

Chapter 2

Bat Echolocation: Adaptations for Prey Detection and Capture

Abstract Bats have evolved a plethora of adaptations in response to the challenges of their diverse habitats and the physics of sound propagation. Such adaptations can confound investigations of adaptations that arise in response to prey. Here, we review the adaptations in the echolocation and foraging behaviour of bats. Bats use a variety of foraging modes including aerial hawking and gleaning. The main challenge to bats echolocating in clutter is increased resolution to detect small objects, be they insects or twigs, and overcoming the masking effects that result from the overlap of echoes from prey and the background. Low-duty-cycle echolocating bats that aerial hawk in clutter have evolved short, frequency-modulated calls with high bandwidth that increase resolution and minimizes masking effects. Bats that glean prey from the vegetation have similar adaptations but in addition use passive listening and/or 3-D flight to ensonify substrate-bound prey from different directions. High-duty-cycle echolocating bats have evolved Doppler-shift compensation which allows the detection of acoustic glints from the flapping wings of insects. Bats that aerial hawk in the open have to search large volumes of space efficiently and use narrowband, low-frequency (for decrease atmospheric attenuation) echolocation calls that maximize detection distance. The wings and echolocation of bats form an adaptive complex. Bats that forage in clutter where distances are short have short broad wings for slow, manoeuvrable flight. Bats that hunt in the open where detection distances are long have long narrow wings for fast, agile flight.

2.1 An Introduction to Echolocation

Echolocation is the location of objects in time and space using reflected sound (i.e. an echo) rather than the reflected light used in vision. The use of reflected sound means that echolocation can be used in complete darkness. The sophisticated echolocation of modern bats probably evolved in the context of the detection and capture of small insects on the wing in complete darkness (Griffin 1944). During echolocation, bats generate their echolocation pulses or calls using their larynx and

vocal chords, in much the same way humans do when we speak. The call travels through the air in the form of concentric sound pressure waves, and when these waves are reflected off objects, echoes are generated and these in turn travel back through the air from the object as another series of sound pressure waves that the bats' ears can detect. The bat's brain interprets differences between its emitted call and the returning echo to form a three-dimensional image of its surroundings in much the same way we use our eyes and light to form three-dimensional images of our surroundings.

The echolocation systems used by bats are sophisticated and complex, but the manner in which echolocation functions can be understood through acoustics, the theory of sound. Acoustics has allowed the documentation of the diversity of echolocation types/systems among bats. In combination with flight, echolocation has allowed bats to colonize just about every conceivable nocturnal niche and adaptations to these niches have given rise to more than 1270 species of bats (Matthias et al. 2016). This has led to an enormous diversity in form and behaviour, making bats the most ecologically diverse group of mammals.

Although all bats fly, not all of them echolocate and about 184 species, commonly known as Flying foxes rely almost exclusively on vision. However, at least three species of Flying fox, *Rousettus aegyptiacus*, *R. amplexicaudatus* (Novick 1958; Griffin 1958; Holland et al. 2004; Yovel et al. 2011), and *R. leschenaulti* (Novick 1958; Raghuram et al. 2007; Fenton and Ratcliffe 2014) also use a rudimentary form of echolocation in which echolocation calls are generated by tongue clicks (lingual echolocation) rather than by the larynx (laryngeal echolocation). Although it has been suggested that other species of Flying fox may also use lingual echolocation (Funakoshi et al. 1995; Schoeman and Goodman 2012), this has not been confirmed. A third type of echo sensing, considered to be rudimentary because it does not allow the accurate estimation of object distance, involves the generation of clicks using the wings (Gould 1988; Boonman et al. 2014). Old World fruit bats are able to use echoes from these wing clicks to detect objects in complete darkness (Boonman et al. 2014).

2.1.1 Detection and Classification of Targets

During echolocation, a bat will typically emit a series of calls which will be reflected off objects as echoes. The bat hears the echoes with its ears and the bat's brain can match the spectral and temporal properties of the emitted call with that of the echo to form a three-dimensional image of its surroundings in much the same way we use vision to do so. Calls of laryngeal echolocators can be emitted either through their mouths (mouth echolocators) or nostrils (nasal echolocators), depending on the species. The complex folds and flaps of skin around the nostrils of nasal echolocators and the shape of the pinnae and head of all bats are associated with the emission and reception of sound during echolocation (Pedersen 1993; Obrist et al. 1993; Goudy-Trainor and Freeman 2002; Zhuang and Müller 2006).

