. 2010).

3.7 Origin of Bats

Although Jepsen (1970) argued that bats evolved in caves, I prefer the suggestion that they evolved in forests with open understory. The protobat has been depicted as being arboreal (Hill and Smith 1984) and presumed to have glided in pursuit of flying insects (Fig. 3.7). Norberg (1985) proposed a model that demonstrated the feasibility of such a transition from gliding to powered flight. Coordinated elongation of arm, hand and finger bones has been shown to be under genetic control during development (Sears et al. 2006). A related scenario applies to the webbing (patagium) of bat wings but not their hind feet (Weatherbee et al. 2006).

Fenton et al. (1995) argued that to function in detecting and tracking flying insects, echolocation signals had to be more intense to increase the effective range of the call. They contended that the use of high-intensity signals in echolocation constituted a “breakthrough”, providing access to a previously inaccessible food source (flying nocturnal insects). Maltby et al. (2009) proposed that the ancestral echolocation call in laryngeally echolocating bats was short, narrowband and multiharmonic. In the initial phase, I think that the protobat would have glided in pursuit of its prey, being a more fundamental step in detecting and tracking targets than the more complicated scenario of when both predator and prey are flying.

This hypothesis makes the prediction that fossil protobats will have laryngeal cartilages robust enough to anchor the cricothyroid muscles that adjust tension on the



Fig. 3.6 J. D. Smith's proposed protobat (Hill and Smith 1984)

vocal cords. These cartilages will match increased subglottal pressures associated with echolocation. Precise control of the vocal cords must have been mirrored by simultaneous development of cricothyroid muscles. The appearance of the stylohyal-tympanic connection may have appeared after development of echolocation, followed by diversification and elaboration of facial and ear structures associated with echolocation. It may be that only exceptionally well-preserved fossils will provide the detail necessary to address and perhaps resolve this prediction.

3.8 Conclusions

The diversity of bats and echolocation behaviour provides as many opportunities for further work as it did 50 years ago; new discoveries open many doors than definitive answers to old questions close. The present array of tools for examining the details of what bats do and how they do it enhances our capacity for better understanding the evolution and diversification of bats. Additional fossil finds may well oblige us to adjust our theories about the origin of bats and echolocation.

Box 3.1 Echolocation: Units, Terms

- Attenuation—absorption of acoustic energy as it moves through air, influenced by frequency
- Audiogram—frequency sensitivity of audiogram measured as strength of signal to evoke neural (or behavioural) response at different frequencies
- Broadband—bandwidth of an echolocation call measured in kHz (Fig. 3.1)
- CF—constant frequency call (or call component) (Fig. 3.1)
- CF-FM—an echolocation call with CF and FM components (Fig. 3.1)
- Click—broadband sound produced by clicking the tongue (Fig. 3.1)
- Clutter—echoes from other than the target (see also Denny 2007)
- dB—decibels (see dB SPL at x cm)
- Duration—the duration of a call
- FFT—fast Fourier transform (frequency versus energy) (Fig. 3.1)
- FME—frequency with maximum energy (kHz) usually measured from a fast Fourier transform power spectrum (Fig. 3.1)
- FM—frequency modulated call (or call component) (Fig. 3.1)
- Frequency—pitch measured in kHz
- Fundamental frequency—lowest frequency of a periodic waveform, sometimes called the first harmonic
- Harmonic—overtone, doubling of frequency over fundamental (Fig. 3.1)
- Highest frequency—in an echolocation call (HF)
- Intensity—measure of signal strength (dB SPL at x cm from source)
- Inter-call interval—time between calls (sometimes called interpulse interval), measured from the start of the first call to the start of the next)
- kHz—kilohertz measure of frequency or pitch
- Loudness—psychometric measure, how loud a signal sounds (a function of hearing sensitivity—audiogram)
- Lowest frequency—in an echolocation call (LF)
- ms—milliseconds (measure of time)
- Narrowband—bandwidth of an echolocation call measured in kHz (Fig. 3.1)
- Power spectrum—distribution of energy in a call by frequency (Fig. 3.1)
- qCF—quasi-constant frequency signal (narrowband) (Fig. 3.1)
- Spectrogram—changes in frequency over time. a three dimensional display with energy represented by the colour or blackness of the display (Fig. 3.1)
- SPL—sound pressure level (usually in the context of dB SPL at a given distance from sound source). Root mean square (rms) values are, for the same signal, 9 dB lower than for peak-to-peak measures
- Spreading loss—energy dissipation as sound moves away from a source (en route to and from a target)
- Wavelength— λ of a sound

