Chapter 4
To Scream or to Listen? Prey Detection and Discrimination in Animal-Eating Bats

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4.1 Introduction

Around 1940, Donald Griffin (Griffin 1944) and Sven Dijkgraaf (Dijkgraaf 1943, 1946) independently demonstrated that some bats use biological sonar while in flight. Soon thereafter, Griffin coined the term "echolocation" to describe how bats use the returning echoes from their vocalizations to orient and to locate objects in their path (Griffin 1944, 1958). Their experiments revealed a previously unconfirmed way of sensing. As a result, the concept of an animal's internal representations of the outside world was changed forever, and echolocation soon became part of popular discourse. In an essay published in 1974, the philosopher Thomas Nagel made famous the question, "What is it like to be a bat?" (Nagel 1974). Nagel used the question rhetorically as a metaphor for the position that understanding another person's experience of reality and, thus another's mind, is reductionist and ultimately absurd. Specifically, he argued that if one cannot fathom how bats "see" the world through their ears, how can one hope to describe and quantify another person's subjective experience? A reader of this volume, however, will be given the

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opportunity to appreciate the extraordinary progress researchers have made since 1974 in understanding what it might be like to be an echolocating bat.

Throughout this volume, the chapters describe the sensory ecology and neurobiology of bat echolocation, from signal design, reception, and processing, to the role of echolocation in niche divergence, and the secondary social uses of biosonar signals for communication. For example, Surlykke, Simmons, and Moss (Chapter 10) discuss the latest ideas about how a bat "sees" with its ears through a well-developed and experimentally supported concept of auditory scene analysis. In this chapter, the research discussed concentrates specifically on the production and processing of auditory information in predatory (i.e., animal-eating) echolocating bats in nature and under conditions meant to simulate nature, especially in those species that hunt airborne prey (hawkers) and take prey from surfaces (gleaners).

Once undetected, and for the most part undetectable by human ears, advances in high-frequency recording technology now make echolocation one of the most measurable and accessible of senses. Simply put, call design indicates which sound frequencies will be (and will not be) in the returning echoes, call rate approximates how often bats update their auditory scene, and call directionality indicates where bats are directing their acoustic gaze. Similarly, one can record and analyze the sounds generated by would-be prey and assess behaviorally which kinds of sounds bat most easily detect. Researchers can also identify the sounds that are more or less attractive to bats or sounds that can even deter hunting bats.

This chapter concentrates on how animal-eating bats, including those that consume exclusively arthropods, use echolocation and prey-generated sounds to detect, discriminate, and locate prey. Most of today's more than 1,000 echolocating bat species are animal-eating (Simmons 2005; Fenton and Ratcliffe 2010), taking their prey either from the air, from surfaces, or both (Schnitzler and Kalko 2001). A small number of echolocating bats, perhaps a dozen species from a number of families, take some of their prey from water surfaces. These trawling species are not discussed in this chapter, other than to say that they use prey detection strategies similar to those used by aerially hawking bats (Siemers et al. 2001). "To scream or to listen," a component of this chapter's title, refers to a relationship first proposed by Griffin (1958). Specifically, aerially hawking bats tend to use calls of much higher intensity than those of bats gleaning prey from terrestrial surfaces. While researchers now know that there are many bats that both glean and hawk prey, this relationship between call intensity and foraging strategy still holds (Hackett et al. 2014). The calls of gleaning bats are less intense because they can be. At shorter distances between a bat and its would-be prey, the echoes returning from even faint calls will be as loud as or louder at the bat's ears than those returning from flying insects at longer distances.

Aerial hawking bats tend to rely on echolocation for prey detection and for all, or most, of the information about prey position and identity. Most substrate gleaning bats, in contrast, are listening for prey-generated sounds to determine prey position (Bell 1985). These two foraging behaviors are often distinguished as active listening (echolocation) and passive listening (using prey-generated cues). Among extant bats, and throughout evolutionary time, locating prey in the air by echolocation and

finding prey on substrates by listening for prey cues probably have been the two important strategies for prey localization (Simmons and Geisler 1998). Whether gleaning bats can use echolocation alone to detect perched prey has been an area of lively debate for some time (Arlettaz et al. 2001).

Aerial hawking and substrate gleaning require different echolocation and flight behaviors and, perhaps, differential reliance on spatial memory and learning (Hulgard and Ratcliffe 2014). Our chapter has three sections focused on these two foraging strategies. In the first we discuss the evolution of echolocation and the foraging behaviors likely used by ancestral bats to set the stage for our examination of foraging in extant animal-eating bats. The second section describes the behavior of aerial hawkers and their complex relationship with insect prey, especially between aerial hawking bats and eared moths that respond to bat echolocation calls. The third section examines substrate gleaning bats and their reliance on prey-generated cues, with particular emphasis on eavesdropping bats that listen in on prey mating calls. Throughout we also discuss the effects of each of these foraging strategies on prey and prey adaptations to thwart bat detection. Together, these sections emphasize the diverse array of behaviors used by foraging bats to identify and localize their animal prey, highlighting the progress that bat researchers have made in answering Nagel's once rhetorical question, "What is it like to be a bat?"

