

# Chapter 4

## Hearing for Defense

Gerald S. Pollack

**Abstract** The appearance of echolocating bats approximately 65 million years ago presented a life-or-death challenge to nocturnally active insects, particularly those that fly at night. In response, ultrasound-sensitive ears and bat-avoidance behaviors have evolved repeatedly in insects. Avoidance responses include steering away from a distant bat, last-chance maneuvers such as diving to the ground or flying erratically to avoid capture in close encounters, and sound production to startle the bat, to warn it of the prey's distastefulness or to interfere with the bat's ability to echolocate. Some bat-avoiding insects use ultrasonic signals for intraspecific communication, presenting them with the challenge of discriminating between potential predators and mates. Evolution of the predator–prey relationship between bats and insects is ongoing, with each participant adopting new strategies to counter those of its opponent.

**Keywords** Acoustic startle • Bat avoidance • Echolocation • Evolutionary arms race • Negative phonotaxis • Predator–prey relations

### 4.1 Introduction

Most of the chapters in this volume focus on the use of acoustic signals for intraspecific communication. Yet the majority of insect auditory systems evolved in the context of predator detection (Greenfield, Chapter 2). The same characteristics of sound that favor it as a method for communication, namely its ability to be detected at a distance from its source and its capacity to encode considerable information in its spectral and temporal structure, also apply to its use for predator detection. Terrestrial predators may reveal their approach through noise produced as they walk on or through vegetation (Fullard 1988), and the vocalizations and wingbeat sounds of birds may warn of their approach (Fournier et al. 2013). The most powerful

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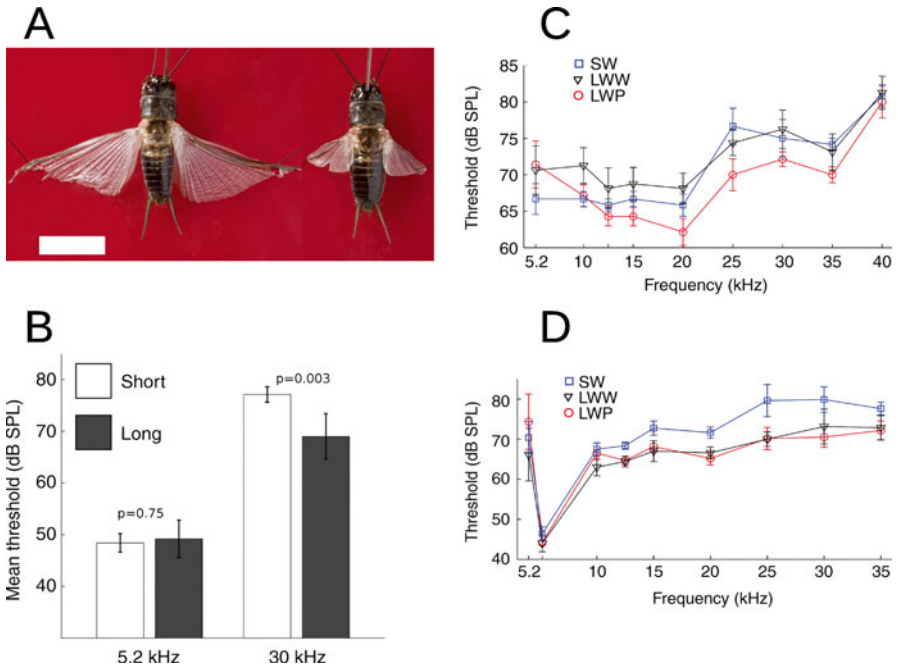
selection pressure favoring the evolution of predator-detecting ears, however, is exerted by bats. Of the more than 1,100 extant species of bat, approximately 70 % feed primarily on insects (Jones and Rydell 2003), which they detect and localize either by homing in on the sounds that the insects produce (e.g., mating calls) or, more commonly, by analyzing the echoes of their own ultrasonic calls that are reflected by the bodies of their flying insect prey. The appearance of these nocturnal aerial predators some 65 million years ago presented a profound challenge to night-flying insects that, until then, had the night sky essentially to themselves. Of the 24–29 independently evolved insect auditory systems known so far, at least 14 are specifically tuned to ultrasound and appear to have evolved as a direct response to bat predation (Greenfield, Chapter 2). In other cases, such as crickets and katydids, ears and mechanisms for sound production were in place and, presumably, used for intraspecific communication long before bats appeared, and ultrasound detection and avoidance were add-ons to well-established acoustic behaviors.

Predation by bats is an ongoing selection pressure that continues to shape the auditory systems of insects. Although ultrasound-sensitive ears are generally broadly tuned, the range of frequencies to which they are most sensitive is often matched to the dominant sound frequencies of the local bat community (Fullard 1998; ter Hofstede et al. 2013). Insects that evolved in or migrated to bat-free habitats tend to be less sensitive to ultrasound compared to those in bat-rich habitats, presumably because of the genetic drift that release from selection allows (Fullard 1994; Fullard et al. 2010). It is worth noting, however, that bats have also responded to the evolution of ultrasound sensitivity in insects, for example, by lowering the intensity of their echolocation calls (Goerlitz et al. 2010), by shifting their sound frequencies above or below the range to which their prey is most sensitive (Fenton et al. 1998), or by broadening the beam of their echolocation calls so as to maintain tracking of insects even as they attempt to escape (Ratcliffe et al. 2013).

