How Some Insects Detect and Avoid Being Eaten by Bats: Tactics and Countertactics of Prey and Predator

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Some insects have evolved audition and evasive behaviors in response to selective pressure from bats, and other insects were preadapted to detecting ultrasonic signals. Some bats have evolved in turn, improving the range or resolution of sonar signals and serendipitously making them less detectable by insects. In other words, there is a kind of evolutionary escalation going on between bats and insects. Our aim with this review is to present the complex interactions between echolocating bats and insects with bat-detecting ears and show how these interactions may be advantageous for predator or prey. To document our examples, we cite mostly newer studies and reviews in which the reader can find references to original works.

Insects occupied all terrestrial habitats at least 300 million years ago, long before bats appeared in the Eocene, about 50 million years ago. Ears have appeared independently 19 times in the class Insecta. In the period before bats, ears and complex acoustical behaviors appeared independently in at least seven orders of insects (Hoy et al. 1989, Robert et al. 1992, Yager 1999). Antibat tactics, which must have appeared in insects since the Eocene, are now known in members of four orders: Lepidoptera (moths and nocturnal butterflies), Orthoptera (crickets), Dictyoptera (praying mantids), and Neuroptera (green lacewings), and possibly also in the Diptera (flies) and Coleoptera (beetles).

Insect tympanal organs, or ears, consist basically of an external, thin membrane (the tympanum) and associated internal air sacs, or tracheae. The auditory (sensory) cells attach to the tympanum or to an internal membrane (Yager 1999). Tympanal organs of most modern tympanate insects respond to a wide band of frequencies extending well into the ultrasonic range (above 20 kHz), as was probably true for pre-Eocene tympanate insects as well. Tympanate insects are physically small animals that can produce high-frequency

> EVOLUTIONARILY SPEAKING, INSECTS HAVE RESPONDED TO SELECTIVE PRESSURE FROM BATS WITH NEW EVASIVE MECHANISMS, AND THESE VERY RESPONSES IN TURN PUT PRESSURE ON BATS TO "IMPROVE" THEIR TACTICS

sounds more efficiently; hence, high frequencies are used by many insects for acoustical communication between conspecifics. Consequently, many sonorous insects were preadapted to the evolution of bats (Hoy 1992).

According to one possible scenario, a vast larder of nocturnal, flying insects awaited exploitation, and a flying mammal, the microchiropteran bat, was one successful exploiter. Echolocation, or biosonar, was a prerequisite for success in darkness, and even the first nocturnal bats probably used it (see Hoy 1992). Most of the nearly 700 microchiropteran bat species eat insects that they detect using biosonar (Schnitzler and Kalko 2001). However, bat biosonar has two major disadvantages: attenuation and forewarning.

The frequencies used by echolocating bats range generally from 20 kHz to 100 kHz, with some outliers using frequen-

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cies below 10 kHz or above 200 kHz. Higher frequencies improve resolution, but they attenuate at a greater rate (Surlykke 1988) and the detection distance is reduced accordingly. The *source level* is the sound pressure level (SPL relative to 20 μPa), in decibels (dB), measured 10 cm in front of the bat's mouth. A bat using a source level of 110 dB at 20 kHz could detect the echo from an object the size of a moth at more than 5 m. Detection would occur at no more than 2.4 m if the bat used 100 kHz (Surlykke 1988). From the insects' perspective, bats advertise their presence with the ultrasonic pulses used to stroboscopically probe the environment. Thus, insects are forewarned if they can hear ultrasound. This coincidentally exerts considerable selection pressure against those insects that either cannot hear or do not react (Miller 1982).

Thus, the stage was set in the Eocene for an evolutionary escalation between bats and insects. Evasive behaviors in existing tympanate insects (presumably crickets, locusts, and mantids) probably appeared in response to selection pressure by bat predation (Hoy 1992). The same selection pressure generated new auditory and motor mechanisms in presumably earless insects (green lacewings and moths). Bats, too, could have developed countermeasures, for example, shifting signals out of the prey's hearing range (Fenton and Fullard 1981) or modifying hunting behaviors (Miller and Olesen 1979).

Avoidance behaviors

Preadaptation. Preexisting auditory systems in insects may have been preadaptively sensitive to bat echolocation. Tympanate insects that were normally diurnal may also have become active at night. Crickets, locusts, and mantids are considered here because they were probably some of the earliest insects with hearing and they are mostly active during the day, but often fly (migrate or disperse) at twilight and at night. However, all crepuscular and nocturnal insects are potential prey for bats.

Crickets. The most intensively studied insect auditory system is that of field crickets (Figure 1a, left). The majority of these studies concern intraspecific communication. The tibia of each foreleg contains an ear (Figure 1a, middle). For example the maximum sensitivity of the cricket *Gryllus bimaculatus* occurs at about 5 kHz as measured electrophysiologically from the auditory nerve. This is also the frequency of the calling song. However, the ear is sensitive to sound frequencies up to 100 kHz at least.

Popov and Shuvalov (1977) first reported that dispersing crickets avoid being hunted by bats. Since then Ron Hoy at Cornell, Andrej Popov in St. Petersburg, and their colleagues have documented avoidance behavior in several species of crickets both behaviorally and neurophysiologically (see Hoy et al. 1989). Crickets in stationary flight steer away from the source of ultrasound (negative phonotaxis), with the most effective frequencies lying between about 10 kHz and 80 kHz (Figure 1a, right). An interneuron in *Teleogryllus oceanicus*

(Int 1) initiates evasive behavior (Hoy et al. 1989), and its homologue in *Gryllus bimaculatus* (AN_2; Popov et al. 1994) presumably does the same. The threshold for AN_2 at 20 kHz is about 20 dB less than that of the behavior (Figure 1a, right), meaning that the neural response is more sensitive than the behavior. Some mole crickets hear ultrasound, in part with special neuronal pathways, and free-flying crickets show avoidance to batlike sounds (Mason et al. 1998).

Bush crickets (Figure 1b, left), like field crickets, have their ears and associated acoustic tracheae in the tibia of the forelegs (Figure 1b, middle). Some species communicate entirely in the ultrasonic range. Many bush crickets can hear bats, but few seem to react to bat echolocation. However, the bush cricket, *Neoconocephalus ensiger,* shows an acoustic startle response during tethered flight in the laboratory (Faure and Hoy 2000). When the insects hear intense batlike sounds with frequencies from 15 kHz to at least 60 kHz (Figure 1b, right), they dive. However, they exhibit no directionality with respect to the sound source, even though bush crickets have directional hearing. A large prothoracic interneuron, the T-neuron, participates in mediating the behavior (Faure and Hoy 2000). The T-neuron is most sensitive to frequencies higher than those of the calling song (13 kHz peak frequency) for the species. The threshold is about 50 dB less than that of the behavior at 20 kHz (Figure 1b, right).