4.2   Evolution of Echolocation

One current hypothesis proposes that echolocation first evolved for orientation and obstacle avoidance as the ancestors of modern bats jumped, glided, or flew between trees while foraging (Fenton et al. 1995; Simmons and Geisler 1998). If correct, this early form of echolocation was presumably quite rudimentary and not functional for prey localization; therefore, these proto-bats most likely located prey by listening for prey-generated cues such as the rustling sounds of arthropod prey moving through leaf litter or for insects flapping their wings against tree bark as they warmed up their muscles for flight (Schnitzler et al. 2003). In this scenario, echolocation was later co-opted for use in prey localization, especially in bats that hunt airborne prey on the wing, an evolutionary trajectory that has likely resulted in the sophisticated echolocators of today (Schnitzler and Kalko 2001). Whether early echolocating bats used their larynxes (like most extant bats) or their tongues (like pteropodid fruit bats in the genus *Rousettus*) to produce echolocation signals is not known. While we cannot be certain how many times laryngeal echolocation has evolved in bats, we favor the hypothesis that laryngeal echolocation evolved once in proto-bats, concurrently with powered flight, and was subsequently lost in the Pteropodidae (Figure 4.1) (Jones and Teeling 2006). The other equally parsimonious hypothesis is that laryngeal echolocation evolved twice: once in the suborder Yangochiroptera, and then a second time in the suborder Yinpterochiroptera after the divergence of the pteropodid bats, a group that includes the flying foxes (Teeling 2009).
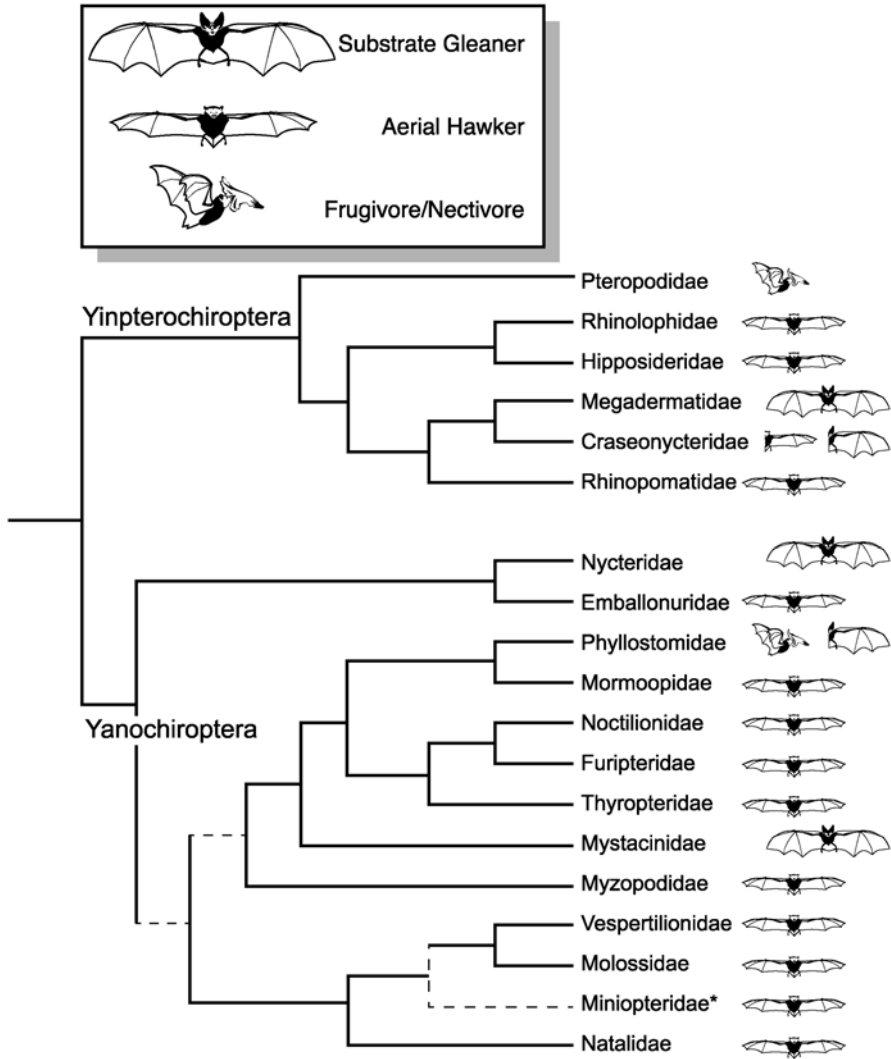
Fig. 4.1 Current phylogeny for bats (Jones and Teeling 2006). To the right of each family name, a Substrate Gleaner icon indicates that, in our opinion, this family is characterized by bat species that rely primarily on a gleaning strategy; all or most of which also take some prey by aerial hawking. An Aerial Hawker icon indicates that the family consists of species most of which primarily use a hawking strategy but includes behaviorally flexible species. Crasoenycteridae comprises a single behaviorally flexible species. A Frugivore/Nectivore icon indicates a family comprised solely or partially of frugivorous and nectivorous species

Each scenario, however, still suggests the same general story (Figure 4.1). That is, early laryngeal echolocating bats used powered flight, hunted animals, and took them in the air. The latter supposition is supported by the fact that most early fossil bats (~50 million years old) had wing designs suited for aerially hawking and not

like those of modern gleaners (Simmons and Geisler 1998; Safi et al. 2005). Therefore, we suppose that while something akin to gleaning may have characterized proto-bats and the very earliest of bats, this trait may have been subsequently lost, at least as a primary means of prey capture, as bats evolved more sophisticated laryngeal echolocation and longer, narrower wings, and then gleaning evolved independently again multiple times (Simmons and Geisler 1998) (Figure 4.1). However, while this idea is supported by fossil evidence (Simmons and Geisler 1998) and phylogenetic trait reconstructions (Safi et al. 2005), it is not clear from a pure parsimony perspective (Figure 4.1), and deserves further attention.

4.3 Aerial Hawking

Echolocation has been well established as the primary means of detecting and locating prey in aerial hawking bats (Griffin 1958; Schnitzler and Kalko 2001). On an interception course with airborne prey, laryngeal echolocating bats from both infraorders (the Yangochiroptera and Yinpterochiroptera) emit calls and listen for echoes arriving at their ears to determine the size, shape, and texture of the would-be target, as well as to update information on the target's 3-D coordinates. The echolocation calls bats use for locating aerial prey can be as loud as 140 dB, measured 10 cm in front of the bat's mouth, and are typically greater than 120 dB, which is louder than a jet engine or a machine gun, and among the loudest biological signals to be described (Holderied and von Helversen 2003; Holderied et al. 2005; Surlykke and Kalko 2008). Griffin's early estimates put these values closer to 100 dB, likely because echolocation calls were assumed to be omnidirectional and measures of intensity using a single-directional microphone were therefore thought to be accurate. We now know that echolocation calls are highly directional, producing a narrow forwardly directed beam (Surlykke et al. 2009a; Jakobsen et al. 2013). As a result, a call must be measured along its acoustic axis to accurately estimate maximum intensity. The recent advent of multi-microphone arrays, made possible through multi-channel, high sampling rate analog-to-digital converters, have revealed how directional (Surlykke et al. 2009a) and loud bats' echolocation signals truly are and also allowed for the identification of the acoustic axis (i.e., the bat's acoustic gaze) (Ghose et al. 2006; Surlykke et al. 2009b). As a result of this 20–40 dB increase in our estimate of call intensity in aerial hawking bats, target detection distance estimates have dramatically increased, from 3–5 m to more than 20 m (Surlykke and Kalko 2008).