In this chapter the focus is on the behavioral strategies employed by insects as countermeasures to bat predation. Although some aspects of the underlying neurobiology are discussed briefly, interested readers should consult Pollack (2015) for a more thorough review of that topic.

## 4.2 Flight and Sensitivity to Ultrasound

Insects are at risk of predation by aerially hawking bats only while flying. Not surprisingly, then, the ability to hear ultrasound is closely correlated with the ability to fly. In some species of mantids, females, the wings of which are reduced or absent, fly little if at all. Concomitantly, the females are less sensitive to ultrasound than males (Yager 1988). Similarly, flight in gypsy moths (*Lymantria dispar*) is limited to males and here, too, female thresholds for ultrasound are higher than those of males (Cardone and Fullard 1988). Even among moths that fly, there is a correlation across species between time spent aloft at night and sensitivity to ultrasound (ter Hofstede et al. 2008). Many species of Orthoptera (crickets, grasshoppers, katydids) are flightless and others are flight dimorphic, with some individuals, which have long wings, able to fly and others, with short or absent wings, flight incapable. Ears



**Fig. 4.1** Ultrasound sensitivity varies with flight capability. (A) Long-winged and short-winged *Gryllus texensis*. The front wings, which do not differ between morphs, have been removed. Scale: 1 cm. (B) Behavioral thresholds of long-winged and short-winged individuals for positive phonotactic steering toward a song model and negative phonotaxis away from ultrasound. (C) Threshold tuning curves of the AN2 neuron for long-winged individuals with functional (*pink*) flight muscles (LWP), long-winged individuals with degenerate (*white*) flight muscles (LWW) and short-winged individuals (SW). (D) As in (C), but for the ON1 neuron [(B)–(D) from Pollack and Martins (2007)]

in the flightless forms are often either absent or poorly developed (Knetsch 1939), although whether the ears of the flight-capable forms are ultrasound sensitive is not known in most cases.

Many cricket species are wing dimorphic, with long-winged, flight-capable and short-winged, flight-incapable individuals (Fig. 4.1A). Crickets use sound for intra-specific communication as well as for predator detection, and long-winged and short-winged individuals of the Texas field cricket (*Gryllus texensis*) are equally sensitive to the relatively low sound frequency that is dominant in their songs. Short-winged individuals, however, are less sensitive to ultrasound than their long-winged counterparts, as measured in both behavioral and neurophysiological experiments (Pollack and Martins 2007; Fig. 4.1B).

Even long-winged individuals may eventually lose the ability to fly because of age-related degeneration of flight muscles. An identified interneuron, AN2, that triggers negative phonotactic steering (Nolen and Hoy 1984; Marsat and Pollack 2006) is less sensitive to ultrasound in long-winged Texas field crickets with degenerate muscles than in those still able to fly (Pollack and Martins 2007; Fig. 4.1C). Because all long-winged crickets have flight-capable muscles early in adulthood, this implies

that the tuning of AN2 shifts when flight ability is lost. Interestingly, tuning of another identified ultrasound-sensitive interneuron, ON1, does not differ between flight-capable and flight-incapable long-winged individuals (Fig. 4.1D). This suggests that the age-related shift in AN2 tuning is not the result of changes at the periphery (otherwise ON1 would also lose sensitivity) and points either to the synaptic connections between ultrasound-sensitive receptors and AN2 or to AN2's intrinsic electrophysiological properties as the likely sites of change in its sensitivity.

The decision to develop as either a long-winged or a short-winged adult is determined during late larval life by developmental hormones and can be manipulated experimentally by exogenous application of juvenile hormone (JH) or an analog, methoprene. Hormone treatment of larvae of the southeastern field cricket (*Gryllus rubens*) that are genetically predisposed to develop with long wings causes them to develop instead with short wings and poorly developed flight muscles (another characteristic of the short-winged form; Zera and Tiebel 1988). Short-winged-like phenotypes can also be induced by hormone treatment even in a species in which all individuals are normally long winged and flight capable (Zera et al. 1998). Hormone treatment of larvae of the Pacific field cricket (*Teleogryllus oceanicus*), a monomorphic long-winged species, results not only in underdeveloped flight muscles in adults but also in poor ultrasound sensitivity (Narbonne and Pollack 2008). Like the sensitivity difference between natural long- and short-winged crickets in dimorphic species, the loss of sensitivity to ultrasound is frequency specific; treated and control individuals are equally sensitive to the frequency used for intraspecific communication. In crickets, then, ultrasound sensitivity seems to be physiologically coupled to other flight-associated characteristics such as wing length and muscle condition, ensuring that those individuals that are able to fly have the sensory equipment required to help them avoid predation by bats.