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References

- Acharya L, Fenton MB (1992) Echolocation behaviour of vespertilionid bats (*Lasiurus cinereus* and *Lasiurus borealis*) attacking airborne targets, including arctiid moths. *Can J Zool* 70:1292–1298
- Acharya L, Fenton MB (1999) Bat attacks and moth defensive behaviour around street lights. *Can J Zool* 77:27–33
- Aldridge HDNJ, Rautenbach IL (1987) Morphology, echolocation and resource partitioning in insectivorous bats. *J Anim Ecol* 56:763–778
- Barclay RMR (1982) Interindividual use of echolocation calls: eavesdropping by bats. *Behav Ecol Sociobiol* 10:271–275
- Bayefsky-Anand S, Skowronski MD, Fenton MB, Korine C, Holderied MW (2008) Variations in the echolocation calls of the European-Free-tailed Bat (*Tadarida teniotis*, Molossidae). *J Zool* 275:115–123
- Bell GP (1985) The sensory basis of prey location by the California leaf-nosed bat *Macrotus californicus* (Chiroptera: Phyllostomidae). *Behav Ecol Sociobiol* 16:343–347
- Brinklov S, Kalko EK, Surylkke A (2009) Intense echolocation calls from two ‘whispering’ bats, *Artibeus jamaicensis* and *Macrophyllum macrophyllum* (Phyllostomidae). *J Exp Biol* 212:11–20
- Brinklov S, Jakobsen L, Ratliffe JM, Surylkke A (2010a) Echolocation call intensity and directionality in flying short-tailed fruit bats, *Carollia perspicillata* (Phyllostomidae). *J Acoust Soc Am* 129:427–435
- Brinklov S, Kalko EK, Surylkke A (2010b) Dynamic adjustment of biosonar intensity to habitat clutter in the bat *Macrophyllum macrophyllum* (Phyllostomidae). *Behav Ecol Sociobiol* 64:1867–1874
- Chadha M, Moss CF, Sterbing-D’Angelo SJ (2011) Organization of the primary somatosensory cortex and wing representation in the big brown bat, *Eptesicus fuscus*. *J Comp Physiol A* 197:89–96
- Chiu C, Xian W, Moss CF (2008) Flying in silence: echolocating bats cease vocalizing to avoid sonar jamming. *Proc Natl Acad Sci USA* 105:13116–13121
- Chiu C, Xian W, Moss CF (2009) Adaptive echolocation behaviour in bats for the analysis of auditory scenes. *J Exp Biol* 212:1392–1404
- Chiu C, Reddy PV, Xian W, Krishnaprasad PS, Moss CF (2010) Effects of competitive prey capture on flight behaviour and sonar beam pattern in paired big brown bats, *Eptesicus fuscus*. *J Exp Biol* 213:3348–3356
- Clare E, Fraser E, Braid H, Fenton MB, Hebert P (2009) Unravelling complex food webs with simple molecules: a generalist predator the eastern red bat (*Lasiurus borealis*) and its arthropod prey. *Mol Ecol* 18:2532–2542. doi:10.1111/j.1365-294X.2009.04184.x
- DeBaeremaeker KR, Fenton MB (2003) Basisphenoid and basioccipital pits in microchiropteran bats. *Biol J Linn Soc* 78:215–233
- Dell L-A, Kruger J-L, Bhagwandin A, Jillani N, Pettigrew JD, Manger PR (2010) Nuclear organization of cholinergic, putative catecholaminergic and serotonergic systems in the brains of two megachiropteran species. *J Chem Neuroanat* 40:177–195
- Denny, M. 2006. *Blip, ping & buzz: making sense of radar and sonar*. Johns Hopkins Press, Baltimore