From target detection to capture, bats produce echolocation calls at emission rates starting out at 20 calls/s, and culminating at >150 calls/s just before contact (Griffin et al. 1960; Simmons et al. 1979). Griffin and colleagues (Griffin et al. 1960) were the first to describe the phases of vespertilionid attack sequences based on little brown bats, *Myotis lucifugus*. First in the sequence is the search phase, where the bat is often producing fewer than 20 calls/s. Second is the approach phase (between 20 and 100 calls/s), in which the bat has detected its prey and plots a course for its interception. The third and final phase is the "terminal buzz," the brief period of extremely high calling rate (>100 calls/s) just before contact with the prey

(Griffin et al. 1960; Simmons et al. 1979). The call rate that characterizes the buzz is thought to reflect the necessity for rapid auditory updates on the prey's position as the bat closes in on its moving target (Griffin et al. 1960).

Since the discovery of bat biosonar, it has been enigmatic how bats can produce buzz calls so quickly and, also, how the bats are then able to accurately process the returning echoes. It has now been shown that "superfast" muscles are responsible for call production during the buzz (Elemans et al. 2011). Superfast muscles can produce power at contraction/relaxation rates greater than 90 cycles/s and are rare in vertebrates (see Rome 2006 for review). Those found in bats are the first to be identified in mammals. How the bat's sonar receiver processes the echoes returning from a target during the buzz is also not well understood. However, echoes from each buzz call should have returned to the bat's ears before the bat produces its next buzz call (Kalko and Schnitzler 1989; Elemans et al. 2011). Researchers also have shown that some species of vespertilionids broaden their biosonar beam, and thus their acoustic field of view, as they close in on their target (Jakobsen and Surlykke 2010). This is largely accomplished by dropping the peak frequency of calls by roughly an octave during the buzz. By widening their field of view and rapidly updating their auditory scene during this terminal phase close to prey, the bats should reduce the chances that the target escapes off to the side of their sonar beam (Ratcliffe et al. 2013).

It is the approach phase, however, that it is characterized by different decision-making processing and, in fact, may be most interesting with respect to better understanding sensorimotor integration and guidance systems in flying animals. The approach phase begins when the bat has detected the target and assessed it as being worthy of further investigation. Kick and Simmons (1984) further classified the approach phase of Griffin et al. (1960) into approach and tracking, the latter term meaning that the bat is actively plotting a course for the target's interception based on estimates of the target's predicted flight path. Plotting a path to interception with an erratically moving target poses a particular challenge. In the laboratory, Ghose et al. (2006) explored this in greater detail and proposed that the big brown bat, *Eptesicus fuscus*, uses a constant absolute target direction strategy for prey tracking, which minimizes time to interception. In this strategy, the bat maintains the absolute direction to the target as a constant by shifting their flight direction and speed in response to changes in prey trajectory. Open space aerial hawking bat species combine long thin wings that enable fast flight (Norberg and Rayner 1987) with loud, directional echolocation calls that allow detection of small prey in open environments (Surlykke et al. 2009a). In many cases the loud echolocation calls that aerial hawking bats produce also provide important information for the hunted prey, as is discussed in the section below.

4.3.1 Echolocating Bats and Insects with Bat-Detecting Ears

Echolocation is an active spatial sensory system where the sender and intended receiver of the echolocation call is one and the same individual. Gillam and Fenton (Chapter 5) discuss the use of echolocation calls by other bats as a means of identifying bat species and, perhaps more often, for identifying potential profitable patches of prey through listening for other bats' feeding buzzes. Many insects, however, have also evolved ears (e.g., moths, mantids, lacewings) or co-opted preexisting ears (katydids and crickets) to detect the echolocation calls of bats (Miller and Surlykke 2001; Fullard et al. 2005). In response to a bat's echolocation calls, these insects typically exhibit evasive flight maneuvers, sometimes simply flying toward (or dropping to) the ground and, in other instances, initiating erratic flight to make themselves more difficult to track and more likely to escape the bat's acoustic field of view (Roeder 1967; Miller and Surlykke 2001). Within the moths alone, ears appear to have evolved multiple times (Hoy 1992; Fullard 1998; Yack et al. 1999). There is evidence that echolocating bats have been the selective force driving the evolution of ears in moths because different populations of moths have ears that are tuned to the frequencies of the echolocation calls of sympatric bats (Fullard 1998; ter Hofstede et al. 2013). The arms race between hearing moths and bats has long fascinated biologists, and this interaction is best explored in the sound-producing tiger moths (Arctiidae).

4.3.2 Case Study: Vespertilionid Bats and Sound-Producing Tiger Moths

The chemically defended tiger moths (Rothschild et al. 1970) are among those groups of moths with ears. Many tiger moths produce high-frequency sounds of their own in response to other high-frequency signals (e.g., bat echolocation calls) as well as in response to tactile stimulation (Blest et al. 1963; Fullard and Fenton 1977). These sounds are clicks: brief (less than 1 ms), broadband (often covering a frequency range from below 10 kHz to well above 100 kHz), and loud (approximately 70–90 dB in intensity) (Blest et al. 1963; Conner 1999). Sound-producing tiger moths produce these clicks (or more accurately, click modulation cycles) using a pair of modified metathoracic episternites, called tymbals. In most, but not all, sound-producing tiger moths, the tymbals buckle asynchronously. Depending on whether the tymbals are striated (i.e., scored by individual grooves called "microtymbals") or not, moths can produce as few as 20 clicks/s to more than 1,000 clicks/s (Barber and Conner 2007; Corcoran et al. 2009).