Even among flight-capable individuals, responses to ultrasound may be evident or robust only while the insect is actively flying. Mantises (*Parasphendale agrionina*: Yager and May 1990) and tiger beetles (*Cicindela marutha*: Yager and Spangler 1997) exhibit steering responses while performing tethered flight (Sect. 4.3.1) but not when they cease flying, even while still tethered above the surface. Pacific field crickets, which respond to ultrasound stimuli with strong and consistent steering responses while flying (Sect. 4.3.1), respond only weakly and transiently while walking (Pollack et al. 1984). Parasitoid flies (*Ormia ochracea*), which locate their singing-cricket hosts through phonotaxis, orient toward both cricket songs and ultrasound stimuli while walking, but while flying they steer toward cricket songs and away from ultrasound (Rosen et al. 2009).

### 4.3 Defensive Strategies

Insects have evolved a number of tactics to avoid bat predation, including avoiding detection, avoiding capture once detected, warning of (or lying about) distastefulness, and interfering with the bat's ability to echolocate accurately.

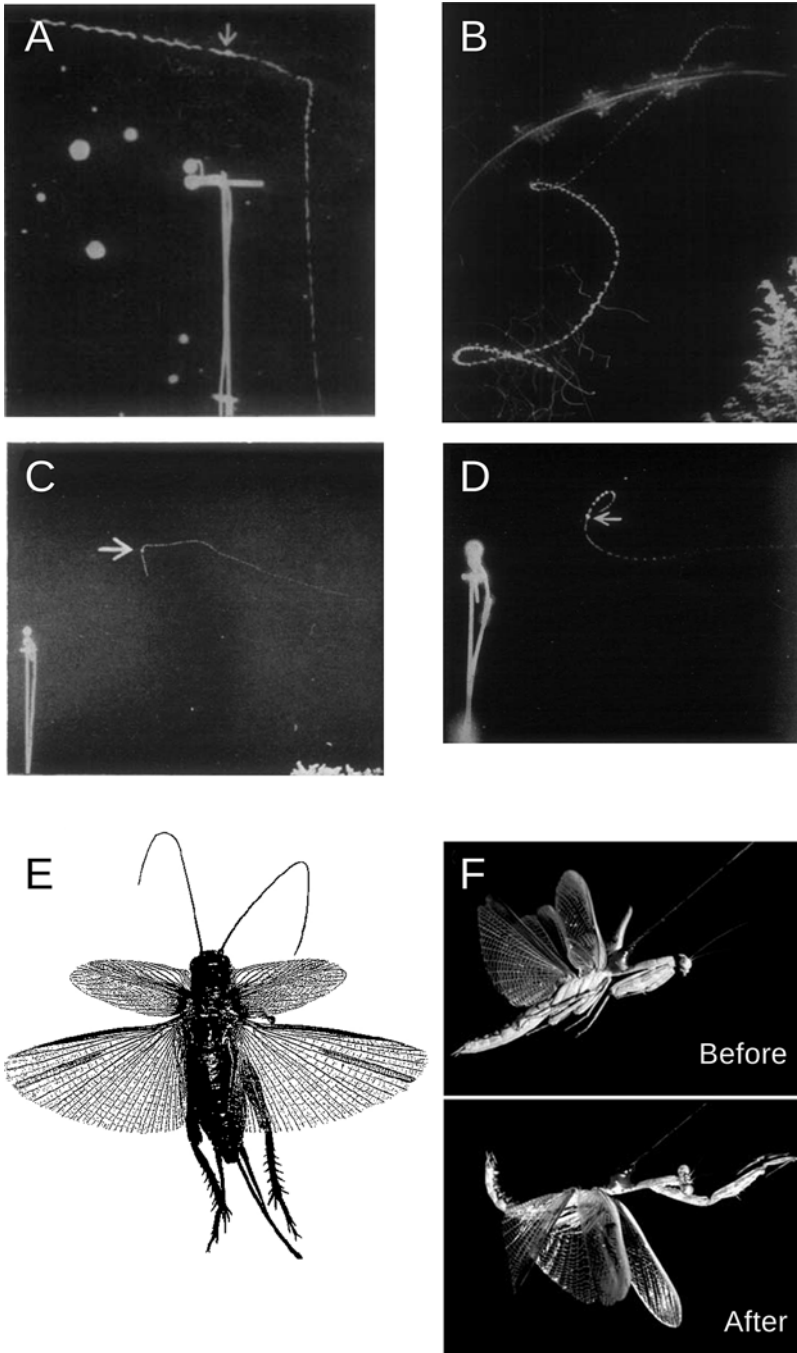
### 4.3.1 Avoiding Detection

The ultrasound probes that bats use for echolocation attenuate rapidly with distance because of atmospheric absorption of high sound frequencies. This, together with the weak echoes returned from the small bodies of insects, limits the operating range of echolocation to only a few meters. By contrast, the sensitivity of insect auditory systems allows detection of a hunting bat at distances of tens of meters (Surlykke and Kalko 2008); thus the insect may hear the bat well before the bat detects the insect. In such cases the safest strategy for the insect may be simply to “disappear,” that is, to leave the region of space being searched by the bat. That moths do just that was demonstrated by Roeder (1962), who used strobe photography to observe the responses of freely flying moths to attacking bats and to artificial ultrasound stimuli. Moths that were close to the source of ultrasound, which was consequently of high amplitude, reacted erratically by flying in loops and/or diving into the vegetation (Fig. 4.2A, B; see Sect. 4.3.2.1), but those that were distant from the sound source, and thus received low-amplitude stimuli, responded by steering systematically away from the sound source (Fig. 4.2C, D), that is, they performed negative phonotaxis. Roeder also demonstrated directed steering attempts away from the sound source during tethered flight by measuring the airflow produced by the beating wings (Roeder 1967). Negative phonotaxis to ultrasound stimuli also occurs in tethered flying crickets (Moiseff et al. 1978; Fig. 4.2E), locusts (Robert 1989), katydids (Schulze and Schul 2001), and parasitoid flies (Rosen et al. 2009). Addition of ultrasound to the normally low-frequency (2.7 kHz) mate-attraction song of southern mole crickets (*Scapteriscus borellii*) reduces the rate at which flying individuals are captured in acoustic traps, demonstrating that they, too, avoid ultrasound (Mason et al. 1998), although the kinematic details have not yet been described.

Green lacewings (*Chrysopa carnea*) respond to stimuli mimicking an approaching bat not by steering away but by folding their wings and dropping passively, a response that would bring them below the hunting bat’s echolocation beam (Miller and Olesen 1979). Katydids may also exhibit a similar flight cessation response to ultrasound (Libersat and Hoy 1991; Schulze and Schul 2001).