Bats are able to use their echolocation to determine the size, shape, material, texture distance of an object and perhaps also the type of insect prey. Bats can also differentiate between echoes from a prey item and those from non-target objects such as the background substrate or vegetation (clutter echoes). All of this information is encoded in the complex temporal and spectral changes that the bat's call undergoes when reflected as an echo. The acoustics involved is very complex but can be simplified as follows. The size of an object is determined simply by the intensity of the echo, larger objects generate echoes of greater intensity than smaller objects. Objects smaller than one wavelength of the echolocation call will not generate any echo or only weak echoes and the bat would not be able to detect it. Echolocation calls are scattered by objects smaller than one wavelength. This is known as Rayleigh scattering (Young 1981; Pye 1993). Rayleigh scattering causes sound reflected by an object smaller than one wavelength of the sound to be scattered in all directions so that very little of it gets back to the bat. As a result, most echolocating bats have to use echolocation calls of short wavelength and therefore high frequency so that echoes are generated from small leaves and twigs (which the bat has to avoid) and from small food items (e.g. small insects) which the bat has to catch and eat. Although most bats echolocate between 20 and 50 kHz (Fullard 1987), the full range of call frequencies used by bats is 9–210 kHz (Fenton et al. 2004; Jacobs 2000).

The speed of sound is constant at atmospheric conditions at which bats operate and bats can therefore determine the distance between it and an object by the time elapsed between when it emits a call and the echo returns from the object. Bats are capable of detecting very small time delays that allow them to differentiate between objects whose distances from the bat differ by as little as 1 mm (Neuweiler 1990). The relative intensity of sound received at each ear and the time delay between arrivals at the two ears provide information about whether the object is to the left or right of the bat, similar to the method first discovered in owls to passively locate prey using the sounds generated by the prey (Payne 1971). Similarly, interference patterns caused by echoes reflecting from the tragus, a flap of skin rising from the bottom margin of the external ear, allow the bat to determine whether the object is below or above the bat (Chiu and Moss 2007).

Echolocation also allows bats to resolve one object from another or from the background and to obtain information about the texture (Schmidt 1988; Simon et al. 2014) of an object. They do so by using calls comprising different wavelengths of sound and by shifting the peak frequency (frequency of maximum energy) of their calls (Neuweiler 1990; Schnitzler and Kalko 2001).

When two objects are close together, the echoes from each of them interfere with those from the other and will produce different patterns of sound waves than those generated by only one object. This allows the bat to discriminate objects that are less than 1 mm apart (Neuweiler 1990). Similarly, objects with very complex surfaces will reflect waves in different directions producing different interference patterns to that generated by objects with smoother surfaces allowing the bat to determine the texture of the object.

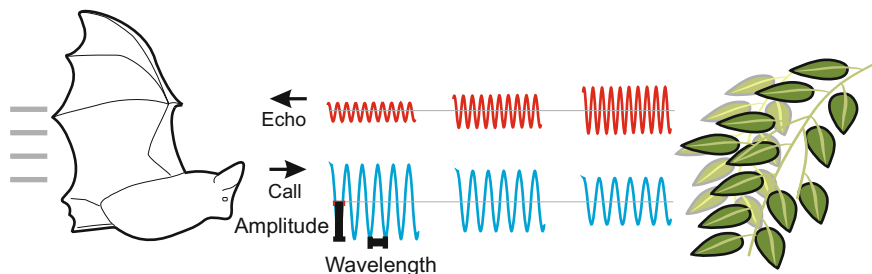


Fig. 2.1 Atmospheric attenuation and Doppler-shift compensation. **Atmospheric attenuation:** The emitted call (in blue) travels through the atmosphere in the form of sound pressure waves. As each pressure wave is formed, some of the energy in the sound is dissipated (indicated by the reduction in the amplitude of wave). When the sound is reflected off the object and travels back to the bat as an echo (in red), the echo is also attenuated. The echo that the bat hears is therefore much softer than the call that impinges on the object. **Doppler-shift compensation:** The bat emits its call (in blue) at a slightly lower frequency than the reference frequency (the frequency of its acoustic fovea—see text). Because of the relative motion of the bat, the echo from the object is shifted up in frequency as a result of the Doppler effect indicated by the shorter wavelengths in the echo in red. The bat compensates for the Doppler effect so that the echo always returns at the reference frequency (color figure online)

Atmospheric attenuation (Fig. 2.1) places limitations on the distance over which echolocation is effective and echolocation is therefore a short-range detection system operating over a few metres only. This is because bats have to use high-frequency sound to detect small objects such as insects and high-frequency sound is especially affected by atmospheric attenuation (Lawrence and Simmons 1982). Apart from frequency of the sound, atmospheric attenuation is also dependent on the temperature and humidity of the air. It is more pronounced for calls of higher frequency and increases as the temperature and humidity increases. All else being equal, bats that echolocate at the higher end of the frequency range used by bats should detect objects at shorter distances than bats that echolocate at the lower end of this range (Luo et al. 2013). However, it appears that bats can compensate for frequency-dependent atmospheric attenuation by increasing the intensity of their echolocation calls. Bat species with similar hunting methods and hunting in habitats from the edge of vegetation to open space away from vegetation or over water have similar detection distances. This is largely because bats echolocating at higher frequencies also use much higher call intensities so that they all have more or less the same detection ranges, i.e., increased intensity can counter frequency-dependent atmospheric attenuation (Surlykke and Kalko 2008).