The adaptive function of tiger moth defensive sound production remains the source of some debate, with three competing hypotheses for the mechanism of bat deterrence. The first hypothesis suggests that the clicks are aposematic warning signals (Dunning 1968). There is strong evidence from naïve bats that the clicks function aposematically. Bats only avoid moths that make clicks if the moths are

distasteful and then only after having experienced this negative pairing of cue and consequence (Hristov and Conner 2005). After being muted, noxious tiger moths are attacked by experienced bats (Ratcliffe and Fullard 2005). Moreover, within a given moth community, there are acoustic mimics in that some sound-producing tiger moths are palatable (Barber and Conner 2007; Barber et al. 2009).

The second hypothesis is that of acoustic startle, which suggests that clicks serve to startle approaching bats (Bates and Fenton 1990). Acoustic startle has received less support in recent years, mostly because bats quickly habituate to startle (Bates and Fenton 1990; Miller 1991), which would require clicking moths to be rare for startle to be effective, and this does not seem to be the case (Dunning et al. 1992).

The third major hypothesis suggests that the clicks act to jam bat echolocation (Fullard et al. 1979). Initially, this hypothesis lacked strong experimental support. However, it has now been confirmed that the incredibly high click rates of the tiger moth *Betholdia trigona* (a relatively palatable species) do jam bat biosonar and prevent the bat from accurately localizing the moth during the approach and terminal phases of attack (Corcoran et al. 2009). Field experiments have shown that bats capture ten times as many of these otherwise edible tiger moths if their sound-producing organs have been ablated than tiger moths with intact organs that are able to jam bat echolocation calls (Corcoran and Conner 2012). Clicking may save a moth's life, but it is energetically costly. The dogbane tiger moth, *Cycnia tenera*, preferentially produces clicks at bats when they are in the middle of their approach phase (Fullard et al. 2007), and they do so based on the activity of a single sensory neuron (Ratcliffe et al. 2009). Producing clicks only during the period of the bat's approach (in which the bat makes its final decision to pursue its would-be prey or to abort its attack) may save the moths energy (Ratcliffe and Fullard 2005; Ratcliffe et al. 2011).

Aerially hawking bats exhibit echolocation and pursuit behaviors that are assumed to be specialized to hunt flying prey in open air. Would-be prey species, in turn, have evolved a variety of strategies to avoid capture, including erratic escape maneuvers and sound production. These behaviors have made aerial hawking bats and their eared insect prey, especially moths, a textbook example of predator–prey interactions. The recent discoveries in moth sound production have highlighted the complexity of this interaction.

4.4 Substrate Gleaning

Based on the hypothesized scenario described at the beginning of this chapter, proto-bat ancestors likely were substrate gleaners that used echolocation for orientation and obstacle avoidance (Fenton et al. 1995; Simmons and Geisler 1998). These proto-bats probably relied on prey-generated cues, such as rustling sounds, to locate food. According to strong fossil evidence, however, the most recent laryngeal echolocating bat species from which all others are thought to have evolved would have been an aerial hawking species (Simmons and Geisler 1998; Safi et al. 2005). Therefore, many bat species and groups of species appear to have independently
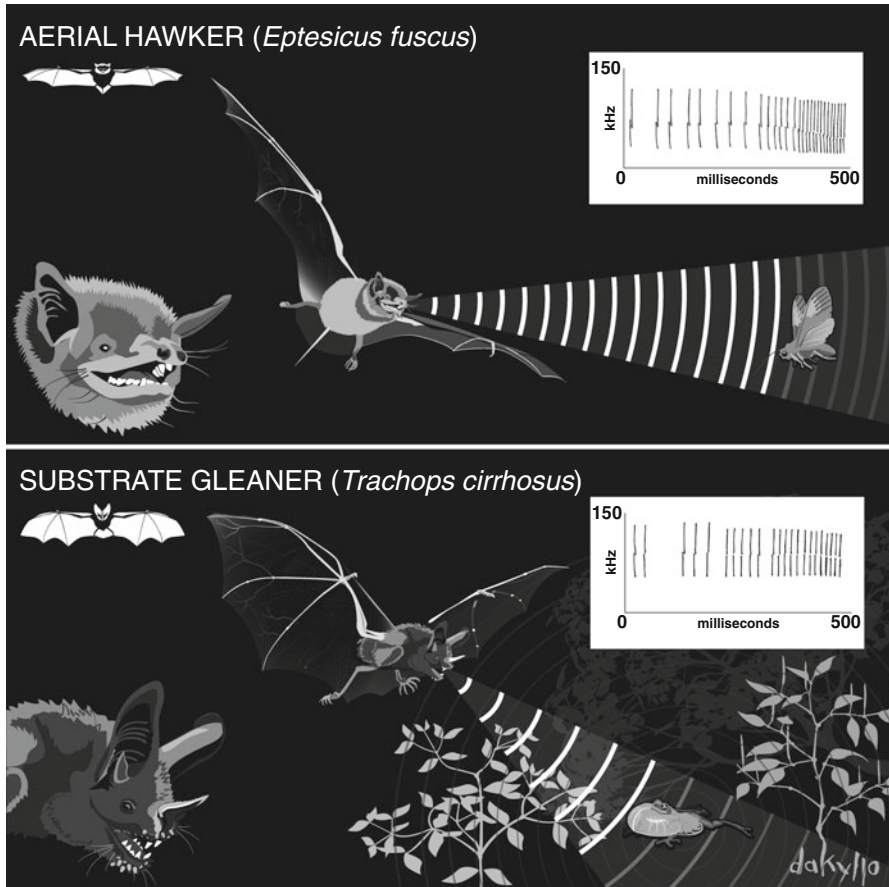
Fig. 4.2 Illustrations depicting two strategies for prey localization in bats. *Above*: Aerial hawk-ing (capturing flying prey in the air) is exemplified here by the big brown bat, *Eptesicus fuscus*, capturing a moth on the wing. *Below*: Substrate gleaning (capturing prey on surfaces, e.g., on the forest floor or on vegetation) is exemplified here by the fringe-lipped bat, *Trachops cirrhosus*, capturing a frog calling in the forest understory. Aerial hawkers tend to rely on echolocation alone for prey detection (active listening); in contrast, substrate gleaners often eavesdrop on prey-emitted sounds to find their prey (passive listening), presumably using echolocation primar-ily for orientation. The divergent wing morphologies associated with these two hunting strategies are illustrated by the silhouettes in the upper left of each panel: Aerial hawkers tend to have long, thin wings for fast flight in open spaces (high wing loading), while substrate gleaners have short, broad wings, which make the bats slower but improve maneuverability for flight in the forest understory (low wing loading). In the upper right of each panel, spectrogram traces depict the echolocation calls emitted by each bat during an attack approach (time on the *x*-axis, frequency on the *y*-axis). As described in the text, the calls of hawking bats are typically louder than those of gleaning bats, which often use calls of shorter duration and broader bandwidth. Gleaning bats often, but not always, drop the terminal buzz from their attacks on substrate-borne prey (Drawings by D. Kyllo)

re-evolved the proto-bat behavior of substrate gleaning (Schnitzler et al. 2003; Figure 4.1). However, the use of specialized echolocation signals (short, high frequency, and broadband) coupled with highly maneuverable powered flight almost certainly sets today's gleaning bat species apart from the earliest progenitors of bats.