Locusts. Another primarily diurnal orthopteran, the locust *Locusta migratoria* (Figure 1c, left), has a pair of general purpose abdominal ears (Figure 1c, middle) that are well studied anatomically, physically, and physiologically. However, the role of hearing in the life of this locust remains poorly understood. One function of hearing may be to mediate negative phonotaxis in response to batlike signals, although to our knowledge there are no published reports of locusts responding to bats. A locust in stationary flight rudders with its abdomen and increases the wingbeat frequency, both of which produce turning in the direction opposite to the sound source (Robert 1989). Negative phonotactic behavior occurs only at frequencies above 10 kHz (Figure 1c, right). Römer et al. (1988) found interneurons sensitive to high frequencies that selectively receive input from auditory afferents. These interneurons control head and abdominal movements and are candidates for controlling negative phonotaxis. Figure 1c (right) shows the auditory sensitivity of one of these (SN-5).

Praying mantids. Praying mantids (Figure 1d, left) are primarily diurnal, but many make dispersal flights at night (Cumming 1996). Although previously thought to be deaf, many species in the suborder Mantodea actually possess ears (Yager and Hoy 1986). The tympanal organ sensitive to ultrasound is hidden deep in a cleft between the two metathoracic coxae (Figure 1d, middle) and consists of two closely opposed, stiff tympanal membranes. A cluster of sensory cells is attached to each tympanal membrane. The ears are thought to function as a single organ (Hoy et al. 1989). Flying mantids (*Parasphendale agrionina*) react at distances as great as
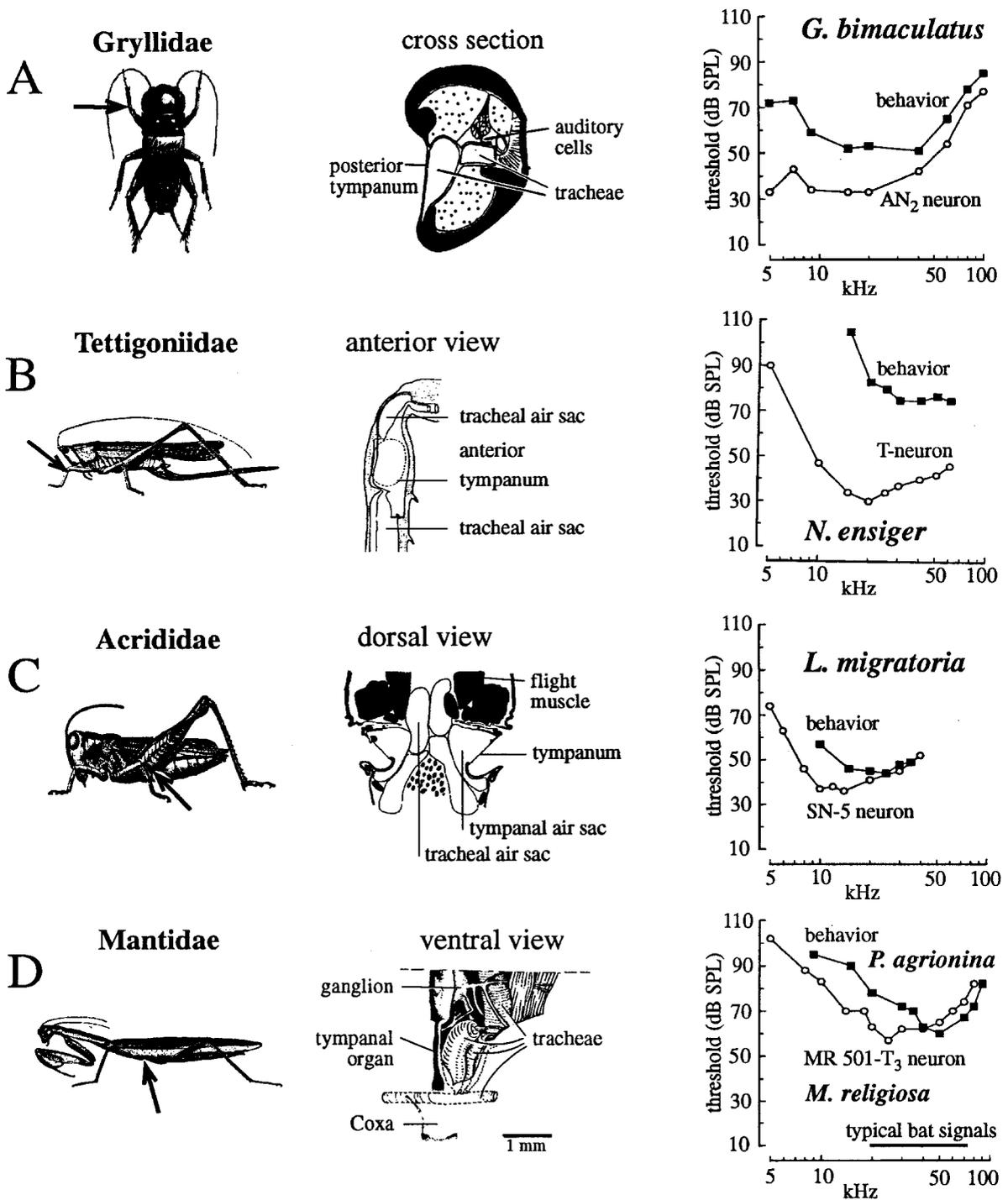
Figure 1. Insects with audition secondarily adapted for hearing bats. Representative insects from the various families are shown in the left column, with the location of the ear as indicated by the arrow. The general anatomy of each ear is shown in the middle column. The tuning curves for avoidance behaviors (negative phonotaxis for orthopterans and nondirectional responses for the mantid) and interneurons thought to be involved with the behaviors are shown in the right column. The frequency range for typical bat biosonar signals is shown on the abscissa (d, right). (a, middle) A cross section of the ear of a cricket, Gryllus bimaculatus (modified from Larsen et al. 1989). (b, middle) A longitudinal section of the ear of an ensiferan, Hemideina cassisens (modified from Ball and Field 1981). (c, middle) A horizontal section through the ear of an acridid, Locusta migratoria (modified from Schwabe 1906). (d, middle) A partial dissection of the ventral surface of a mantid, Mantis religiosa (modified from Yager and Hoy 1986). (d, right) The behavioral data are from Parasphendale agrionina, and the neuronal data are from M. religiosa.