- Denny M (2007) *Blip, ping & buzz: making sense of radar and sonar*. Johns Hopkins University Press, Baltimore, MD
- Eick GN, Jacobs DS, Matthee CA (2005) A nuclear DNA phylogenetic perspective on the evolution of echolocation and historical biogeography of extant bats (Chiroptera). *Mol Biol Evol* 22:1869–1886
- Fattu JM, Suthers RA (1981) Subglottic pressure and the control of phonation by the echolocating bat, *Eptesicus*. *J Comp Physiol A* 143:465–475
- Faure PA, Barclary RMR (1994) Substrate-gleaning versus aerial-hawking: plasticity in the foraging and echolocation behaviour of the long-eared bat, *Myotis evotis*. *J Comp Physiol A* 174:651–660
- Fenton MB, Fullard JH (1979) The influence of moth hearing on bat echolocation strategies. *J Comp Physiol A* 132:77–86
- Fenton MB, Audet D, Obrist MK, Rydell J (1995) Signal strength, timing and self-deafening: the evolution of echolocation in bats. *Paleobiology* 21:229–242
- Fenton MB, Skowronski MD, McGuire LP, Faure PA (2011) Variation in the use of harmonics in the calls of laryngeally echolocating bats. *Acta Chiropterol* 13:169–178
- Fenton MB, Faure PA, Ratcliffe JM (2012) Evolution of high duty cycle echolocation in bats. *J Exp Biol* 215:2935–2944
- Galambos R, Griffin DR (1942) Obstacle avoidance by flying bats: the cries of bats. *J Exp Zool* 89:475–490
- Gillam EH, Ulanovsky N, McCracken GF (2007) Rapid jamming avoidance in biosonar. *Proc Biol Sci* B274:651–660
- Goerlitz HR, ter Hofstede HM, Zeale MRK, Jones G, Holderied MW (2010) An aerial hawking bat uses stealth echolocation to counter moth hearing. *Curr Biol* 20:1568–1572
- Griffin DR (1958) *Listening in the dark*. Yale University Press, New Haven, CT
- Griffin DR, Galambos R (1941) The sensory basis of obstacle avoidance by flying bats. *J Exp Zool* 86:481–506
- Griffiths TA (1978) Modification of *M. cricothyroideus* and the larynx in the Mormoopidae, with reference to amplification of high-frequency pulses. *J Mammal* 59:724–730
- Hartley DJ, Suthers RA (1987) The sound emission pattern and the acoustical role of the noseleaf in the echolocating bat, *Carollia perspicillata*. *J Acoust Soc Am* 82:1900–1987
- Hartley DJ, Campbell KA, Suthers RA (1989) The acoustic behavior of the fish-catching bat, *Noctilio leporinus*, during prey capture. *J Acoust Soc Am* 86:8–27
- Hill JE, Smith JD (1984) *Bats: a natural history*. British Museum (Natural History), London
- Hiryu S, Bates ME, Simmons JA, Riquimaroux H (2010) FM broadcasting bats shift frequencies to avoid broadcast-echo ambiguity in clutter. *Proc Natl Acad Sci USA* 107:7048–7053. doi:10.1037/pnas.100429107, <http://www.pnas.org/cgi>
- Holderied MW, von Helversen O (2003) Echolocation range and wing beat period match in aerial-hawking bats. *Proc Biol Sci* 270:2293–2299
- Holderied MW, Korine C, Fenton MB, Parsons S, Robinson S, Jones G (2005) Echolocation call intensity in the aerial hawking bat *Eptesicus bottae* (Vespertilionidae) studied using stereo videogrammetry. *J Exp Biol* 208:1321–1327
- Holland RA, Waters DA, Rayner JMV (2004) Echolocation signal structure in the megachiropteran bat *Rousettus aegyptiacus* Geoffroy 1810. *J Exp Biol* 207:4261–4369
- Hubner M, Weigrebe L (2003) The effect of temporal structure on rustling-sound detection in the gleaning bat, *Megaderma lyra*. *J Comp Physiol A* 189:337–346
- Jakobsen L, Surlykke A (2010) Vespertilionid bats control the width of their biosonar beam dynamically during prey pursuit. *Proc Natl Acad Sci USA* 107:13930–13935
- Jen PH-S, Suga N (1977) Coordinated activities of middle-ear and laryngeal muscles in echolocating bats. *Science* 950–952
- Jepsen GL (1970) Bat origins and evolution. In: Wimsatt WA (ed) *Biology of bats*, vol 1. Academic, New York, pp 1–64
- Jones G, Holderied MW (2007) Bat echolocation calls: adaptation and convergent evolution. *Proc Biol Sci* B274:905–912