It is apparent that specialized gleaning bats differ from specialized aerial hawking species in both wing shape and echolocation behavior (Figure 4.2). Gleaning bats tend to have shorter and broader wings, which should confer greater maneuverability (Norberg and Rayner 1987). Gleaning bats also make much quieter echolocation calls (reviewed in Hackett et al. 2014), and their attack sequences often, but not always, lack the "terminal buzz" phase seen in aerial hawking species (Ratcliffe and Dawson 2003). The echolocation calls of gleaning bats also tend to be shorter in duration, with a broader bandwidth and a higher peak frequency (Schnitzler and Kalko 2001).

When taking prey from the ground or from vegetation, it had been supposed that instead of using echolocation, gleaning bats listen for prey-generated sounds to detect and localize prey (Schnitzler and Kalko 2001). Indeed, for most bat species that glean some or all of their prey, echolocation is thought to play at most a secondary role, used to orient in 3-D space and avoid obstacles, but not to discriminate their target from background vegetation. Arlettaz et al. (2001) used the phrase "acoustically blind" to describe the problem bats face in resolving prey on complex backgrounds like terrestrial vegetation.

To our minds, the subject is still open to debate for many gleaning species, particularly in light of more recent evidence demonstrating that most, perhaps all, gleaners do not stop echolocating as they close on prey. Instead, they use calls of lower intensity, missed by early recording equipment (Ratcliffe et al. 2005; Russo et al. 2007). Later in this section, a remarkable phyllostomid bat, the common big-eared (leaf-nosed) bat, *Micronycteris microtis*, is discussed. This species uses echolocation alone to detect and discriminate still and silent prey perched on vegetation (Geipel et al. 2013a). While previous work on gleaning bats from a number of families suggests that *M. microtis* may be the exception to the rule, further work is warranted.

4.4.1   Gleaning Bats Use Prey-Generated Cues

Among the prey cues used by gleaning bats are the incidental sounds of prey movement (Arlettaz 1996) and the advertisement signals prey produce to attract mates (Tuttle and Ryan 1981). Incidental sounds may include the rustling sound of prey moving through leaf litter or the sound of prey wing-beats against a hard surface. These incidental sounds are relatively generic to many types of prey, and, therefore, may be particularly useful as they encompass a wide variety of potential prey. Most rustling sounds, such as those created by beetles walking on leaf litter, are broadband, spanning a frequency range of 3–30 kHz with some energy up to 50 kHz and occasionally up to 100 kHz (Goerlitz et al. 2008). The broad range of frequencies encompassed by rustling sounds show substantial overlap with the hearing range of most bats, and their broadband components may make them particularly localizable (Bell 1982; Page and

Ryan 2008). Although generic to many types of prey, rustling sounds can also provide some information as they differ depending on the arthropod's size (Goerlitz and Siemers 2006) and the substrate type (Goerlitz et al. 2008), both of which could be useful for bats in determining which rustling sounds to approach and which to pass over.

Many bat species use prey-generated rustling sounds to locate prey (Bell 1982; Russo et al. 2007). One example is the greater mouse-eared bat, *Myotis myotis*, which forages by flying low over the ground and listening for prey-generated sounds. When *M. myotis* detects rustles, it briefly hovers and then lands on the ground with wings outstretched, often trapping the insect with its body and then picking it up in its mouth (Arlettaz 1996). This foraging strategy appears to be widespread for bats that glean insects from vegetation or the ground and requires specialized wing morphology that allows them to take off from the ground quickly to avoid terrestrial predators (Jones et al. 2003).

Most gleaning bats also flexibly employ aerial hawking strategies (Bell 1982; Ratcliffe et al. 2006). Many are predators on moths and other eared insects and use echolocation when these prey are aloft in open air but listen for the fluttering sounds of their warm-up wingbeats to locate them on surfaces (Ratcliffe and Dawson 2003). While we generally think of moths as prey to aerial hawkers and safe from predation when close to vegetation, this may not always be the case. For example, the western long-eared bat, *Myotis evotis*, can capture moths either by aerial hawking or by gleaning from the ground. When gleaning, *M. evotis* uses moth fluttering sounds to locate prey (Faure and Barclay 1994). This behavior also has been demonstrated in other myotids, the most species-rich genus of bats (Ratcliffe and Dawson 2003). At the extreme, the pallid bat, *Antrozous pallidus*, predominantly consumes arthropods but appears to attack them almost exclusively on the ground in response to prey-generated sounds (Bell 1982). Some predatory gleaning bats have expanded beyond arthropods to consume vertebrate prey. The African heart-nosed bat, *Cardioderma cor*, uses passive listening for prey rustling sounds to localize frog as well as insect prey (Ryan and Tuttle 1987). These and numerous other examples demonstrate that prey localization by passive listening for prey-emitted cues is widespread across gleaning bats from multiple families, as it is likely to be an excellent strategy for locating prey among clutter when echolocation is not as effective. As noted above, however, with the possible exception of *Macrotus californicus*, which has been reported to stop echolocating under bright moonlit conditions in the laboratory (Bell 1985), all gleaning species once thought to be silent have been demonstrated to produce echolocation calls throughout gleaning attacks (Schmidt et al. 2000; Russo et al. 2007), some species even while on the ground (Jones et al. 2003; Ratcliffe et al. 2005) but at lower intensities than when hawking.