10 m from a loudspeaker emitting batlike signals at natural intensities. They react by turning or with dives and spiral flight. The responses are all nondirectional, as would be expected from a functionally monaural system. The lowest threshold for avoidance behavior occurs from 20 kHz to 80 kHz (Figure 1d, right; Yager 1999). Yager identified an interneuron whose tuning curve resembles that of the behavior (Figure 1d, right), albeit in another species (*Mantis religiosa*). The neuron is most likely part of a neural circuit for avoidance behavior, although attempts to elicit avoidance behavior from *M. religiosa* to artificial bat signals have thus far failed.

Flies and beetles. We suspect that some flies can hear and react to bats, but evidence at present is not sufficient to put them on the growing list of bat-detecting insects. The larviparous tachinid flies, *Ormia ochracea* and *Therobia leonidei*, parasitize crickets and bush crickets, respectively (Lakes-Harlan and Heller 1992, Robert et al. 1992). The calling songs of their nocturnal hosts attract female flies. *Ormia ochracea* hears best at 5 kHz as measured electrophysiologically from the neck connective. This frequency is near the peak power output of the host's song, but the fly's hearing extends into the ultrasonic range. The hearing of *T. leonidei* is also tuned to its host, which sings mostly in the ultrasonic range. These flies can surely hear bats, but their reactions to batlike signals or to bats in nature are unknown.

Beetles, the largest order of insects, are heavily preyed on by some bats, and until recently ears were unknown in beetles. The tiger beetle, *Cicindela marutha,* has ears on the first abdominal segment that are sensitive to sound between 30 kHz and 60 kHz. Batlike signals provoke changes in the beetle's behavior during stationary flight, which include the production of ultrasonic clicks, a property shared only with some arctiid moths (see below; Yager et al. 2000). Hearing in tiger beetles may be used for intraspecific communication, especially because they also produce clicking sounds while on the ground. At present we assume that hearing in these beetles has been secondarily adapted for detecting bats.

In response to pulsed ultrasound, flying scarab beetles, *Eutheola humilis,* dropped or flew toward the ground, and walking beetles stopped. They hear best at 45 kHz. The ears are in the neck region and have evolved independently from those in tiger beetles (Forrest et al. 1997), perhaps specifically for bat detection.

New auditory systems. Ears have evolved independently in many families of eight (perhaps nine) superfamilies of moths (Minet and Surlykke 2002). Physiological and behavioral results, when available for Noctuoidea, Pyraloidea, Geometroidea, Sphingoidea, and Drepanoidea, indicate that the ears are adapted specifically for hearing bat signals. Very recently, evasive behavior to batlike ultrasound was documented in nocturnal butterflies of the superfamily Hedyloidea that have ears on their wings (Yack and Fullard 2000). Green lacewings (Chrysopidae) also have ears on their wings that are sensitive to ultrasound and function as bat detectors.

A lack of frequency sensitivity is common to all these hearing organs: Moths and green lacewings are tone deaf. In contrast, audition in orthopterans and mantids, which is probably secondarily adapted for hearing bats, shows frequency selectivity. Nevertheless, selection pressure has shaped the tuning curves, the hearing or behavioral sensitivity to different sound frequencies, of moth hearing. Many Nearctic species of noctuoids hear best between 20 and 40 kHz, whereas tropical noctuoids hear best over a broader range of ultrasonic frequencies and are more sensitive than their Nearctic relatives (Fullard 1984a). A good example of this is the noctuid *Ascalapha odorata.* Its ear is tuned to the biosonar and social calls of the one bat species on the Hawaiian island Kauai. The same or a closely related species of moth in Panama, on Barro Colorado Island, has a lower threshold of hearing and a broader tuning curve. This is probably an adaptation to the broader range of frequencies used by the many insectivorous bat species found there (Fullard 1984a).

Moths. Ken Roeder made noctuid moths famous through his numerous studies of their hearing and behavior (Roeder 1967a). The Noctuidae, Notodontidae, and Arctiidae (all in the superfamily Noctuoidea; Figure 2a, left) have ears on the lateral surfaces of the metathorax (Figure 2a, middle). Behind the thin tympanal membrane is a large air sac, which is separated from other air sacs by tracheal membranes. Two sensory cells, A1 and A2 (but a single A cell in notodontids; see Surlykke 1988) are attached to the tympanum. The two cells have identical tuning curves (Figure 2a, right) and dynamic ranges, but they differ by about 20 dB in sensitivity. Dynamic range is the range over which neural responses occur to sound intensity, measured in dB from threshold to saturation. The noctuid and arctiid moths have a total auditory dynamic range of about 40 dB.

Freely flying, unidentified moths exhibit a variety of behavioral responses to bats and to synthetic batlike signals (Roeder 1967a; for recent results, refer to Acharya and Fenton 1992). Moths far from the source often turn and fly away, whereas those close to the source show zigzag and looping flight, power dives, or passive falls. Presumably the louder sounds recruit the A_2 sensory cells, which trigger the switch from negative phonotaxis to less predictable, evasive flight behavior. However, Roeder (1964) indicated that the percentage of moths showing turning-away responses decreases and the percentage showing looping responses increases as the pulse repetition rate increases. Because of this, Roeder (1964) suggested that the most sensitive sensory cell (A_1) acting alone could release several behaviors, but further experimentation is needed to confirm this.