Besides increasing the intensity of the call, bats are able to increase the distance over which their echolocation is effective by decreasing the band width of the call so that the energy of the call can be concentrated in a narrow range of frequencies or by decreasing the frequency of the call to minimize atmospheric attenuation. However, these strategies have trade-offs associated with them. Decreasing the bandwidth of the call decreases the resolving power of the call. Decreasing the frequency means that the bat will not be able to detect small objects. Thus,

increasing detection range decreases resolution and vice versa. Different species of bats have evolved different ways of dealing with these trade-offs to optimize the effectiveness of echolocation resulting in many different kinds of calls consisting of different components.

Target size and texture, the wing-beat patterns of insects (Rhebergen et al. 2015), and movement of the vocal sac of frogs (Halfwerk et al. 2014) could allow bats to classify the type of prey they are tracking using their echolocation calls. However, some bats using high-duty-cycle echolocation (see section on duty cycle below) are also able to determine the type of insect prey they are tracking from the temporal and spectral information in the echoes reflected off their prey (von der Emde and Schnitzler 1990) and from the wing-beat frequency of the prey (von der Emde and Menne 1989). High-duty-cycle bats detect prey by the amplitude and frequency modulations (acoustic glints, Fig. 1.1) generated when the calls are reflected off the wings of the prey which are at different angles to the impinging echolocation beam during the insect's wing-beat cycle. These bats can accurately measure the wing-beat frequency of insects by measuring the rate at which the acoustic glints are generated. Since wing-beat frequencies are inversely correlated with the size of insects, it can be used as the first step in classification. However, these bats can also use the amplitude and frequency information in the glints and the echoes between glints (which are unique for each type of insect even if they have the same glint frequency) to determine the type of insect, irrespective of the orientation of the insect relative to the bat (von der Emde and Menne 1989; von der Emde and Schnitzler 1990).

2.1.2 Components of Calls

2.1.2.1 Frequency-Modulated Components (FM)

Bat calls are composed of various components of mainly two types, frequency-modulated (FM) and constant-frequency (CF) components but with a range of variations of these two types of components. The calls of most species of bats are dominated by FM components while those of the remainders (largely just three families of bats, Rhinolophidae, Rhinonycteridae, and Hipposideridae) are dominated by CF components. FM calls can be narrowband, with a low range of frequencies or broadband with a high range of frequencies. Narrowband FM signals are good for target detection but not for target localization and classification. Broadband FM calls are good for target localization and classification but because of atmospheric attenuation and the consequent short detection range are not good for target detection (Schnitzler and Kalko 2001).

Broad bandwidth FM calls allow exact target localization through accurate determination of the distance and angle to the target. Echoes from steep FM broadband calls activate the neuronal filters in the brain of the bat for only a short time, producing the precise time markers that allow the accurate determination of

the time delays that encode the distance to the target (Goerlitz et al. 2010). In addition the large bandwidth activates more neuronal filters, improving the accuracy of both the distance (Moss and Schnitzler 1995) and angle determination with increasing bandwidth (Schnitzler and Kalko 2001).

Frequency-modulated signals of broad bandwidth also allow the determination of texture and depth structure of the target. Texture of the target can be determined from the differences in absorption of different frequencies while depth structure can be determined from interference patterns caused by the overlapping of multiple sound waves in the echoes from the target. Determination of these parameters could assist the bat in the classification of the target (Neuweiler 1989, 1990).

To optimize detection range and target localization most bats use a combination of narrowband and broadband FM calls switching from one to the other depending on the situation. Most species also use harmonics (Neuweiler 1984; Schnitzler and Kalko 2001) to broaden the bandwidth of their calls. Echolocation calls consist of the fundamental or 1st harmonic, and a series of harmonics of higher frequency called the 2nd, 3rd and 4th harmonics and so on. Not only are these harmonics important because they allow the bat to resolve smaller objects than they otherwise would have been able to, but they also help the bat to distinguish echoes from the target and echoes from non-target objects (i.e. clutter) in the background or to the periphery of the target (Bates et al. 2011).