Simultaneously listening to prey-generated sounds and echolocating raises some challenges. Barber et al. (2003) showed that for the gleaning vespertilionid pallid bat, *Antrozous pallidus*, attempting to process both forms of auditory information simultaneously may result in lower foraging performance overall. While this bat preferentially uses prey-generated sounds over echolocation to detect prey, its reliance on one modality or the other may reflect processing constraints limiting the ability to effectively integrate both at once. It has been proposed that the inferior colliculus is larger in gleaning species than aerial hawking species as a response to

the challenge of processing both echolocation information and prey-generated sounds simultaneously (Baron et al. 1996; Reep and Bhatnagar 2000). However, a more recent comparative study did not find support for this hypothesis (Ratcliffe et al. 2006), suggesting, as do the results of Barber et al. (2003), that dual processing may be constrained by limited attention.

4.4.2   Gleaning Bats That Eavesdrop on Signaling Prey

Some bat species not only use generic rustling sounds to locate prey but also eavesdrop on species-specific mating calls of their prey. Eavesdropping is defined by Peake (2005) as "the use of information in signals by individuals other than the primary target" and differs from the use of inadvertent prey-generated cues, such as rustling sounds, in its reliance on signals rather than cues. Signals are defined as traits that evolved to communicate information (Karlson and Lüscher 1959). Cues are defined as incidental features present in the environment (Seeley 1995). Both signals and cues can be produced by a given prey species and can be used by predators. Signals, unlike cues, are specific to particular groups and even species and sexes of prey. This specificity may generate selection on the morphology and cognition of eavesdropping bats in order to successfully locate and identify calling prey.

Eavesdropping gleaning bats from a number of families prey on katydids (Orthoptera: Tettigoniidae) (Belwood and Morris 1987; ter Hofstede et al. 2008; Jones et al. 2011; Falk et al. 2015), which produce high-frequency and broadband calls (Korsunovskaya 2008). Some eavesdropping bats are reliant on katydid calls to locate them. The northern long-eared bat, *Myotis septentrionalis*, eavesdrops on the calls of the sword-bearing conehead katydid *Neoconocephalis ensiger* (ter Hofstede et al. 2008) and in captivity will attack speakers broadcasting this katydid's song. If the song is stopped before a bat lands on the speaker, the bat will abort its attack even if there is a katydid on the speaker. This demonstrates the dependence of *M. septentrionalis* on prey-emitted cues for localization and arguing against a role for echolocation in prey localization, at least in this species (ter Hofstede et al. 2008). As is the case with many eavesdropping predators, the response of *M. septentrionalis* is specific to the prey cue. For example, *M. septentrionalis* does not respond to the calls of the allopatric oceanic field cricket *Teleogryllus oceanicus* (ter Hofstede et al. 2008). Katydids are widespread throughout the world and likely are prey to other bat species whose foraging behavior has not yet been documented.

4.4.3 Case Study: The Fringe-Lipped Bat

Insects are not the only potential prey making loud, conspicuous signals. One of the most studied of the eavesdropping bats is the fringe-lipped bat, *Trachops cirrhosus*, that hunts frogs by approaching their calls (Tuttle and Ryan 1981). *T. cirrhosus* also eavesdrops on the calls of katydids (Falk et al. 2015) but preferentially approaches frog calls over katydid calls (Tuttle et al. 1985). During attacks on prey, *T. cirrhosus* echolocates throughout (Barclay et al. 1981). *T. cirrhosus* in the area surrounding the Panama Canal hunt the túngara frog, *Physalaemus pustulosus*, which calls from small puddles. Male túngara frogs can produce simple calls consisting of a ~350 ms frequency sweep ("whine"), and they can also make complex calls consisting of a whine followed by 1–7 broadband, approximately 40–80 ms, harmonic bursts ("chucks") (Ryan 1980). The foraging behavior of *T. cirrhosus* is worth discussing in depth for two reasons: it is the eavesdropping bat for which we have the best morphological, cognitive, and evolutionary explanations for response to prey cues, and it is a species that has been demonstrated to have remarkable learning capabilities.

Female túngara frogs (Ryan 1980) and *T. cirrhosus* (Ryan and Tuttle 1982) preferentially approach complex calls over simple calls. All male túngara frogs can produce complex calls, but complex call production is not correlated with male size (Ryan 1980). In female frogs, the preference for complex calls has apparently emerged from a perceptual bias for call complexity (Ryan et al. 1990; Phelps and Ryan 1998; but see Ron 2008). For *T. cirrhosus*, there are a number of potential factors that may produce this preference for call complexity. Complex calls contain more broadband frequency components than simple calls, which, in addition to their greater overall duration and the sharp onset and offset of the chucks, may make the calls easier signals to localize (Ryan 1985). Flight cage experiments confirm that complex calls are easier for bats to localize under certain conditions (Page and Ryan 2008). Another possibility is that bats prefer complex calls because frogs are more likely to make complex calls when there are other frogs calling nearby (Bernal et al. 2007); thus complex calls are indicative of higher prey densities. Bats may learn to associate complex calls with higher capture success because there are more available prey items when bats approach complex calls than when bats approach simple calls. *T. cirrhosus* have been shown to learn associations between acoustic stimuli and high prey rewards extremely quickly (Page and Ryan 2005; Jones et al. 2013), so it is likely that preference for call complexity has a learning component.

It is unclear whether, like female frogs, *T. cirrhosus* have a sensory bias for complex calls. In Ecuador the sister species of the túngara frog, Peter's dwarf frog (*Physalaemus petersi*), has populations that make complex calls and populations in which males only make simple calls (Boul and Ryan 2004). *T. cirrhosus* in Ecuador exhibit more passes over field playback speakers broadcasting complex calls than speakers broadcasting simple calls, even in populations where the local frogs do not make complex calls, suggesting a perceptual bias for complex calls (Trillo et al. 2012). In contrast, at the La Selva biological station in Costa Rica where túngara frogs are absent, captured *T. cirrhosus* individuals show no preferential response to

complex versus simple calls of this allopatric frog in flight cage playback experiments (Jones et al. 2014).