Size and sensitivity are correlated in moths, complicating matters further. Big moths reflect more intense echoes than small moths and may be detected by bats as far away as 10 m. However, results from noctuid moths show that big moths are also more sensitive and may detect approaching bats as far away as 100 m. Thus, there seems to be a fairly constant 10-fold margin of safety; that is, noctuid moths can detect bats
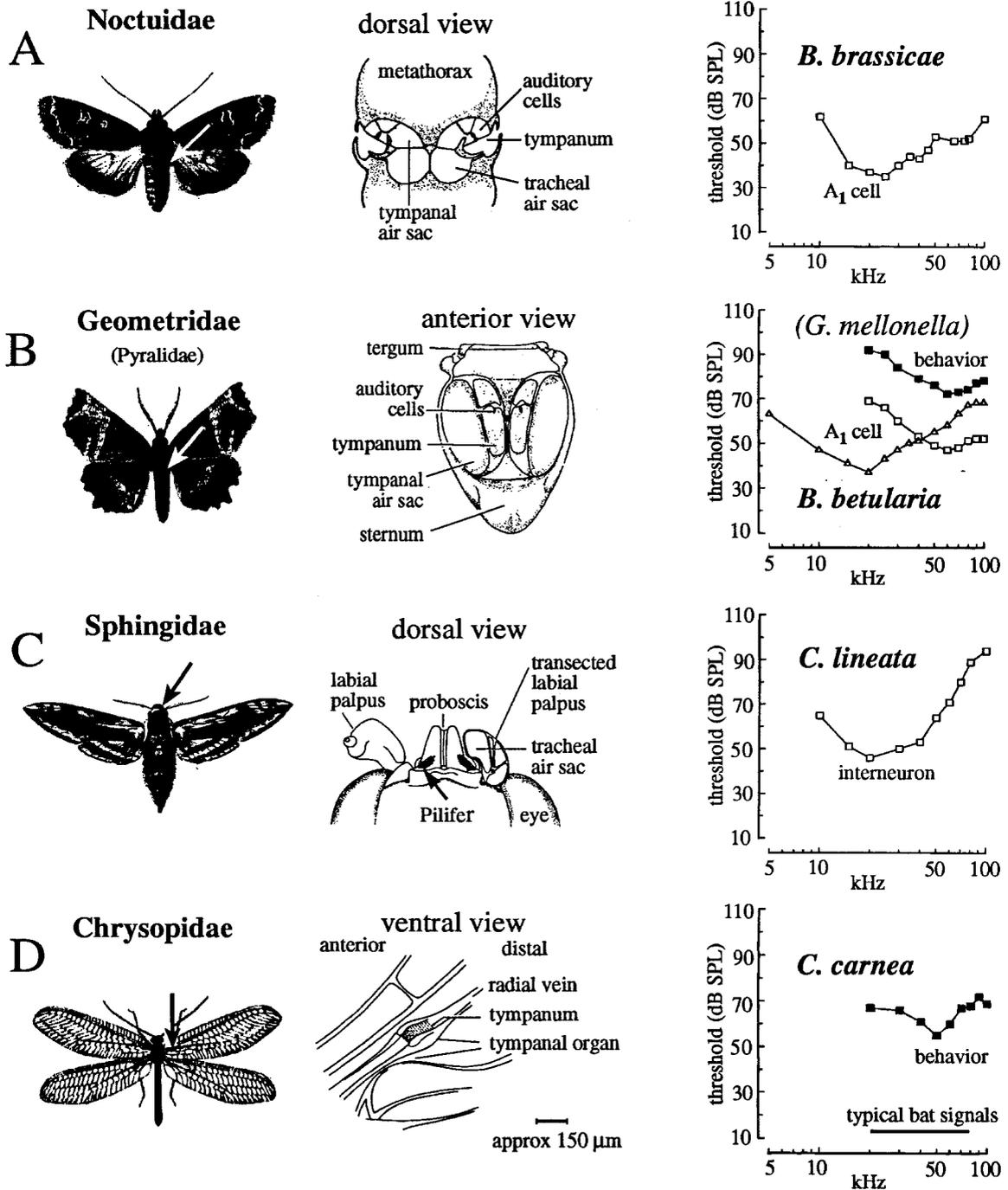
Figure 2. Insects with audition adapted specifically for hearing bats. Representative insects from the various families are shown in the left column, with the location of the ear indicated by arrow. The general anatomy of each ear is shown in the middle column. The tuning curves for flight cessation (behavior), the A1 sensory cells, and an interneuron are shown in the right column. The frequency range for typical bat biosonar signals is shown on the abscissa (d, right). (a, middle) A horizontal section through the metathorax of a noctuid moth (modified after Eggers 1919). (b, middle) A cross section through the first abdominal segment of a geometrid moth viewed from the inside (modified after Kennel and Eggers 1933). A single tympanal air sac occupies the space behind the tympana (not seen in this drawing). The pyralid ear (e.g., Galleria mellonella) is anteroabdominal like that of the geometrid. (b, right) Data for a geometrid, Biston betularia (modified from Surlykke and Filskov 1997), as well as for a pyralid, Galleria mellonella. (c, middle) The head of a sphingid moth, Celerio lineata, with one labial palp in longitudinal section. The sound receivers (pilifers) are seen on the lateral surface of the proboscis (modified from Roeder et al. 1970). (d, middle) The ventral surface of the base of the wing of the green lacewing, Chrysoperla carnea (modified after Miller 1975). References for tuning curves are given in the text.

at about 10 times the distance over which bats can detect moths (Surlykke et al. 1999).

Many interneurons in the thoracic and cephalic ganglia of noctuids have been characterized (Roeder 1975, Boyan and Fullard 1986). For example, two identified neurons receive direct input from the A_1 afferent in parallel, but they process temporal information differently (Boyan and Miller 1991). Synaptic input to some motor neurons controlling the up–down movement of the wings occurs only when the A_2 sensory cell is activated (Madsen and Miller 1987). The role individual interneurons play in eliciting behavior is speculative, principally because the responses of moths are exceedingly difficult to study under controlled conditions (Roeder 1967b).

Arctiid moths behave like noctuids but are more reluctant to do so. In addition, some arctiids produce ultrasonic clicking sounds from tymbal organs when they hear bat signals or are touched. (The clicks have various effects on bats, as described below.) *Cycnia tenera* starts clicking before it stops flying in response to ultrasonic stimuli (Fullard 1979). The threshold for flight cessation is about 10–20 dB above that for clicking, and repetition rates from 17–40 pulses per second are best at eliciting clicking (Fullard 1984b). Also the rate of motor spikes to the tymbal muscles increases when the stimulus rate increases (Northcott and Fullard 1996). So, both amplitude and pulse repetition rate of the ultrasonic stimulus influence behavioral responses from noctuid and arctiid moths.

The Geometridae, Pyralidae, and Drepanidae have ultrasound-sensitive ears on the first abdominal segment (Minet and Surlykke 2001). In the geometrids (Figure 2b, left), the tympana are adjacent to the midline and point caudally (Figure 2b, middle). The tympana in pyralids point rostrally and have a slight tilt ventrally. Four sensory (A) cells attach to each tympanum. The dynamic range for hearing in the geometrid *Biston betularia* is about 50 dB because each cell covers a smaller range (10–15 dB) than the A cells in a noctuid ear. The frequency range of hearing extends to at least 100 kHz in all species studied thus far (Figure 2b, right, *B. betularia;* Surlykke and Filskov 1997). Some geometrids show flight cessation and other responses to ultrasound (Rydell et al. 1997). Pyralid wax moths respond to bat cries (Spangler and Takessian 1983), and *Galleria mellonella* shows a number of behavioral responses while in stationary flight, the most noticeable of which is flight cessation (Skals and Surlykke 2000). Flight cessation, which is the behavior with the highest threshold, occurs at +20 to +25 dB with respect to the threshold for the A_1 cell (Figure 2b, right, *G. mellonella*). Actually, avoidance behavior to bat echolocation is so powerful that some pyralid (and noctuid) moths abort sexually oriented flight to females broadcasting pheromones (Acharya and McNeil 1998).