Echoes from clutter can interfere with the bats processing of target echoes, especially when the two kinds of echoes arrive at the bats auditory system at the same time. This masking of target echoes by echoes from clutter (Fig. 2.2) makes it difficult for the bat to use time delays to determine distances to the target. The horizontal width of the echolocation beam is dependent on the frequency of the sound; the higher frequency of higher harmonics has a narrower beam than the lower frequency of the 1st harmonic and therefore generates fewer echoes and echoes of lower amplitude from the clutter than from the target. The target reflects echoes from both the 1st and the higher harmonics that are of higher amplitude than echoes from clutter allowing the bat to focus on echoes from the target. This is analogous to visual images of objects directly in front of us and those in our peripheral vision. The harmonic structure of echolocation calls also assists in isolating echoes from the target from background clutter because the higher-frequency sounds of higher harmonics attenuate more quickly in air. Echoes generated by the higher harmonics reflect more weakly off the more distant background than off the closer target. Echoes from the target therefore are of higher amplitude than echoes from the background allowing the bat to detect an insect, for example, against the background clutter (Bates et al. 2011).

Although it is possible that a bat could increase its bandwidth by calls sweeping from higher to lower frequencies instead of harmonics, the duration of such calls would be longer than calls with harmonics and would increase the potential of temporal overlap of background echoes with all or parts of the call, interfering with the bat's ability to process target echo time delays. The facility with which FM components can be used to resolve targets while avoiding call echo overlap when close to clutter makes them ideal for hunting in dense vegetation where resolution is

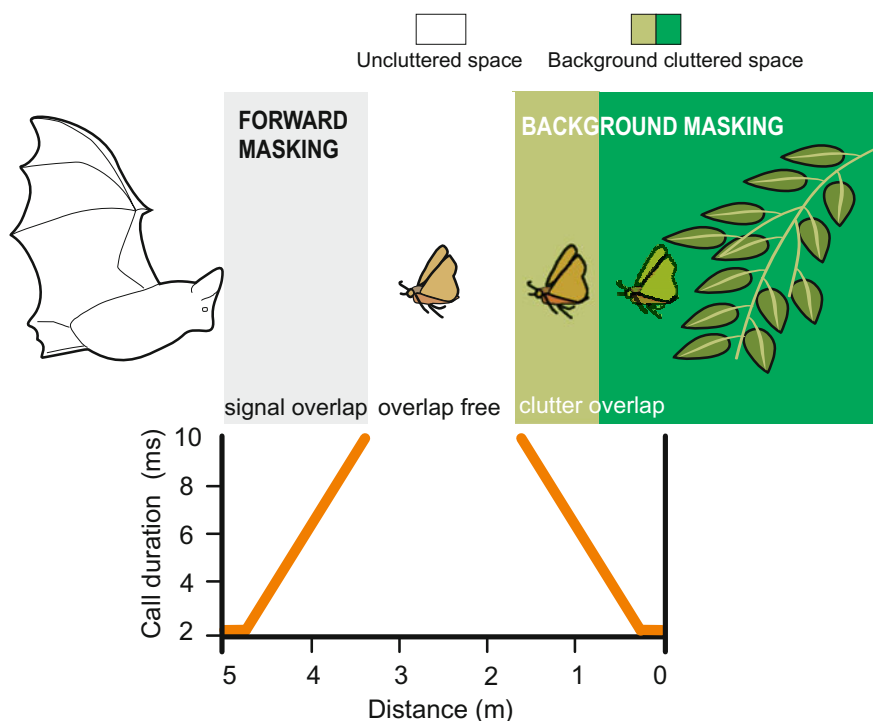


Fig. 2.2 Masking effects. **Forward masking** is the overlap of call and echo and occurs in the zone immediately in front of the bat (*grey area*). **Backward masking** is the overlap of target echo with echoes from the background (*green areas*). There is an overlap-free zone some distance from the bat and the vegetation. This zone increases in size (*orange lines*) as the bat decreases the duration of its calls. Adapted from Schnitzler and Kalko (2001) (color figure online)

of greater importance than detection distances (Schnitzler and Kalko 2001). The distance between bat and objects is small in cluttered situations in any case.

2.1.2.2 Constant-Frequency (CF) Components

Constant-frequency (CF) components of calls are components in which there is no change in frequency with time. In such components, the energy is concentrated into a single or narrowband of frequencies allowing the sound to travel through the atmosphere for greater distances, before atmospheric attenuation dissipates the energy, than that in FM components in which the energy is spread over several frequencies. Focusing all of the energy in a narrowband of frequencies also allows the CF signal to be of longer duration than FM signals. The operational range of CF components is therefore further than that of an FM signal because echoes returning within the narrow-frequency band are of higher amplitude and can be summed by

the bat's auditory system over the entire length of the call. This maintains a constant frequency for up to 100 ms compared to that in a FM signal where each frequency has an effect that lasts only a few milliseconds. The longer call duration also increases the probability of part of the call being reflected off a distant object (Schnitzler and Flieger 1983; Schnitzler and Kalko 2001). Constant-frequency components are therefore good for detecting objects but because they consist of a single or narrow range of wavelengths, they are not good at localizing objects in time and space. Consequently, these signals are well-suited in open spaces where distances to objects are likely to be long and detection range is therefore more important than localization. They are also good for bats that wait on perches for prey to fly past. The long, narrowband signal allows the bat to detect Doppler shifts, which would be produced by an insect moving either towards or away from a perched bat.