Flight cage experiments in Panama also have tested for perceptual bias in bat preference for complex túngara calls over simple ones (Fugère et al. 2015). Captive bats were offered a choice between an unmodified simple túngara frog call versus a simple call modified to possess one of several acoustic properties differentiating complex calls from simple ones (e.g., longer duration, increased bandwidth, quick onset/offset amplitude modulation). With the exception of weak evidence suggesting that increased call duration could contribute to the bats' preference, there was no support for the perceptual bias hypothesis in *T. cirrhosus*. Rather, it is postulated that extreme flexibility and rapid learning abilities bypass any potential perceptual biases in shaping this bat's foraging behavior (Fugère et al. 2015). To further understand the mechanics underlying this bat's preference for call complexity, it may be particularly fruitful to examine the development of this preference in juvenile bats.

4.4.4 Auditory and Behavioral Adaptations to Eavesdropping

Hunting by eavesdropping may produce particular selective pressures on the hearing of predatory bats to improve detection and localization of prey calls. This has not been examined for eavesdropping bats that hunt insects, as insect calls generally have higher frequency components that overlap with the hearing range of most bats. *T. cirrhosus*, on the other hand, hunts frogs with <5 kHz calls (Tuttle and Ryan 1981). *T. cirrhosus* has auditory specializations for hearing low frequency sound, characterized by an unusual cochlear structure with peak neuron density in the apical portion of the cochlea, that part of the cochlea proposed to detect low frequency sound (Bruns and Burda 1989). It is unknown whether other eavesdropping bats have similar specializations for locating prey calls.

Eavesdropping on prey cues may also drive changes in behavior. As mentioned previously, *M. septentrionalis* eavesdrops on calls of the katydid *N. ensiger* but does not respond to the calls of the allopatric cricket species, *T. oceanicus* (ter Hofstede et al. 2008). Such specificity in eavesdropping also characterizes *T. cirrhosus*, which responds to the calls of palatable frog species but not to the calls of poisonous toads (Tuttle and Ryan 1981). Also, *T. cirrhosus* exhibits population variation in response to some prey calls depending on the availability of that species (Jones et al. 2014). Although bats respond to some prey calls and not to others, *T. cirrhosus* do generalize their responses to include similar-sounding novel calls (Ryan and Tuttle 1983). *T. cirrhosus* also can learn novel associations between prey cues and prey quality very quickly through both individual learning (Page and Ryan 2005) and social learning (Page and Ryan 2006; Jones et al. 2013). The learning capabilities of *T. cirrhosus* may be a solution to the challenge posed by eavesdropping as a foraging strategy, where each prey item is associated with a specific signal.

4.4.5   Sensory Niche Partitioning in Gleaning Bats

The two forms of passive listening for prey-generated cues (listening for the rustling sounds of prey moving across the substrate and eavesdropping on prey mating calls) can enable niche partitioning between closely related species of gleaning bats through different sensory ecologies. Bats that listen for prey-emitted rustling sounds do not necessarily respond to prey calls, as evidenced by *A. pallidus* and their lack of a response to orthopteran calls (Bell 1982) and *Cardioderma cor* (Megadermatidae) and their lack of an attack response to frog calls (Ryan and Tuttle 1987).

Sensory niche partitioning has been demonstrated for the European greater and lesser mouse-eared bats, *Myotis myotis* and *M. blythii oxygnathus*, which are morphologically very similar and roost together in the same caves. *M. myotis* predominantly eats carabid beetles, which it locates using the rustling sounds of beetles moving through leaf litter (Russo et al. 2007), and *M. b. oxygnathus* predominantly eats katydids, which it locates by eavesdropping on the katydid calling songs (Jones et al. 2011). Differences in the types of prey cues used by these two closely related species may therefore enable niche partitioning. Similarly, while *T. cirrhosus* preferentially approaches frog calls over katydid calls, a closely related species, the white-throated round-eared bat, *Lophostoma sylvicolum*, only approaches katydid calls and does not respond to frog calls (Tuttle et al. 1985). Further research compared two other closely related phyllostomid bats, *Tonatia saurophila* and *Micronycteris microtis*, and demonstrated that each of these four gleaning species differs in which acoustic features of katydid calls best predict their attacks (Falk et al. 2015). Such differences in foraging behavior potentially partition niches for these four often sympatric Neotropical phyllostomid bats.

Passive listening versus active prey localization through echolocation can also enable niche partitioning, as appears to be the case for the closely related *Myotis bechsteinii* and *M. nattereri*. *M. bechsteinii* relies more on prey-generated cues while *M. nattereri* relies more on echolocation to locate prey (Siemers and Swift 2006). These studies suggest that the means by which bats locate prey can have important consequences for species divergence. Interestingly, these and other European vespertilionid bats also exhibit signs of sensory niche partitioning with respect to aerial hawking, with those species able to produce calls containing very high frequencies best able to exploit airborne prey close to background vegetation (Siemers and Schnitzler 2004). Dietary evidence for these different niches is somewhat lacking, however, and DNA barcode analysis is required to better document who eats what and even when (Clare et al. 2009). Niche partitioning between sympatric bat species is discussed further in Chapter 6 (Denzinger, Kalko, Tschapka, Grinnell, and Schnitzler).

4.4.6   Challenges in Relying on the Use of Prey-Emitted Acoustic Cues

For prey hunted by eavesdropping predators, the best recourse to avoid being eaten is to stop calling. Many katydid species stop calling when they hear bat echolocation calls (ter Hofstede et al. 2008, 2010), and túngara frogs stop calling when they see a bat fly overhead (Tuttle et al. 1982). As the bat approaches the prey, therefore, the prey-generated cue stops. Bats that hunt prey by listening for their rustling sounds may face a similar challenge if the rustling prey can hear bat echolocation calls and cease moving. In order to detect the motionless and silent prey, these gleaning bats may require echolocation. It is possible that the use of prey-generated cues gives bats general information on the location of the prey, and they then use echolocation in the final stage of attack. This has been demonstrated for *T. cirrhosus*, as they continue to use echolocation as they approach calling prey and update their information about prey size if the prey that is available is manipulated (Page et al. 2012).