Mantises are unique among hearing animals in having a nondirectional auditory system, with a functionally single midline ear that provides no binaural cues for determining the azimuth of a stimulus (Yager and Hoy 1986). In tethered flight, mantises respond to ultrasound with a deimatic display in which they extend their forelegs and dorsiflex the abdomen (Fig. 4.2F). This is combined with steering attempts to the left or right; the steering direction, however, is random with respect to the location of the stimulus (Yager and May 1990). In free flight, lateral steering is often accompanied by diving (Yager et al. 1990).

In contrast, tiger beetles have distinct left and right ears capable of encoding substantial binaural differences in the amplitude of an ultrasound stimulus that, in principle, could support determination of sound azimuth (Yager and Spangler 1995). Nevertheless, they, like mantises, steer randomly to one side or the other in response to ultrasound stimuli (Yager and Spangler 1997). Presumably even these



**Fig. 4.2** Steering responses to ultrasound stimuli. (A)–(D) are strobe photographs showing flight paths of moths in response to artificial ultrasound stimuli (A, C, D) or in a close encounter with a bat (B). Flight paths appear as dotted lines because of the periodic stroboscopic illumination of the

randomly directed course changes suffice to remove the insect from the bat's awareness, at least some of the time.

Although, as noted in Sect. 4.2, sensitivity to ultrasound and flight ability are often linked, nonflying insects may also be at risk of predation by gleaning bats (Faure and Barclay 1994), which detect them both through echolocation and by homing in on the sounds that the insects produce (Geipel et al. 2013; Falk et al. 2015). Male wax moths (*Achroia grisella*) and katydids (*Neoconocephalus ensiger*) attract females with mate-calling songs that are rich in ultrasonic frequencies, but they fall silent when presented with bat-like ultrasound stimuli (Faure and Hoy 2000; Greenfield and Baker 2003). Female wax moths interrupt their approach to a calling male when presented with a bat-like stimulus (Greenfield and Weber 2000). The females discriminate between these two ultrasonic signals based on their differing temporal patterns. In another moth species, *Spodoptera litura*, females do not discriminate between male songs and bat calls, a situation that the males exploit by eliciting freezing responses in females, thus allowing the males to mate with the immobile females (Nakano et al. 2010).

In many moth species, stationary females attract distant males by emitting pheromones, which they disperse by fanning their wings. On presentation of bat-like stimuli, they cease wing fanning and lower their bodies close to the substrate, both of which actions presumably make them less conspicuous acoustically (Acharya and McNeil 1998).

### 4.3.2 Avoiding Capture Once Detected

#### 4.3.2.1 Last-Chance Evasive Flight Maneuvers

Bats are fast and agile fliers, capable of speeds of 10 m/s or more (Hayward and Davis 1964). Although some insects can match this, speeds of <2 m/s are more typical (Dudley 2002). An insect, then, once detected, stands little chance of outflying a pursuing bat. Rather than relying on speed, many insects adopt erratic, unpredictable flight paths to elude capture. As mentioned in Sect. 4.3.1, moths that are presented with high-intensity ultrasound stimuli undergo a series of loops and dives rather than flying directly away from the stimulus (Roeder 1962). While performing tethered flight, Pacific field crickets steer away from low-intensity ultrasound stimuli but steer alternately to the left and right when stimulus intensity is high (Nolen