Such long-duration CF signals are optimal for detecting the amplitude and frequency changes, called acoustic glints (Fig. 1.1; Neuweiler 1984; Schnitzler and Kalko 2001), which occur in the echo when the signal impinges on the wings of insects when the insect is flying or flapping its wings while sitting on the substrate (Schnitzler and Flieger 1983; Neuweiler 1984; Schnitzler et al. 2003). Bats hunting from a perch using these signals with long-duration CF components are unable to detect prey against background clutter but can do so quite readily when the insect is flapping its wings. This is possible because the bat is able to generate constant echoes from the stationary background, (see Doppler-shift compensation in the section on high-duty-cycle bats below and Fig. 2.1). Superimposed on this constant background echo are changes in frequency and amplitude, called acoustic glints, generated when the call is reflected by the fluttering insect wings (Schnitzler and Flieger 1983; Neuweiler 1984; Schnitzler and Kalko 2001). When the long-duration CF signal impinges upon a wing, the amplitude and frequency of the echo are dependent on the position of the wing and whether the wing is moving towards the bat or away from it, respectively. Remember that the strength (i.e. amplitude) of an echo is dependent on the size of the object generating it. When the insect wing is in an upright position or at the bottom of its arc and perpendicular to the impinging echolocation signal all of its surface area reflects the signal producing an echo of maximum amplitude. When the wing is halfway through its cycle only its edge is exposed to the impinging signal and a very weak echo is produced. Similarly when the insect wing closest to the bat is moving down towards the mid-point of its cycle, it is moving towards the bat and the Doppler effect shifts the frequency of the echo up relative to the frequency in the bat's signal. When the wing is moved past the mid-point of its cycle and towards its lowest point, it is moving away from the bat and the echo is Doppler shifted lower than the bat's signal. These changes in the amplitude and frequency in the echoes of a bat's call from flapping insect wings are perceived by the bat as amplitude and frequency glints against the constant echo from the background clutter collectively called acoustic glints (Schnitzler and Flieger 1983; Neuweiler 1984; Schnitzler and Kalko 2001), which allow the bats to detect flapping insect wings against the background clutter. Acoustic glints are

analogous to coloured lights of different brightness flashing on and off against a background lit by a light of constant colour and intensity.

2.1.3 Duty Cycle

Bats emit their echolocation signals as discrete packets of sound or calls. These calls are thus separated by silence during which the bat is emitting no sound. The ratio of the duration of the call to the period of the call (call duration + time to the next call) is the duty cycle (Fenton 1999) and is usually expressed as a percentage.

2.1.3.1 Low-Duty-Cycle (LDC) Bats

Low-duty-cycle (LDC) bats have call durations that are short relative to the period of the call. The reason for this is the way in which these bats avoid being deafened by their own calls. Atmospheric attenuation at the high frequency at which bats operate means that bats have to emit their calls at very high intensities (measured as 110–135 dB at 10 cm in front of the bat) to have a functional range of detection. However, the inner ears of the bat have to be sensitive enough to pick up the faintest of echoes. Such a sensitive ear is likely to be damaged by sounds great than 90 dB emitted only millimetres from the ear. To avoid damage to the inner ear, LDC bats switch off their ears. In the middle ear of bats, the three small ossicles are linked in tandem and transmit sound from the ear drum to the cochlear (or inner ear). Attached to the ossicles are small muscles. Just before the bat emits its echolocation call, these muscles contract and disrupt the linkage between the three ossicles preventing the transmission of sound to the cochlear, thereby protecting the sensitive inner ear. The bat then emits the echolocation call. After emission of the call, it relaxes the muscles and restores the link between the ossicles allowing sound to be transmitted to the cochlear. The bat thus separates the emitted call and returning echo in time and has to wait until the echo from one call returns before emitting the next call so that the echo from one call does not return while the ear is functionally deaf during the emission of the next call. This is why there is a relatively long period of silence between each call and why the duty cycle is therefore low (Fenton 1999).