- Jones G, Teeling EC (2006) The evolution of echolocation in bats. *TREE* 21:149–156
- Kalko EK, Schnitzler H-U (1989) The echolocation and hunting behavior of Daubenton's bat, *Myotis daubentonii*. *Behav Ecol Sociobiol* 24:225–238
- Kick SA (1982) Target-detection by the echolocating bat, *Eptesicus fuscus*. *J Comp Physiol* A145:431–435
- Kingston T, Rossiter SJ (2004) Harmonic-hopping in Wallace's bats. *Nature* 429:654–657
- Kruger J-L, Dell L-A, Bahgwandin A, Jillani NE, Pettigrew JD, Manger PR (2010) Nuclear organization of cholinergic, putative catecholaminergic and serotonergic systems in the brains of two microchiropteran species. *J Chem Neuroanat* 40:210–222
- Lancaster WC, Speakman JR (2001) Variations in respiratory muscle activity during echolocation when stationary in three species of bat (Microchiroptera: Vespertilionidae). *J Exp Biol* 204:4185–4197
- Lancaster WC, Henson OW Jr, Keating AW (1995) Respiratory muscle activity in relation to vocalization in flying bats. *J Exp Biol* 198:175–191
- Lawrence BD, Simmons JA (1982a) Echolocation in bats: the external ear and perception of the vertical positions of targets. *Science* 218:481–483
- Lawrence BD, Simmons JA (1982b) Measurements of atmospheric attenuation at ultrasonic frequencies and the significance for echolocation by bats. *J Acoust Soc Am* 71:585–590
- Lazure L, Fenton MB (2011) High duty cycle echolocation and prey detection by bats. *J Exp Biol* 214:1131–1137
- Li G, Wang J, Rossiter SJ, Jones G, Zhang S (2007) Accelerated FoxP2 evolution in echolocating bats. *PLoS One* 9:e900
- Li G, Wang J, Rossiter SJ, Jones G, Zhang S (2008) The hearing gene *Prestin* reunites echolocating bats. *Proc Natl Acad Sci USA* 105:13959–13964
- Maltby A, Jones KE, Jones G (2009) Understanding the evolutionary origin and diversification of bat echolocation calls. In: Brudzynski SM (ed) *Handbook of mammalian vocalization, an integrative neuroscience approach*. Academic, Oxford, Chapter 2.4
- Miller G (2005) Bats have a feel for flight. *Science* 310:1260–1261
- Möhres FP (1966) Communicative characters of sonar signals in bats. In: Busnel R-G (ed) *Animal sonar systems: biology and bionics, vol 2*. Laboratoire de Physiologie Acoustique, Jouy-en-Josas, pp 939–945
- Mora EC, Macias S (2007) Echolocation calls of Poey's flower bat (*Phyllonycteris poeyi*) unlike those of other phyllostomids. *Naturwissenschaften* 94:380–383
- Mora EC, Macias S, Vater M, Coro F, Kossel M (2004) Specializations for aerial hawking in the echolocation system of *Molossus molossus* (Molossidae, Chiroptera). *J Comp Physiol* A190:561–574
- Mueller R (2004) A numerical study of the role of the tragus in the big brown bat. *J Acoust Soc Am* 116:3701–3712
- Mueller R, Lu H, Zhang S, Peremans H (2006) A helical biosonar scanning pattern in the Chinese noctule, *Nyctalus plancyi*. *J Acoust Soc Am* 119:3092–4083
- Neuweiler G (1989) Foraging ecology and audition in echolocating bats. *TREE* 4:160–166
- Neuweiler G (1990) Auditory adaptations for prey capture in echolocating bats. *Physiol Rev* 70:615–641
- Norberg UM (1985) Evolution of vertebrate flight: an aerodynamic model for the transition from gliding to active flight. *Am Nat* 126:303–327
- Norberg UM, Rayner JMV (1987) Ecological morphology and flight in bats (Mammalia, Chiroptera) – wing adaptations, flight performance, foraging strategy and echolocation. *Philos Trans R Soc Lond B Biol Sci* 316:337–419
- Obriest MK, Fenton MB, Eger JL, Schlegel PA (1993) What ears do for bats: a comparative study of pinna sound pressure transformation in Chiroptera. *J Exp Biol* 180:119–152
- Oppenheim AV, Schaffer RW, Buck JR (1999) *Discrete-time signal processing*. Prentice Hall, Garden City, NY
- Parsons S, Riskin DK, Hermanson JW (2010) Echolocation call production during aerial and terrestrial locomotion by New Zealand's enigmatic lesser short-tailed bat, *Mystacina tuberculata*. *J Exp Biol* 213:551–557