The bat-detecting ear of some hawk moths (Figure 2c, left) consists of air-filled labial palps that transmit sound energy to the pilifers located on either side of the proboscis (Figure 2c, middle). Other hawk moths have scale plates on the labial palps rather than air-filled palps. Neurophysiological recordings from the labial nerve or from interneurons reveal the auditory characteristics in both types of hawk moths (Figure 2c, right). They are most sensitive to frequencies between 20 and 30 kHz with a threshold of 40–50 dB sound pressure level. The dynamic range of the single auditory sensory neuron in the pilifer is about 20 dB, resembling that in the ear of notodontid moths. Hawk moths in tethered flight respond to ultrasound with changes in flight speed, with nondirectional turning, and sometimes by emitting sound. The behavioral threshold is about 70 dB SPL, or 20 dB above the sensory threshold (Roeder et al. 1970, Göpfert and Wasserthal 1999).

Green lacewings. The ear of the green lacewing (Figure 2d, left) is located in a bulge near the base of the radial vein in each forewing (Figure 2d, middle). It is a true tympanal organ, which is mostly fluid filled and contains a small trachea. It is the smallest tympanal organ known. Perhaps only 6 of the 25 sensory cells actually respond to ultrasound (see Miller 1984 for a review). Like wax moths, green lacewings in stationary flight show a number of responses to lower intensity stimuli before ceasing their flight (Miller 1975). Flight cessation (Figure 2d, right) occurs most reliably to ultrasonic signals broadcast at rates of 1–50 pulses per second. High stimulus repetition rates alone were ineffective in stopping the flight of restrained green lacewings.

A more realistic picture of behavior emerged from studies on freely flying green lacewings and bats (Figure 3). Bat signals at low repetition rates, possibly combined with low intensities, cause insects to fold their wings and passively dive. The green lacewing shows this nondirectional early-warning response to bats' searching signals (Figure 3, between flashes 2 and 3). The bat increases its call rate as it approaches a falling insect (Figure 3, flashes 3 to 4). Just before capturing its prey, the bat increases its repetition rate to a maximum of about 200 signals per second in the terminal phase for most bats (Figure 3, flash 5). During the terminal phase, the insect suddenly flipped open its wings (Figure 3, flash 5 arrow), presumably in response to the high repetition rate signals. This last-chance response breaks the dive and foils the bat in this case, after which the insect continues its dive (Figure 3, flash 6). Artificial bat signals mimicking the sequence shown in Figure 3 evoke the same behavior (Miller and Olesen 1979). By repeating the experiments with deafened green lacewings, we showed that the selective advantage of reactors over nonreactors was 47%, or about the same as that found for moths (see Miller 1982). Unidentified neurons in the prothoracic ganglion respond to ultrasound, but their role in eliciting behavior is unknown (Miller 1984).

Conclusions about insect behaviors

We can draw some conclusions and make predictions based on what we know about avoidance behaviors. Looking at all the behavioral response types for all the insects mentioned above, we find that the best frequency, the frequency at which neural or behavioral responses have the lowest threshold, lies between about 20 and 60 kHz with thresholds between about 30 and 70 dB SPL. The response latencies range from 40–70 ms at +15 dB with respect to the behavioral threshold.
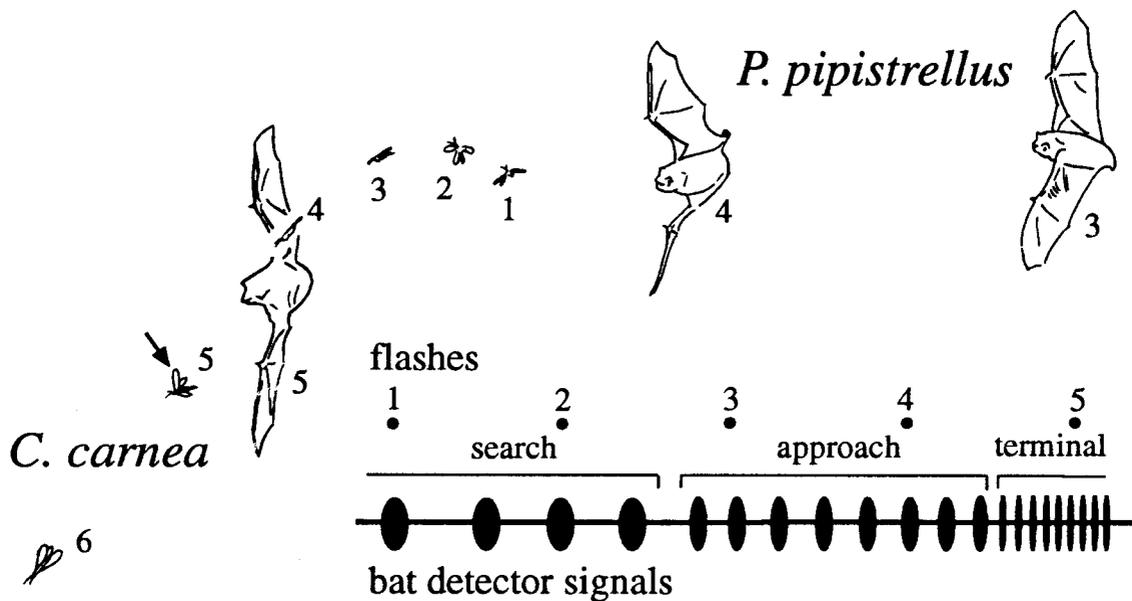
Figure 3. The behavioral responses of a green lacewing to a hunting pipistrelle bat. The behavior was photographed in a large flight cage using stroboscopic flashes at 70-ms intervals. The biosonar signals that the bat emitted during the various stages of hunting were simultaneously recorded. The signals are schematic, and only the intervals are accurately shown. Modified from Miller and Olesen 1979.

Because the distance at which the insects respond to 40 kHz sounds varies from 6.5–37 m for bats using intense signals, the insects have several tenths of a second to avoid even fast-flying bats (Surlykke 1988). The situation is somewhat different for whispering bats, which use intensities of less than about 75 dB SPL and hunt near vegetation. Here the response distances for flying insects are from 0.1–2.7 m, depending on the hearing threshold. However, bats can detect a moth-sized echo at about 0.6 m, putting the less-sensitive insects in danger. Many of the insects mentioned above are open-air fliers and normally do not meet whispering bats.