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**Fig. 4.2** (continued) moth's wings. (A) Power dive of moth that was close to the loudspeaker (at the top of the vertical shaft) when stimulated; time of stimulation is indicated by the arrow. (B) Looping dive following close encounter with a bat, the path of which is seen above. (C, D) Two examples of directional responses away from the loudspeaker. (E) Steering response of a tethered cricket in response to an ultrasound stimulus presented from the left. Flexion of the legs, antennae, and abdomen to the right are diagnostic of an attempted right turn. (F) Deimatic display of a tethered flying mantis in response to ultrasound stimulation [(A)–(D) from Roeder (1962); (E) from Moiseff et al. (1978); (F) from Yager (2012)]

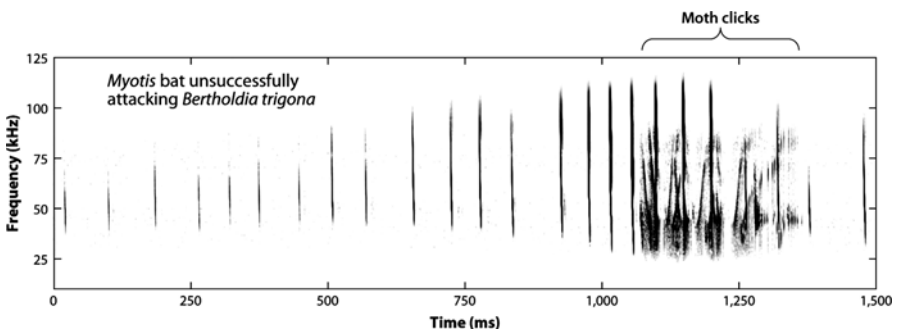
and Hoy 1986a). Similarly, katydids (*Tettigonia viridissima*) that steer away from low-intensity stimuli cease flight and dive in response to high-intensity ultrasound (Schulze and Schul 2001). The diving turns of mantises, described in Sect. 4.3.1, become spiral in form when stimulus intensity is high (Yager et al. 1990).

Another auditory cue for insects about the proximity of an approaching bat is the temporal structure of the bat's echolocation calls. These occur at rates of a few per second while the bat is searching for a target (search phase), increase to tens per second once a target is acquired (approach phase), and to 100 or more per second just before the capture attempt (terminal buzz) (Griffin et al. 1960; Fenton et al. 2014). Green lacewings, on hearing a terminal buzz, often interrupt their passive drop by extending their wings, thus perturbing their otherwise predictable trajectory (Miller and Olesen 1979).

#### 4.3.2.2 Sound Production

Tiger moths (Arctiinae), geometer moths (Geometridae), hawkmoths (Sphingidae), and tiger beetles (Cincindelidae) have independently evolved mechanisms for producing ultrasonic clicks in response to bat-like stimuli (Fig. 4.3). Tiger moths and geometer moths use specialized cuticular structures, tymbals, that generate clicks when buckled or relaxed under muscular control (Corcoran and Hristov 2014). Hawkmoths stridulate by rubbing specialized scales on their genitalia against the abdomen (Barber and Kawahara 2013). The mechanism for sound production by tiger beetles is unclear, although they do possess structures on their wings that seem well-suited for stridulation (Freitag and Lee 1972). In some of these cases, sound production has secondarily been exploited for intraspecific communication (Nakano et al. 2015; Greenfield, Chapter 2). The focus here, though, is on sound production as a defensive mechanism.

In most cases, sound production is a late component of the insect's response to echolocation calls. Like the wing-extension response of green lacewings, clicking



**Fig. 4.3** Sound production by a moth in response to an unsuccessful bat attack. The dense sound produced by this species, *Bertholdia trigona*, thwarts attacks even by naïve bats, suggesting that it interferes with the bat's ability to echolocate accurately (From Conner and Corcoran 2012)



by the tiger moth (*Cycnia tenerea*) occurs toward the end of the bat's sequence of echolocation calls, where it appears to be triggered by the sound-pulse rates typical of approach-phase calls (Ratcliffe and Fullard 2005). The geometer moth *Eubaphe unicolor* also tends to click in the latter portion of the call sequence (Corcoran and Hristov 2014). The response latency of clicking by tethered tiger beetles is longer than that of other phonotaxis-related components of their response to ultrasound (Yager and Spangler 1997). Thus sound production, like the adoption of erratic flight paths, may be a last-chance response to avoid capture.

There are several ways in which sound production might offer protection against an attacking bat. First, it may simply startle the bat, momentarily disrupting its attack and allowing the insect to escape (Fenton and Bates 1990). Second, it might serve as an aposematic warning that the potential prey is distasteful or dangerous. Indeed, tiger moths are rejected by a number of potential predators because of their sequestration of noxious compounds from their food plants (reviewed by Dunning 1968). Third, sound production may, through Batesian mimicry, allow species that are not themselves distasteful nevertheless to dissuade bats that have learned, through their encounters with distasteful sound producers, to associate prey-produced ultrasound with unpalatability. Fourth, the prey-produced ultrasound might interfere with the bat's echolocation system, causing it to misjudge the location of the insect.