- Pedersen SC (1995) Cephalometric correlates of echolocation in the Chiroptera; II fetal development. *J Morphol* 225:107–123
- Pedersen SC (1996) Skull growth and the presence of auxiliary fontanelles in rhinolophid bats (Microchiroptera). *Zoomorphology* 116:205–212
- Pedersen SC (1998) Morphometric analysis of the chiropteran skull with regard to mode of echolocation. *J Mammal* 79:91–103
- Pettigrew JD (1991) Wings or brain? Convergent evolution in the origins of bats. *Syst Zool* 40:199–216
- Pye JD (1968) How insects hear. *Nature* 218:797
- Ratcliffe JM (2009) Predator–prey interaction in an auditory world. In: Dukas R, Ratcliffe JM (eds) *Cognitive ecology II*. University of Chicago Press, Chicago, IL, pp 201–228
- Ratcliffe JM, Jakobsen L, Kalko EKV, Surlykke A (2011) Frequency alternation and an offbeat rhythm indicate foraging behaviour in the echolocating bat, *Saccopteryx bilineata*. *J Comp Physiol A Neuroethol Sens Neural Behav Physiol* 197:413–423. doi:10.1007/s00359-011-0630-0
- Roeder KD (1967) *Nerve cells and insect behavior*, revised edn. Harvard University Press, Cambridge
- Schnitzler H-U, Kalko EKV (2001) Echolocation by insect-eating bats. *Bioscience* 51:57–569
- Schnitzler H-U, Kalko EKV, Kaipf I, Grinnell AD (1994) Fishing and echolocation behavior of the greater bulldog bat, *Noctilio leporinus*. *Behav Ecol Sociobiol* 35:327–345
- Schuchmann M, Siemers BM (2010) Behavioral evidence for community-wide species discrimination from echolocation calls in bats. *Am Nat* 176:72–82
- Sears KE, Behringer RR, Raswweiler JJ IV, Niswander LA (2006) Development of bat flight: morphologic and molecular evolution of bat wing digits. *Proc Natl Acad Sci USA* 103:6581–6586
- Siemers BN, Schnitzler HU (2004) Echolocation signals reflect niche differentiation in five sympatric congeneric bat species. *Nature* 429:657–661
- Simmons NB (1994) The case for chiropteran monophyly. *Am Mus Novit* 3103:1–54
- Simmons NB (2008) Taking wing. *Sci Am* 2008:96–103
- Simmons NB, Geisler JH (1998) Phylogenetic relationships of *Icaronycteris*, *Archaeonycteris*, *Hassianycteris*, and *Palaeochiropteryx* to extant bat lineages in Microchiroptera. *Bull Am Mus Nat Hist* 235:1–182
- Simmons JA, Stein RA (1980) Acoustic imaging in bat sonar: echolocation signals and the evolution of echolocation. *J Comp Physiol A* 135:61–84
- Simmons NB, Novacek MJ, Baker RJ (1991) Approaches, methods and the future of the chiropteran monophyly controversy: a reply to J.D. Pettigrew. *Syst Zool* 40:239–243
- Simmons NB, Seymour KL, Habersetzer J, Gunnell GF (2008) Primitive early Eocene bat from Wyoming and the evolution of flight and echolocation. *Nature* 451:818–821
- Simmons NB, Seymour KL, Habersetzer J, Gunnell GF (2010) Inferring echolocation in ancient bats. *Nature* 466:E8
- Speakman JR, Racey PA (1991) No cost of echolocation for bats in flight. *Nature* 350:421–423
- Stamper SA, Bates ME, Benedicto D, Simmons JA (2009) Role of broadcast harmonics in echo delay perception by big brown bats. *J Comp Physiol A* 195:79–89
- Surlykke A, Kalko EKV (2008) Echolocating bats cry out loud to detect their prey. *PLoS One* 3:e2036. doi:10.1371/journal.pone.0002036
- Surlykke A, Ghose K, Moss CF (2009a) Acoustic scanning of natural scenes by echolocation in the big brown bat, *Eptesicus fuscus*. *J Exp Biol* 212:1011–1020
- Surlykke A, Pederson SB, Jakobsen L (2009b) Echolocating bats emit a highly directional sonar sound beam in the field. *Proc Biol Sci* 276:853–960
- Suthers RA, Thomas SP, Suthers BJ (1972) Respiration, wing-beat and ultrasonic pulse emission in an echo-locating bat. *J Exp Biol* 56:17–48
- Suthers RA, Hartley DJ, Wenstrup JJ (1989) The acoustic role of tracheal chambers and nasal cavities in the production of sonar pulses by the horseshoe bat, *Rhinolophus hildebrandti*. *J Comp Physiol A* 162:799–813
- Swartz 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