The tuning of neurons suspected to be involved in avoidance behavior in preadapted insects such as crickets, grasshoppers, and preying mantids poorly match the behavioral tuning. This discrepancy suggests that these auditory neurons have been molded into an antibat circuitry as a result of selection pressure. Behaviors, such as turning in midflight or flight cessation, have thresholds typically 20 dB higher than those for sensory neurons or interneurons (except premotor interneurons) in the same insects. Consequently, yet undiscovered behaviors to low stimulus intensities may provide additional survival advantage.

Insect avoidance behaviors and their underlying mechanisms are undoubtedly complicated. Take for example the variability of responses. The behaviors cannot be reliably predicted, and the same individual may show different responses or no response at all to the same stimulus. Roeder called this the "evitability" of behavior, which provides a survival advantage by making it difficult for the predator to predict what the prey will do. The characteristic feature of evitability makes it difficult to study, but it seems to be present in the behavior and

physiology of some moths (Roeder 1975, Madsen and Miller 1987) and green lacewings (Miller and Olesen 1979). Nevertheless, the auditory and behavioral mechanisms presented here, found in many families in several orders of insects, give an overall picture of convergent evolution in response to bat predation.

Insects living in bat-free environments

Spatial isolation. Some moths escape from the risk of predation by insectivorous bats simply by living in places where no bats occur. Bats are found on all continents except Antarctica and on the majority of islands, but some remote islands are free of bats, for instance, the Faroe Islands in the North Atlantic and the islands in French Polynesia.

In general, moth hearing sensitivity tends to reflect the characteristic frequencies and intensities of the local bat fauna. However, moths from the Faroes (Surlykke 1986) as well as those from Tahiti (French Polynesia; Fullard 1994) have retained auditory sensitivity in complete isolation from bats. Isolated moths have thresholds at the best frequencies that are comparable to the thresholds of moths sympatric with bats in similar habitats, temperate or tropical. Moths from High Arctic areas also show evasive maneuvers to ultrasound (Rydell et al. 2000). The reason these moths have retained sensitive hearing, which seems totally superfluous, is not known. It may simply be due to the slow regression of a character if there is no selection pressure against it. In contrast, a character that has adaptive value may spread through the population after only a few generations, as shown by melanism in the peppered moth, *Biston betularia*.

Temporal isolation. This is another strategy to avoid bats. The Cuculliinae (Noctuidae) include moths that are active in the winter. Several species (e.g., *Lithophane grotei* and *Eupsilia vinulenta*) were captured in Massachusetts in November over a 3-week period, when snow covered the ground and nightly bat censuses revealed none. All captured moths had functional ears tuned to bat sounds with thresholds as low as their relatives flying in the summer (Surlykke and Treat 1995). A study of hearing in winter-active geometrid moths gave a similar result (Rydell et al. 1997). Apparently, nocturnally active winter moths do not use their hearing, even for intraspecific communication. Isolated moths retain their ultrasonic hearing, which indicates that it is not very costly, evolutionarily speaking, to retain ears if they provide winter moths with additional protection, such as from the possibility of occasionally overlapping with bats.

The nocturnal noctuid moth *Rileyana fovea* (formerly *Thecophora fovea*) from Central Europe emerges in late October to early November after bat activity has decreased. *Rileyana fovea* communicates with ultrasound. The males sing in flight by scraping the file of the hind tarsus against the fovea, which is an inflated bubble on the hindwing supported by the heavily sclerotized radial vein (Figure 4). The intense sounds (80 dB at 1 m) have peak power around 30 kHz, which would make the moths very conspicuous to bats. The moths are readily eaten by captive bats. However, by being active at a time of the year with few bats, *R. fovea* can use ultrasound for intraspecific communication. Hence, it seems that a complete conversion of hearing from a defensive context to a sexual one has occurred secondarily in *R. fovea* (Surlykke and Gogala 1986). Ultrasound-producing organs have developed independently in distantly related species of moths that are protected from bats in different ways. This suggests that the pre-

hindwing
stridulatory fovea
hindleg
femur
tibia
tarsus
scraper
T. fovea
2 mm
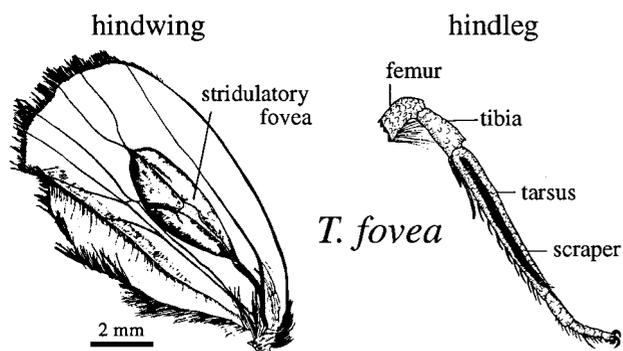
Figure 4. Male stridulatory organ used for the production of intraspecific communication sounds by the noctuid moth Rileyana fovea *(formerly* Thecophora fovea*). Sound pulses with carrier frequencies of about 30 kHz are produced by scraping the file on the tarsus of the hind leg against the stridulatory swelling (fovea) on the hindwing. Modified from Surlykke and Gogala 1986.*

existing ear prompted the development of intraspecific acoustic communication in certain moths (Conner 1999, Skals and Surlykke 1999).

Some moths have changed to diurnal life, a secondary adaptation perhaps in response to predation by bats. Often, diurnal moths are protected by toxins and warning colors, like some butterflies. These day fliers include many tiger moths (Arctiidae), especially from the subfamily Ctenuchinae. Only relatively few Noctuidae are day fliers. One example is the Australian whistling moth, *Hecatesia thyridion* (Agaristinae), which is brightly patterned and probably toxic. Male whistling moths produce sounds that are audible, but most of the energy is in the ultrasonic range where their hearing is best. They use sounds to defend their territories and to attract females (Surlykke and Fullard 1989). Some diurnal moths are silent, and apparently their hearing has no function at all. For example diurnal notodontid moths in the subfamily Dioptinae from Venezuela show varying degrees of auditory degeneration ranging from almost normal sensitivity in some species to very reduced sensitivity, especially at ultrasonic frequencies, in other species (Fullard et al. 1997). Similarly, the diurnal geometrid *Archiearis parthenias* is practically deaf to ultrasonic frequencies (Surlykke et al. 1998).

Sound as defense

Many arctiids possess tymbal organs located on the sides of the metathorax (Figure 5a; Conner 1999). Special muscles buckle the tymbal membrane, generating one click or a burst of clicks per activation cycle (Figure 5b). Click amplitudes vary from about 50–90 dB SPL measured at 5 cm, with maximum sound energy falling between 30 and 80 kHz (Figure 5c; Fullard and Fenton 1977, Surlykke and Miller 1985). Flying arctiids may click when they hear the biosonar signals of bats. Thresholds for clicking can be as low as 60–75 dB SPL for simulated search-phase signals (Fullard 1979, Surlykke and Miller 1985), but considerably higher for short signals (about 2 ms; Fullard 1984b).