Discriminating among these alternatives is possible by observing whether/how the bat's behavior changes as a result of repeated encounters with an insect, an approach that has been pursued with studies of bat-moth interactions. Startle, unless predictive of unpalatability, should be effective only for the bat's initial capture attempts, after which the bat will have learned that the prey is harmless and palatable despite its sound production. Indeed, this is precisely what happened in laboratory tests with the big brown bat (*Eptesicus fuscus*), both when recorded moth sounds were paired with presentation of palatable prey (Fenton and Bates 1990) and when a palatable but sound-producing moth (a Batesian mimic) was offered to naïve bats (Hristov and Conner 2005). If, on the other hand, naïve bats are offered unpalatable, sound-producing prey, they should initially capture and taste them but then learn their unpalatability and avoid them. Laboratory trials demonstrated this scenario as well (Hristov and Conner 2005). Finally, if sound production interferes with the bat's ability to detect or localize the prey, then it should be equally effective against naïve and experienced bats. To date, such "jamming" has been demonstrated for only a single moth species, the tiger moth (*Bertholdia trigona*; Corcoran and Conner 2009), although field tests have demonstrated the impressive effectiveness of this defense mechanism, moths that were muted by puncturing their tymbals were more than 10 times as likely to be captured than intact individuals (Corcoran and Connor 2013).

Moth sounds fall into two general classes that seem to be well-suited for aposematic warning (or mimicking) and for jamming, respectively. Sound in the aposematic class, which includes those of known distasteful moths or their mimics, have relatively few clicks per tymbal activation and low duty cycle and are demonstrably sufficient to warn off an attacking bat. Sounds in the jamming class, which includes *B. trigona* along with many other potential but as yet untested jammers, have many clicks and high duty cycles and thus are more likely to present a stimulus at a time

when it might be misinterpreted by the bat as an echo or otherwise interfere with the time-crucial processing of ultrasound in the bat's auditory system (Corcoran et al. 2011; Conner and Corcoran 2012).

### 4.3.3 *Nonauditory Defenses*

It is worth noting that hearing is not the only defense that insects have against bat predation. Indeed, nearly half of the approximately 140,000 species of moths are earless (Barber et al. 2015). Behavioral adaptations, such as avoiding flight at times and places where bats hunt, offer protection in many cases (Soutar and Fullard 2004).

Structural, rather than neurobehavioral, adaptations are another evolutionary strategy. The scales of moth wings have a honeycomb-like structure that resembles that of some man-made sound-absorbing materials. The scales enhance the absorption of sound frequencies between 40 and 60 kHz, that is, the same range most common in the echolocation calls of bats, thereby decreasing the amplitudes of echoes that the bat would receive. It is estimated that this might decrease the bat's detection range by 5–6 % (Zheng et al. 2011).

Luna moths (*Actias luna*) are large and earless. Their hindwings have long, swallowtail-like extensions that trail behind the moth and oscillate during flight. In laboratory tests, nearly half of the attacks by big brown bats were directed toward these extensions, which presumably are acoustically conspicuous, rather than toward the moth's body per se, thus leaving the vital organs of the mid-body unharmed (Barber et al. 2015). The wing extensions were often bitten off by the bat but with little impact on the moth's ability to fly. Comparison of capture rates of intact moths with those in which the wing extensions were ablated showed that the extensions afforded a level of protection, approximately 47 %, similar to that of ultrasound-sensitive ears in tympanate insects. Of course, unlike ears, the wing extensions offer protection only against one or two attacks; once they've been lost, the moth would be left completely vulnerable.

## 4.4 Interactions Between Defense and Reproduction

### 4.4.1 *Attraction to a Mate Versus Repulsion by a Predator*

In many cases, an insect may be en route to a potential mate when defensive action is called for. Male moths, for example, locate distant females by following their pheromone plumes. Anti-bat defensive behaviors such as negative phonotaxis or erratic loops and dives risk taking the moth far from the plume, which it might not regain, thus potentially losing a mating opportunity. Interestingly, moths are able to titrate the opposing tendencies to mate and to escape against one another, weighing

the proximity of an approaching bat, as reflected by the amplitude of ultrasound, against the quality and quantity of female pheromone. In a laboratory assay, moths (*Spodoptera littoralis*) walked toward a pheromone source while being challenged with ultrasound stimuli. As mentioned in Sect. 4.3.1, walking moths freeze when presented with ultrasound. The threshold level of ultrasound required to elicit freezing was elevated by 10 to more than 40 dB in the presence of pheromone, depending on the quality and concentration of the olfactory stimulus (Skals et al. 2005).

A similar suppression of avoidance responses by mating-associated signals occurs in Pacific field crickets. The negative phonotactic response to ultrasound of females performing tethered flight is suppressed by the simultaneous presentation of a stimulus with the relatively low sound frequency that is dominant in the song that males sing to attract females (Nolen and Hoy 1986b). Response suppression in this case is ascribable to neural inhibition by low-frequency stimuli of the AN2 interneuron (Nolen and Hoy 1986b). As in the case of moths, the attractive and repulsive stimuli play off against one another quantitatively; the more intense the ultrasound, the higher the amplitude of a low-frequency signal required to suppress the avoidance response. In this case, the function of suppression may be to prevent crickets from being repelled by the high-frequency harmonics that are present in song. As a female approaches a male, these harmonics might, in the absence of low-frequency suppression, become sufficiently intense to excite the high frequency-tuned bat-avoidance circuits in the nervous system and elicit inappropriate avoidance responses (Nolen and Hoy 1986b). The neural inhibition elicited by low-frequency stimuli prevents this from happening.