LDC bats are very diverse in their echolocation calls, flight behaviour, and habitat. The calls of most LDC bats are dominated by a broadband FM component which is well suited to the habitat in which they hunt and their mode of hunting. Because FM components are good for localization and distinguishing clutter from target echoes, these bats hunt in habitats where they forage close to vegetation either in dense vegetation or at the edges of vegetation near the ground or water. LDC bats can be specialists spending most of their time in dense vegetation whereas others are more flexible and can move from open habitats to edges of

vegetation, near the ground or water. These bats are able to switch from narrowband calls in open space to broadband calls when hunting close to clutter. Bats with calls dominated by FM components are generally slow manoeuvrable flyers with some flexibility and this is reflected in the shapes of their wings. Some of them have short broad wings for gleaning (taking prey from a substrate) or aerial hawking (catching prey in flight) in dense vegetation while others have intermediate wings for flying in edge habitats (Norberg and Rayner 1987). The FM-dominated calls of some LDC bats that hunt in the open have a quasi-CF component that increases their range of detection. These bats usually have long narrow wings for rapid and agile flight in open habitats, e.g., away from vegetation or high above the ground and water (Schnitzler and Kalko 2001).

2.1.3.2 High-Duty-Cycle (HDC) Bats

High-duty-cycle bats have call durations that are long relative to the silent period between calls (Fenton 1999). These bats are able to have relatively short silent periods and therefore high duration to call period ratios because they avoid self-deafening by separating the emitted call and returning echo in frequency rather than time. High-duty-cycle bats are restricted to the Old World families, Rhinolophidae, Rhinonycteridae, and Hipposideridae and a single species in the Americas, *Pteronotus parnellii*. High-duty-cycle bats emit calls of long duration (up to 100 ms) dominated by a CF component preceded and followed by a brief FM component (Schnitzler and Flieger 1983; Neuweiler 1984). Unlike LDC bats which place most of the call energy in the fundamental, HDC bats place most of the call energy into the second harmonic (Neuweiler 1984; Schnitzler and Kalko 2001). HDC bats have a region in their auditory cortex known as the ‘acoustic fovea’. This region has an over-representation of neurons sensitive to a unique and narrow range of frequencies called the reference frequency (Schuller and Pollak 1979). Echoes from the bat’s call will return at a slightly higher frequency than the emitted call because of the Doppler effect on frequency as a result of the bats’ flight speed relative to that of the target. To ensure that the returning echo falls within the narrow range of frequencies of the acoustic fovea, the bat lowers the frequency of the emitted call a phenomenon known as Doppler-shift compensation (DSC; Fig. 2.1; Schnitzler and Flieger 1983; Neuweiler 1984; Schnitzler and Denzinger 2011). As a result of DSC, the frequency of the emitted call does not therefore fall within the acoustic fovea protecting it from the high intensities at which the calls are emitted and preventing self-deafening. Because the ears are not ‘switched off’ during echolocation, the bat can emit calls and receive echoes at the same time unlike LDC bats. HDC bats can also hunt from a perch and when stationary emit calls that are 100–300 Hz lower than the reference frequency. These calls are referred to as the ‘resting frequency’ (RF; Schuller and Pollak 1979).

2.1.4 Tracking Targets

Bats have to adjust their echolocation calls to keep track of a moving object and as the distance between the bat and the object decreases. Bats do so by changing the temporal and spectral parameters of their calls in a systematic way. Echolocation attack sequences can therefore generally be divided into three phases (Griffin et al. 1960): a search phase (narrow bandwidth, long calls with long inter-call intervals), approach phase (shorter, broadband calls and shorter intervals), and the terminal or feeding buzz stage (much shorter calls and intervals with very narrow bandwidth). When a bat searches for prey, it scans as far ahead as possible and as widely as possible to increase the volume of space that it is searching at any one time, maximizing the chances of detecting prey. To do so it uses calls that are of long duration, relatively lower frequency and narrow bandwidth and therefore less affected by atmospheric attenuation. Because the bat is probing further, it takes longer for echoes to return so it emits calls at a slower rate. Longer calls will also increase the probability of at least part of the call being reflected off a distant object as an echo. After detection, the bat switches to the approach phase which allows the bat to classify and localize the object accurately in time and space. This requires greater resolution so it increases the bandwidth of its calls and the call rate while decreasing the duration of the calls. During the approach phase, the bat will have identified the object as edible or something to avoid. If it is prey, the bat homes in on the object switching to the terminal or feeding buzz phase of its attack. During these final stages of the attack, the bat just needs to pinpoint the object in time and space to make an accurate capture. Call rate increases even more, calls get even shorter in duration, and the bandwidth decreases. Calls are now so rapid that instead of discrete calls they appear to be one long buzz of sound, hence the name ‘feeding buzz’ (Griffin et al. 1960).