Some bats and insects share the same hibernacula, and marauding bats feed on hibernating insects. Nymphalid butterflies sense the vibrations in the substratum as the bat crawls toward it. The torpid butterfly opens its wings in a characteristic manner, which produces intense ultrasonic clicks from a special area of the wing membrane (Møhl and Miller 1976). What purpose do the clicks serve? There are three likely functions of clicking sounds: They could startle bats; they could interfere with the bats' biosonar system; or they could warn bats of a distasteful prey, as many arctiid moths contain toxins in their body tissues or in special glands.

Startle and interference. The clicks of nymphalid butterflies startle bats and thus provide a chance for the insect to escape. However, a bat quickly habituates to the sounds and eats these butterflies (Møhl and Miller 1976). For experienced bats, clicks can act as a dinner bell. Arctiid clicks can startle inexperienced and naive bats (*Eptesicus fuscus*), but these bats also habituate rapidly (Bates and Fenton 1990, Miller

P. fuliginosa

tymbal organ

A

1mm

Coxa III

B

0   1   2
ms

C

20 dB

power

0   100   200
kHz
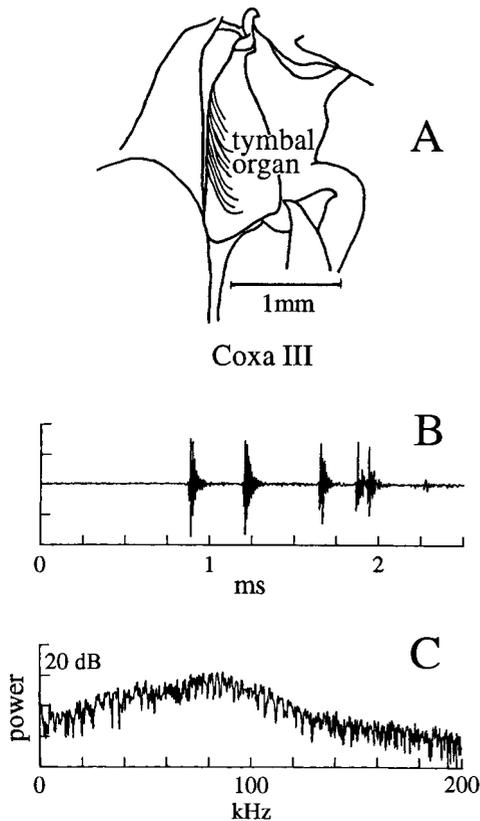
Figure 5. Arctiid tymbal organ and clicks. (a) The tymbal organ on the lateral surface of the metathoracic segment of the arctiid Phragmatobia fuliginosa. *(b) The tymbal organ produces a burst of clicks each time it buckles. (c) The power spectrum of the burst has a maximum at about 80 kHz. (a) Modified from Surlykke and Miller 1985; (b) and (c) modified from Miller 1991.*

1991). Thus, clicks must be used sparingly to have survival value as startle signals.

The ultrasonic clicks of arctiids might disturb bat biosonar in two ways: by simulating multiple targets (Fullard et al. 1979, 1994) and by interfering with range determination (Miller 1991). The arctiid *Cycnia tenera* produces long trains of clicks at high rates. Fullard et al. (1979, 1994) hypothesized that clicks of *C. tenera* could function as acoustical camouflage by simulating multiple targets (false echoes) near the moth and thus jam a bat's (*Eptesicus fuscus*) biosonar. They based their conclusion mainly on the ability of the moth to time its clicking to the terminal phase of the bat's signals. Miller et al. (forthcoming) tested this idea using bats (*Pipistrellus pipistrellus*) trained to catch catapulted meal worms after which natural click sequences from the arctiid *Phragmatobia fuliginosa* were played back during the bats' terminal phase. The bats reacted by increasing the harmonic structure of their terminal signals, but clicks did not influence the success rate of

prey capture. The results suggest that the clicks produced by *P. fuliginosa* do not interfere with the bats' sonar system, perhaps because the click rate is too low. However, in psychophysical experiments, the clicks from *P. fuliginosa* did interfere with the ability of bats (*Eptesicus fuscus*) to determine range differences (Miller 1991). When clicks, triggered by the bats' own signals, fall repeatedly within a critical time window of about 1.5 ms before an echo, the bat's discrimination of range differences deteriorated by as much as 40-fold. A single artificial click placed within the critical window interferes with range difference determination (Tougaard et al. forthcoming) and with neural responses (Tougaard et al. 1998). In either case, a bat would miss its target if clicks represent false echoes from phantom objects or if they interfere with the bat's ranging mechanism.

Warning sounds, toxins, and mimicry. Several facts point to the warning function of clicks as suggested by Dunning (1968). The Arctiidae (including the Ctenuchinae) are generally unpalatable, and arctiids are the only noctuoid moths that click in response to bat sonar sounds. Arctiid clicks could warn the bat of a noxious prey. Evidence supporting a warning function comes from studies in the laboratory and the field. In experimental studies, bats (*Pipistrellus pipistrellus* and *Eptesicus fuscus*) habituated to arctiid clicks when given palatable rewards (Surlykke and Miller 1985, Bates and Fenton 1990). However, the same bats learned very quickly to associate moth clicks with a distasteful reward. Field studies indicated that bats (*Lasiurus* sp.) foraging around street lights often aborted their attacks in the approach or terminal phase when the prey was the noisy arctiid moth, *Hypoprepia fucosa* (Acharya and Fenton 1992). Wild *H. fucosa* did not take visible evasive action to attacking bats. Bats avoided more than 90% of the moths released and dropped the few they captured, usually undamaged. The bats showed no evidence of habituation, although *H. fucosa* were abundant, composing more than 30% of the moth population. *Hypoprepia fucosa* has classic warning coloration and patterns associated with toxic species. Evidence favors the assumption that arctiid clicks are acoustical aposematic signals, warning bats that the moths taste bad (Dunning and Krüger 1996).