#### 4.4.2 *Discriminating Mate from Predator*

In contrast to the higher harmonic components of cricket song, which are present at relatively low levels and thus would be detectable only close to the source, songs of some other insects are dominated by high frequencies that could be detected by bat-sensitive insect ears at a distance. For example, males of many moth species court females with ultrasonic songs (Nakano et al. 2015), and songs of many katydids are rich in ultrasonic frequencies that overlap the frequency range that bats use for echolocation (e.g., Mason and Bailey 1998; Montealegre-Z et al. 2006). How do these insects discriminate potential mates from potential predators?

As mentioned in Sect. 4.3.1, in some moths no such discrimination occurs; the walking female's response to courtship song, freezing, is identical to her response to bat calls. Other moths, however, clearly discriminate between courtship song and bat calls. Moth ears are exceedingly simple, comprising only one to four auditory receptor neurons, and there is no indication that they are capable of frequency discrimination. Any strategy based on distinguishing between the spectra of courtship songs and bat calls is thus ruled out. Rather, the moths rely on differences in the temporal structures, or rhythms, of the signals. Male wax moths court females with a series of brief ultrasonic clicks delivered at a rate of 80–100 per second. Females

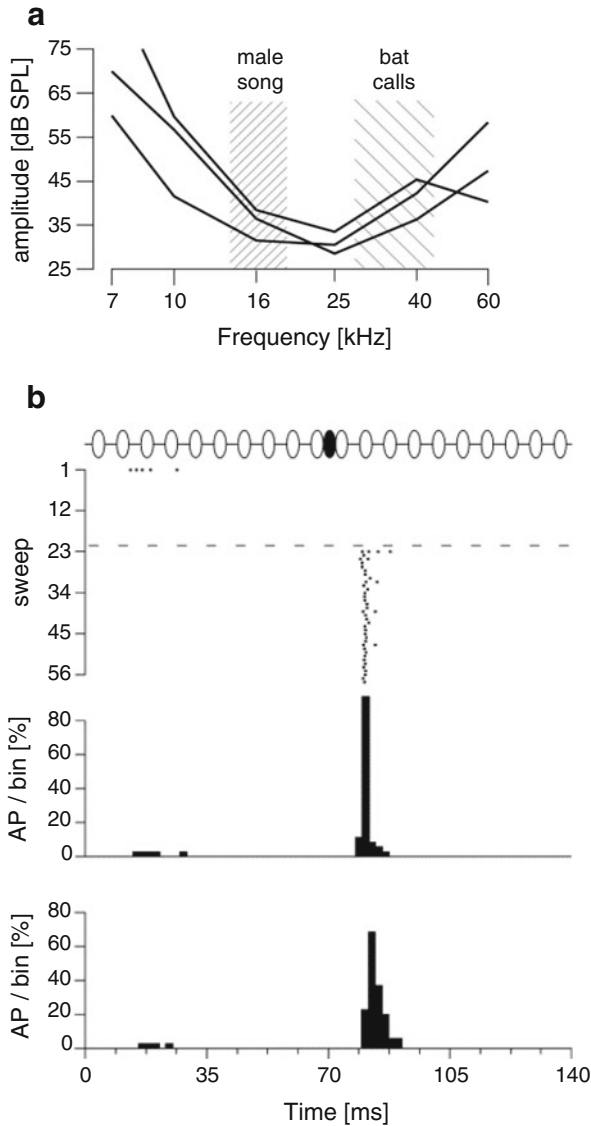
perform positive phonotaxis by walking toward this signal, but they freeze if pulses are delivered at rates of less than 30 per second, which are similar to those used by bats during the search phase of their behavior. Males cease singing in response to the same, low pulse rate signal (Greenfield and Weber 2000). Reliance on a signal's temporal pattern as the basis for its identification is a common theme in insect auditory systems (see Hedwig and Stumpner, Chapter 8 and Ronacher, Chapter 9).

Unlike moth ears, katydid ears can support sophisticated frequency discrimination. The 20–40 sensory neurons in each ear are arranged tonotopically, with neighboring neurons most sensitive to different sound frequencies in a manner reminiscent of the mammalian organ of Corti (Stolting and Stumpner 1998; Montealegre-Z et al. 2012). Thus, in principle, katydids could exploit even small spectral differences between their own high-frequency calls and those of bats to discriminate between the two signals. The separation of frequency sensitivity at the periphery is, however, blurred in the central nervous system by the convergent projections of differently tuned afferents onto central neurons. One of these neurons, T1, has a large-diameter axon that promotes rapid conduction of action potentials, suggesting that it may play a role in bat-avoidance responses. Because of afferent convergence, T1 responds both to the 15-kHz frequency that is dominant in the songs of katydids in the genus *Neoconocephalus* and to the higher frequencies of bat calls. Nevertheless, when exposed to both signals simultaneously, T1 responds selectively to bat-like stimuli (Schul and Sheridan 2006; Fig. 4.4). It is able to do so because of sound frequency-specific adaptation to stimuli with high pulse rates. Frequency specificity is possible because tonotopy is expressed not only in the ear but also in the central projections of auditory afferents (Römer 1983; Stolting and Stumpner 1998). Although differently tuned afferents converge onto TN1, they do so at different places within T1's dendritic arbor. As a result local, thus frequency-specific, depression of afferent-to-T1 synapses is possible (Triblehorn and Schul 2013), allowing T1 to adapt to the high pulse rate song while remaining sensitive to lower pulse rate bat calls.