2.1.5 Bat Foraging Modes

Bats occupy a diverse range of habitats, and they have evolved different flight modes and echolocation behaviour which allow them to deal with the conditions in these different habitats.

2.1.5.1 Aerial Hawking in Open Habitats

Bats foraging in open areas away from or above vegetation use aerial hawking, i.e. catching flying prey on the wing. Aerial hawkers fly fast to search a large area quickly and to chase down fast-flying prey. They therefore have to probe far in front of them to detect targets at greater distances to give them sufficient time to intercept any target that is detected. In open areas, resolution of targets from each other or

from the background vegetation is not necessary and detection and classification are more important. Aerial hawkers use long-duration, narrowband echolocation calls of low frequency, all of which increase detection range. The calls are also narrowly frequency-modulated but aerial hawkers can change both their bandwidth and frequency to improve localization and classification of targets (Neuweiler 1984; Schnitzler and Kalko 2001).

2.1.5.2 Aerial Hawking Near Vegetation

Bats catching insects on the wing near vegetation such as at forest edges and in forest gaps have to distinguish echoes from the target from the much louder echoes coming from the vegetation while keeping track of the vegetation so that they do not collide with it. Bats foraging in such areas use a mixture of very shallow FM or quasi-constant-frequency (QCF) and steep FM calls. Some may also use calls that have both steeply FM and QCF components. Different species of bats hunting in background cluttered space can use different combinations of these types of calls (Schnitzler and Kalko 2001). The narrowband components of these mixed signals allow detection of prey, and the broadband FM components facilitate localization and classification of the background and insect. These bats avoid background masking effects (Fig. 2.2) by searching for and detecting prey in areas where the echo from the prey does not overlap with echoes from the background vegetation. They can also minimize masking effects by using short-duration calls (Neuweiler 1984; Schnitzler and Kalko 2001; Schnitzler et al. 2003).

Dealing with Clutter

Bats hunting in dense vegetation can use aerial hawking, ambush hunting (searching for prey from a perch and intercepting detected prey), and gleaning (taking prey from a substrate, e.g., from a branch or the ground using their mouths or from the surface or just below the surface of water using their feet, fish eagle style) (Fig. 2.3).

2.1.5.3 Gleaning

Bats hunting within dense vegetation (Fig. 2.3) have to be able to resolve target echoes from background clutter and have to deal with both forward (overlap between call and echo) and backward masking (Fig. 2.2) overlap between echoes from the target and background) effects. Target resolution and localization are achieved by using calls of wide bandwidth and high frequencies usually with multiple harmonics. Masking effects are minimized by using calls of short duration, 1–3 ms and maintaining a distance from the target, during localization and classification, that places the target in the overlap-free zone, i.e., where echoes do not

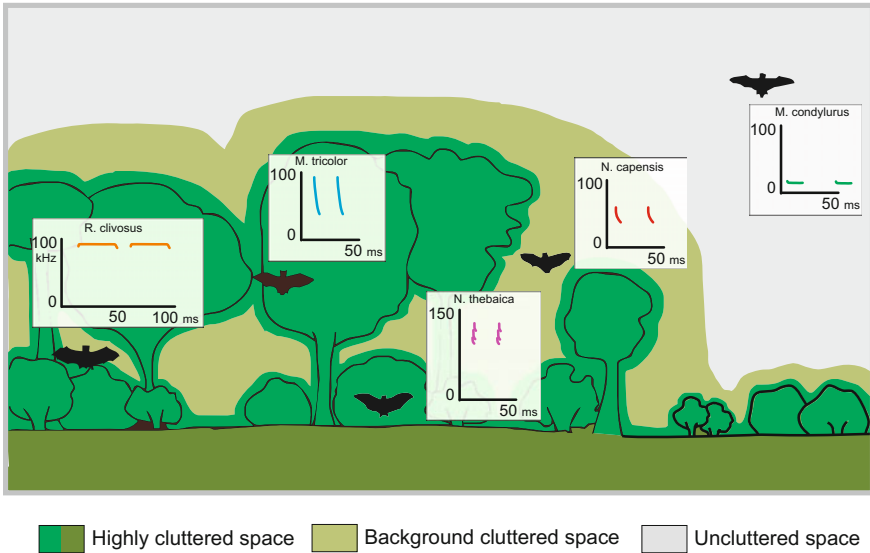


Fig. 2.3 Bat foraging habitat and duty cycle. Depicted are three habitat categories based on the challenges to echolocation with the wing shape and echolocation calls associated with each category (redrawn from Jacobs 2016). With the exception of *R. clivosus* which is a **high-duty-cycle** echolocator (indicated by the high ratio between call duration and call period —see text) all the other bats are **low-duty-cycle** echolocators (color figure online)

overlap with the emitted call or echoes from the background (Fig. 2.2; Schnitzler and Kalko 2001; Geipel et al. 2013). Because these bats operate in confined spaces, the operation range of their echolocation is short and they are able to use very quiet calls and are often referred to as ‘whispering bats’ (Schnitzler and Kalko 2001).