Combining acoustic defenses. The startle, interference, and warning hypotheses are not mutually exclusive. In areas where arctiid moths are scarce, the clicks may mostly startle bats. Because bats quickly adapt to the clicks, a warning function is most likely in areas where arctiid moths are abundant. Warning seems especially likely for toxic arctiids like *Arctia caja*, which produce few, but intense clicks in response to batlike signals (Surlykke and Miller 1985). At least some species of arctiids begin clicking to the searching signals of aerial hawking bats at distances of about 2–4 m (Surlykke and Miller 1985). At these distances the bat should be able to hear the clicks, giving an experienced predator ample time to avoid the distasteful prey. There is sufficient time for the bat to change its behavior even if the warning comes during the approach or

terminal phases of the bat's pursuit (Acharya and Fenton 1992). Should the moth's clicks arrive at the bat's ear just before the echoes, the bat's estimation of range to the prey blurs, perhaps causing the bat to miss the target. Moths using long trains of click bursts could exploit this strategy. All three possibilities, startle, interference, and warning, offer selective advantages for arctiid moths in addition to those provided by changes in flight behavior.

Potential countertactics for bats

The diet of many bats contains very few moths, perhaps because of their effective defenses. However, some barbastelle bats prey almost exclusively on tympanate moths, and just how they do this is not known (Sierro and Arlettaz 1997). Here we present some possible double-edged strategies that may explain bat adaptations.

Changing signals. Echolocating bats announce their presence to all potential prey equipped with auditory bat detectors, and bats may use different acoustic strategies to reduce their conspicuousness. One strategy would be an adaptation that moved frequencies of sonar signals out of the range where tympanate insects are most sensitive (Dunning and Krüger 1996). Some bats use very high frequencies, which make them less audible to most noctuoid moths. However, small moths such as some geometrids (Surlykke and Filskov 1997), the pyralid *Galleria mellonella* (Figure 2b, right), and many tropical noctuoids (Fullard 1988) are quite sensitive to high frequencies. The attenuation of high frequencies reduces the useful range of bat sonar, so the advantage of this strategy may be limited. If emission of high frequencies were a countermeasure against tympanate insects, one would expect to find bats exploiting this strategy in temperate regions where many moths do have poor sensitivity at high frequencies (Fullard 1988). The only temperate nongleaning bats that use relatively high frequencies are small ones (e.g., *Pipistrellus* spp.), which detect small prey. While the emission of high frequencies may be a response to insect defenses, it may also be a way to increase resolution and, thus, increase the ability of bats to detect smaller insects (Surlykke et al. 1993).

A second strategy would be for bats to emit very low frequencies, which would make them less conspicuous to moths (Rydell and Arlettaz 1994). This strategy is employed mostly by fast-flying bats that hunt aerial insects far from the ground and vegetation (Neuweiler 1989, Fenton 1990). Low frequencies increase the bats' range but lower the resolution of the bats' biosonar, making only large insects detectable (Barclay 1986).

A third strategy would be an adaptation for bats to reduce the intensity of their signals. *Sound intensity* is a measure of sound energy and is proportional to the sound pressure. (The dB scale is adapted such that any change in sound pressure and the corresponding change in sound intensity result in the same change in dB value.) The advantage would be that the sound intensity decreases with the square of the distance, but the echo intensity decreases with the fourth power of the

distance (Surlykke 1988), making the bat less detectable to the tympanate insect. We do not know if any bats exploit this strategy, but we know that all bats studied so far, when gleaning, use low-intensity sounds if they emit any signals at all (Neuweiler 1989, Miller and Treat 1993, Faure and Barclay 1994). For a gleaning bat, the reduction of detection range is probably not an important restriction, because reducing sound intensity gives the additional advantage of reducing clutter echoes from the background (see Schnitzler and Kalko 2001). In contrast, field studies using techniques to calculate the distance and direction to the bat indicate that at least some bats hunting aerial insects in the open emit intense signals with source levels up to 125 dB SPL, the highest levels yet measured (Jensen and Miller 1999). Also, bats that display both gleaning and aerial-hawking modes of foraging, such as, for instance, *Myotis evotis* (Faure and Barclay 1994) and *M. septentrionalis* (Miller and Treat 1993), emit high intensities when hunting flying insects.

Finally, shorter echolocation signals should be less conspicuous to prey. However, shorter signals mean shorter echoes with less energy, which are less conspicuous to the bats, too. Also, short search signals are recorded mainly from bats using frequency-modulated calls and hunting close to clutter (Neuweiler 1989, Fenton 1990). Hence, we believe that short calls probably are not a countermeasure against insect hearing, but rather an adaptation for reducing the overlap between echoes from clutter and those from prey.

Listening to prey sounds. The most effective way for a bat to sneak close to tympanate prey is to cease echolocating altogether and detect prey using passive sensory cues. If the insects produce sound, bats may find them using passive hearing. Gleaning bats such as *Plecotus auritus* and *Myotis evotis* usually have large pinnae (Faure and Barclay 1994). They react with very fast positive phonotaxis to insect-produced sounds, such as the sound of wings fluttering or of an insect crawling on a surface. Some gleaning bats emit the full repertoire of biosonar signals, including the terminal phase (Schumm et al. 1991). However, gleaners generally stop calling before the attack and produce no terminal phase (Neuweiler 1989, Faure and Barclay 1994). Whether omission of the terminal phase reduces the insect's chance of escaping is difficult to say, because tympanate insects probably detect echolocating bats long before the terminal phase (Roeder 1967a, Surlykke et al.1999). However, omitting the terminal phase may prevent last-chance escape maneuvers (Miller 1984). On the other hand, sedentary moths stay motionless or freeze when hearing echolocation signals. Turning off the sonar in the final phase may not be a countermeasure against tympanate insects; it may simply be that the bat does not need to continuously update the estimated position of a motionless insect. In contrast, the prey of aerial hunters change position continuously in three dimensions, thus forcing the bat to use its biosonar nearly to the moment of capture.

It is difficult to determine if the acoustical adaptations of bats are responses to constraints of the environment or to the

bats' hunting strategies or are intended to overcome insect defenses. In any case, some bat echolocation signals are less conspicuous to tympanate prey.

Concluding remarks

The evolutionary arms race continues between bats and their insect prey, and undiscovered strategies await to be revealed. Some suspected strategies, such as acoustical mimicry, need to be documented by laboratory and field studies. Experimental studies in the field can elucidate some questions about bat and insect interactions. For example, wild gleaning bats hunting at familiar sites (Miller and Treat 1993, Faure and Barclay 1994) offer unique opportunities to test some hypotheses about echolocation behavior and the functions of clicks as interfering or warning signals. Employing modern digital systems that can reproduce clicks and simulate insect echoes will assist in such studies.

Some questions will be difficult to answer. An individual bat can modify at least some of its strategies through learning, whereas insect counterstrategies appear through the slower process of natural selection. Does this mean insect strategies lag behind those of their predators? Perhaps not. The variability of an individual insect's antibat behaviors might be a response to the predator's ability to learn. Perhaps the "evitability" of the prey's behavior (Roeder 1975) makes learning by the predator less effective.

Acknowledgments

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