## 4.5 Summary

The repeated evolution of ultrasound-sensitive ears among insects attests to the strong selection pressure exerted by echolocating bats. Despite the many evolutionary routes that led to ultrasound sensitivity and bat-evasive strategies, some common themes are recognizable across taxa, such as the correlation between sensitivity to ultrasound and risk of predation and the selection of different evasive behaviors depending on the proximity of an attacking bat. This chapter has concentrated on behavior, but studies on the underlying neurobiology have also revealed many examples of convergent evolution, including large-diameter neurons that conduct action potentials rapidly, and neural mechanisms that discriminate between probable threats and innocuous ultrasonic stimuli (reviewed by Pollack 2015).

The correlation between flight and sensitivity to ultrasound begs explanation, particularly in cases where members of the same species face different exposure to



**Fig. 4.4** Selective responsiveness of the katydid T1 neuron to bat-like sound in the presence of ongoing song. **(a)** Threshold tuning curves of the T1 neuron of three individuals of the katydid *Neoconocephalus retusus*. The neuron is approximately equally sensitive to the sound frequencies found in conspecific songs and in bat calls, as indicated by the *hatched vertical bars*. **(b)** *Top trace* shows stimulus pattern, with sound pulses in the model song shown in *white*, and a single bat-pulse mimic shown in *black*. *Second panel from top* shows raster display of TN1 responses to repeated stimulation; spikes are indicated as *dots*. The neuron responded with a few spikes on trial 1 but quickly adapted to the high pulse rate of the song model. It responded reliably to the single bat-pulse model (sweeps 23–56) despite its continued adaptation to the song stimulus. *Bottom graphs* are peristimulus-time histograms summarizing the response when both song and bat models are presented at the same amplitude, 70 dB SPL, and when the bat model is presented at 12 dB lower amplitude (From Schul and Sheridan 2006)

aerially hawking bats, whether because of differences in bat fauna across the species' range or because of developmental-, sex-, or age-related differences in flight behavior. In the former case, loss of ultrasound sensitivity in bat-poor environments may be explained by genetic drift that is permitted by the relaxation of selection pressure. Drift cannot, however, account for differences in sensitivity related to flight dimorphism, sex, or age because in these cases the flight-capable and flight-incapable individuals share the same evolutionary history. Here, the negative correlation between flight and ultrasound sensitivity suggests that the ability to hear ultrasound might be costly. Could unnecessary neural processing of ultrasound stimuli in flightless individuals impose a significant metabolic cost that would be recouped by sacrificing auditory sensitivity (Lauglin et al. 1998)? Might detection of nonthreatening ultrasound signals elicit needless startle responses that could distract individuals from activities such as foraging or mating? Examination of the relationships among an individual's condition, sexual receptivity, and ultrasound sensitivity might help to answer these questions. Further research on the cellular mechanisms linking flight and hearing would also be profitable. In crickets, JH regulates both flight-muscle condition and ultrasound sensitivity. The cellular mechanisms by which JH regulates flight-muscle development and degeneration are beginning to be understood (Zera et al. 1999; Nanoth Vellichirammal et al. 2014), but the mechanisms linking JH and poor sensitivity to ultrasound are completely unexplored.

In many insects, bat detection and evasion were the primitive functions of hearing, whereas in others bat detection was incorporated into an auditory system that had long been used for intraspecific communication, possibly by repurposing neurons and neural circuits with properties that were specialized for analyzing communication signals. Do traces of these differing evolutionary trajectories persist in the present-day bat-evasion behavior of these insects? For example, positive phonotaxis in a specific direction toward a potential mate might require more accurate sound localization than negative phonotaxis away from an approaching bat, where any maneuver that removes the insect from the bat's "search light" might suffice to avoid capture. Similarly, recognizing the songs of one's own species, and perhaps even discriminating among individuals, might require more sophisticated analysis of acoustic features than bat detection. Comparative studies of ultrasound-elicited evasive behaviors between insects in which bat detection is primitive, for example, moths, and those in which it is derived, for example, crickets or katydids, focusing on aspects such as accuracy of sound localization and analysis of acoustic features of stimuli, might offer insights into how new behavioral requirements are incorporated into existing repertoires.

The ongoing evolutionary dialog between bats and their insect prey has attracted the attention of biologists for decades, and it can be expected to continue to do so well into the future.

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