Nevertheless, target detection, localization, and classification is still very difficult and almost impossible leading to the suggestion that gleaning bats hunting in clutter can only locate prey by using cues other than echoes such as olfactory (Thies et al. 1998) and visual (Bell 1985; Ekloef and Jones 2003) ones as well as prey-generated sounds such as mating calls (see Chap. 4 and 6; ter Hofstede et al. 2008; Jones et al. 2011) and noises of walking or flying insects (Siemers and Swift 2006; Russo et al. 2007; Jones et al. 2011).

Although it has been demonstrated that some gleaning bats are unable to locate and classify prey in clutter using echolocation alone (Arlettaz et al. 2001) other gleaning species appear to use echolocation throughout a gleaning attack (Schmidt et al. 2000; Swift and Racey 2002; Ratcliffe and Dawson 2003) and some of them appear to be able to localize and classify prey using echolocation alone (Geipel et al. 2013). The gleaning bat *Micronycteris microtis* can do so by combining short-duration, high-frequency broadband calls with three-dimensional hovering flight to minimize the masking effects of echoes from the substrate on which the prey rests (Fig. 2.2). The three-dimensional flight allows the bat to take advantage

of the acoustic mirror effect of the substrate at certain angles of ensonification. The substrate acts as an acoustic mirror reflecting echoes from the background away from the bat, minimizing the clutter in which echoes from the prey are embedded, allowing the bat to use its echolocation to localize and classify prey (Geipel et al. 2013). However, whether this is a species-specific strategy not used by other gleaning bats or a more general strategy remains to be determined.

2.1.5.4 Aerial Hawking

Bats in the Old World families, Rhinolophidae, Rhinonycteridae, and Hipposideridae and the New World mustached bat and *Pteronotus parnellii* (Mormoopidae) are HDC bats that use aerial hawking to search for and catch fluttering insects in highly cluttered space close to vegetation or the substrate (Fig. 2.3). The echolocation system of these bats (see sect. ‘High-duty-cycle (HDC) bats’ above) allows them to generate acoustic glints off the wings of fluttering prey, be the prey stationary or flying, while keeping the echoes from the background constant. This effectively circumvents the problem of backward masking, allowing these bats to locate and classify prey flying close to or sitting on the background. This is achieved by the long-duration CF component of their calls which is therefore clutter insensitive (Schnitzler and Kalko 2001). However, these bats still have to be able to determine the distance to the prey with a degree of precision that allows capture. Such ranging tasks are probably enabled by the FM components at the beginning and end of the CF component (Schnitzler 1968; Schuller et al. 1971; Schnitzler and Denzinger 2011) as is evidenced by increase in the bandwidth and duration particularly of the terminal FM component in response to clutter (Fawcett et al. 2015). Such ranging tasks would also be important for a stationary bat tracking a moving target and explain why even stationary HDC bats include FM components in their calls (Mutumi et al. 2016, S1). These FM components are, however, not clutter insensitive and it is not known how these bats deal with masking effects (Fig. 2.2).

2.1.6 Eavesdropping

Many bats that glean prey use prey-generated acoustic cues, e.g. calls of insects and frogs (Tuttle and Ryan 1981; Ryan et al. 1982; Belwood and Morris 1987; Arlettaz et al. 2001) or rustling noises of insects walking on leaf litter or fluttering their wings (Faure and Barclay 1994; Siemers and Swift 2006; Russo et al. 2007; Jones et al. 2011) for detection, classification, and localization of prey. Many gleaners are characterized by large ears that facilitate passive (i.e. non-echolocating) acoustic localization of prey. However, it appears that gleaners may always emit echolocation signals in flight to determine the position of the site with food, to navigate, and to avoid collisions (e.g. see Ratcliffe et al. 2005) and may use calls of low

amplitude to prevent overloading of the hearing system with loud clutter echoes (Schnitzler and Kalko 2001). Passive listening may be a strategy to overcome masking effects that arise from the overlap between target and clutter echoes.

Bats have evolved a plethora of adaptations allowing them to circumvent the acoustic challenges of a diversity of habitats. This has allowed them to prey on an even greater diversity of prey in these habitats, from arthropods to vertebrates. Adaptations to the acoustic challenges of the habitat in which bats forage can confound investigations into the co-evolution between bats and their prey. This is also true of prey defences. The identification of co-evolved traits is therefore dependent on the extent to which we can separate the influence of habitat from that of the predator-prey interaction on the evolution of bats and their insect prey.

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