T. cirrhosus can obtain echoacoustic information not only from the prey per se but from perturbations made by prey in the surrounding environment. When túngara frogs call, the repeated inflation and deflation of the vocal sac produces ripples on the water surface. *T. cirrhosus* uses echolocation to key in on these ripples and prefers calls coupled with ripples to calls with no ripples present (Halfwerk et al. 2014). Ripples are a particularly salient cue because even if a calling frog detects an approaching bat and goes silent, the frog cannot immediately stop the trail of ripples that continue for another several seconds, thus leaving an unavoidable "footprint" of the frog's presence. The continual use of echolocation while approaching prey-generated cues has been demonstrated for a number of bat species (Schmidt et al. 2000; Russo et al. 2007) and indicates the importance of echolocation even for gleaning bats that do not require echolocation to locate prey.

Bats that locate prey using prey-generated cues may be particularly susceptible to interference from background noise in prey detection. *Myotis myotis* avoids areas with anthropogenic traffic noise, presumably because of the interference between such background noise and prey-generated rustling sounds (Schaub et al. 2008). Similarly, *T. cirrhosus* does not approach the calls of the pug-nosed treefrog, *Smilisca sila*, when they are masked by the water sounds that are common at the bubbling stream sites where *S. sila* chooses to call (Tuttle and Ryan 1982). Although aerial foraging bats that rely on echolocation to locate prey also may be negatively impacted by background noise, they are likely less impacted than passive-listening bats due to the high frequency of echolocation calls.

4.4.7 Case Study: The Common Big-Eared Bat Defies Categories

For decades it was thought that bats hunting in highly cluttered conditions, such as the dense forest understory, could not use echolocation alone to glean silent, motionless prey. Foraging in such conditions is a very difficult sensory task. Weaker echoes from prey overlap with stronger echoes from the surrounding vegetation, resulting in backward masking, while the bats' emitted signals and their returning echoes can also become confounded, resulting in forward masking (Neuweiler 1989). Due to both these masking effects, it was argued that bats could not use echolocation alone to find prey when gleaning in dense clutter (Schnitzler and Kalko 1998; Arlettaz et al. 2001; Schnitzler et al. 2003). Geipel et al. (2013a), however, made a striking discovery with the Neotropical common big-eared bat, *Micronycteris microtis*, that proved this assumption wrong.

Micronycteris microtis seems do the "impossible": They take silent, motionless dragonflies and other insect prey, including stick insects, off of the surface of leaves in the dense rainforest understory at night. *M. microtis* fly up and down individual plants, hover in front of resting prey, and then move in for capture. By offering *M. microtis* manipulated dragonfly prey in a small flight cage and recording their hunting behavior with high-speed video, Geipel et al. (2013a) showed that the strategy used by *M. microtis* for hunting prey consists of two main components. First, their stereotypical 3-D hovering likely enables them to shift the angle between the target and background, reducing interference between returning echoes and enabling the bat to pinpoint the prey on the leaf precisely and to assess its quality. Second, the bat's short, broadband, high-frequency echolocation calls (broadcast at a high repetition rate for a gleaning bat) are likely short enough in duration that a bat that stays a sufficient distance from its prey can discriminate outgoing calls from incoming echoes. Like some other gleaners, *M. microtis* lacks a terminal phase buzz.

The combined strategy of 3-D hovering and emitting short, high-frequency echolocation calls allows these bats to be quite selective in their assessment of prey. In flight cage experiments the bats successfully rejected dummies that had incorrect shape, surface structure, or material. *M. microtis* apparently has an echo-acoustic search image for its prey and has the ability to detect, localize, and assess prey among leaves using echolocation alone. This skill may take some time to perfect, as evidenced by the observations that mothers continue to feed young well after weaning, when the young are already foraging for themselves (Geipel et al. 2013b). Whether other gleaning bat species have similar capabilities remains to be seen, as does the possibility that many gleaning bats possess the more modest ability to track prey moving on substrate based on changes in echo timing and structure from one echolocation call to the next (Ratcliffe et al. 2005; Ratcliffe 2009).

4.5 Summary

Animal-eating bats fall predominantly in three groups: aerial hawkers, substrate gleaners, and those that use both strategies. The latter may include the majority of species. All appear to be descended from a laryngeal echolocating bat that fossils indicate was an aerial hawking species. Over the course of the 50 million years or more since the evolution of echolocation in modern bats, this extraordinary sensory system has been highly modified for different tasks and challenges. One of the drivers of this evolution is the arms race between echolocating bats and their would-be prey, which have evolved a number of strategies to avoid capture and have likely required bats to develop the remarkable echolocation abilities that characterize aerial hawkers (for example, the low-intensity aerial hawking bat, *Barbastella barbastellus*; Goerlitz et al. 2010).

However, there are many bats, from many different families, that have reverted to the proto-bat ancestor's hunting strategy of gleaning prey from terrestrial surfaces. At the two extremes, specialized substrate gleaning species differ from open space aerial hawkers in wing shape, echolocation call design, and perhaps even cognitive abilities (Norberg and Rayner 1987; Fenton 1990; Schnitzler and Kalko 2001; Ratcliffe 2009; Hulgard and Ratcliffe 2014). Another important difference between substrate gleaning bats and aerial hawking species is the use of prey-generated cues. The echo-acoustic challenge of locating prey among leaves on a surface makes listening for the rustling sounds of prey moving or the calls that prey make to attract mates, particularly advantageous for gleaning bats. In turn, listening for prey cues drives a number of sensory adaptations, such as the large ears characteristic of substrate gleaners, as well as different auditory and cognitive processing. This foraging behavior also generates selective pressure on prey mating signals and behaviors (Tuttle and Ryan 1981).

While some animal-eating bats fall squarely into these two categories of aerial hawkers that rely on echolocation to locate prey and substrate gleaners that use prey-generated cues, it would appear that most species flexibly and opportunistically recruit the two strategies (Ratcliffe and Dawson 2003; Ratcliffe et al. 2006). However, there are also some remarkable exceptions, such as the gleaning common big-eared bat (*Micronycteris microtis*) that can find silent stationary prey amongst leaves using echolocation alone (Geipel et al. 2013a) and the aerial hawking species *B. barbastellus* that uses calls of intensities similar to those used by gleaning bats (Goerlitz et al. 2010). In this chapter we have attempted to succinctly summarize the auditory information and foraging behaviors used by animal-eating bats to find their prey, and we have demonstrated some of the progress researchers have made toward providing an answer to Nagel's question, "What is it like to be a bat?"

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