- Teeling EC (2009) Hear, hear: the convergent evolution of echolocation in bats? *TREE* 24:351–354
- Thomas JA, Moss CF, Vater M (eds) (2002) *Echolocation in bats and dolphins*. University of Chicago Press
- Ulanovsky N, Fenton MB, Tsoar A, Korine C (2004) Dynamics of jamming avoidance in echolocating bats. *Proc Biol Sci* 271:1467–1475
- Vanderelst D, deMey F, Peremans H, Kalko E, Firzlaff U (2010) What noseleaves do for FM bats depends on their degree of sensorial specialization. *PLoS One* 5:e11893. doi:[10.1371/journal.pone.0011893](https://doi.org/10.1371/journal.pone.0011893)
- Veselka N, McErlain DD, Holdsworth DW, Eger JL, Chhem RK, Mason MJ, Brain KL, Faure PA, Fenton MB (2010a) A bony connection signals laryngeal echolocation in bats. *Nature* 463:939–942
- Veselka N, McErlain DD, Holdsworth DW, Eger JL, Chhem RK, Mason MJ, Brain KL, Faure PA, Fenton MB (2010b) Reply to Simmons et al. *Nature* 466:e9–e10
- Voight-Heucke S, Taborsky M, Dechmann DKN (2010) A dual function of echolocation: bats use echolocation calls to identify familiar and unfamiliar individuals. *Anim Behav* 80:59–67
- Von Helversen D, von Helversen O (2003) Object recognition by echolocation: a nectar-feeding bat exploiting flowers of a rain forest vine. *J Comp Physiol A* 189:327–336
- Von Helversen D, von Helvesen O (1999) Acoustic guide in bat-pollinated flower. *Nature* 398:759–760
- Weatherbee SD, Behringer RR, Rasweiler JJ IV, Nisander LA (2006) Interdigital webbing retention in bat wings illustrates genetic changes underlying amniote limb diversification. *Proc Natl Acad Sci USA* 103:15103–15107
- Yovel Y, Franz MO, Stilz P, Schnitzler H-U (2008) Plant classification from bat-like echolocation signals. *PLoS Comput Biol* 4:e1000032. doi:[10.1371/journal.pcbi.1000032](https://doi.org/10.1371/journal.pcbi.1000032)
- Yovel Y, Falk B, Moss CF, Ulanovsky N (2010) Optimal localization by pointing off axis. *Science* 327:701–704
- Zhuang Q, Mueller R (2006) Noseleaf furrows in a horseshoe bat act as resonance cavities shaping the biosonar beam. *Phys Rev Lett* 97:218701