Sound Strategies: The 65-Million-Year-Old Battle Between Bats and Insects

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Abstract

The intimate details regarding the coevolution of bats and moths have been elucidated over the past 50 years. The bat-moth story began with the evolution of bat sonar, an exquisite ultrasonic system for tracking prey through the night sky. Moths countered with ears tuned to the high frequencies of bat echolocation and with evasive action through directed turns, loops, spirals, drops, and power dives. Some bat species responded by moving the frequency and intensity of their echolocation cries away from the peak sensitivity of moth ears, and the arms race was on. Tiger moths countered by producing anti-bat sounds. Do the sounds advertise moth toxicity, similar to the bright coloration of butterflies; do they startle the bat, giving the moth a momentary advantage in their aerobatic battle; or do they jam the sonar of the bat? The answer is yes. They do all and more in different situations and in different species. Any insect that flies at night must deal with bat predation. Beetles, mantids, true crickets, mole crickets, katydids, green lacewings, and locusts have anti-bat strategies, and we have just scratched the surface. In an exciting new twist, researchers are taking the technologies developed in the laboratory back into the field, where they are poised to appreciate the full richness of this remarkable predator-prey interaction.

Keywords
acoustic aposematism, arms race, coevolution, echolocation, mimicry, predator-prey interaction, sonar jamming
Tymbal organ: the sound-producing structure in arctiine moths

INTRODUCTION
An ancient battle rages high above our heads in the night sky. Bats, the consummate nocturnal predators, hunt their insect prey using ultrasonic sonar. Insects counter with myriad behaviors including aerobatic evasions, stealthy adaptations, and anti-bat sounds. The bat-moth story is one of the pillars of neuroethology—predator and prey interactions at their most sophisticated. It rests squarely on the shoulders of two research giants. Donald Griffin laid out the basics of bat echolocation in his classic text *Listening in the Dark* (54), and Kenneth Roeder illuminated insects’ counteradaptions in *Nerve Cells and Insect Behavior* (97). In one of his last scientific papers in 2001, Griffin referred to the bat-moth story as a magic well that continues to provide scientists with refreshing insights (55). Here we share what we and researchers in other laboratories have learned from these charismatic animals and their duels in the dark. For treatments from additional perspectives, see Fullard (40), Miller & Surykkke (84), Waters (120), and Ratcliffe (93).

BAT ECHOLOCATION
One of the most important factors in the successful adaptive radiation of bats is their effective echolocation system. All but some Old World fruit bats use echolocation as a means of spatial orientation in the dark, and a large number actively pursue prey either partially or completely guided by sonar (32, 69, 89, 102, 103). Laryngeal echolocation appears to have evolved once in an ancestor of extant species, followed by a rich radiation of echolocation strategies with considerable convergence on successful paradigms (68, 69). Echolocating bats emit ultrasonic pulses and listen for the presence, delay, and harmonic structure of the echoes reflected from objects in the environment. The frequency of the echolocation calls varies from 8 to 215 kHz depending on the bat species. The pulse repetition rate of the calls can vary from roughly 3 to approximately 200 pulses s⁻¹ (103, 105). The echolocation prowess of bats has reached its highest expression in the aerial insect-eating bats, which use echolocation to detect, locate, identify, and track prey in flight (Figure 1). The echolocation sequence of hunting insectivorous bats involves three main phases: search, approach, and terminal (buzz) (56, 105). During the search phase the bat’s flight is relatively straight and the bat produces echolocation calls with a low repetition rate (3–15 Hz) and relatively long duration (5–30 ms). The approach phase begins when a bat first responds to a target by turning toward it and increasing the pulse repetition rate. During the terminal (buzz) phase the bat emits a group of short pulses (0.5–1.0 ms) at a high rate (100–200 Hz) as it closes on its airborne target (71, 72, 103, 105). Echolocating bats vary the intensity, pulse repetition rate, frequency-time structure, directionality, and harmonic components of their echolocation calls according to the situation (50, 51, 108). This plasticity allows them to avoid obstacles and locate objects in different habitats. Bats typically have wing morphologies and echolocation repertoires specialized for the habitat in which they forage (92), and they impose a strong selective pressure for defensive counteradaptations by insects (40, 84). It is appropriate to consider the implications of this predation pressure on the defenses of insects.

MOTH HEARING
Tympanic organs (ears) sensitive to ultrasound have evolved multiple times in nocturnal Lepidoptera and exist in nearly half of extant species (93, 98, 104). High-frequency ears arose from vibration-sensitive proprioreceptors in the thorax (e.g., Noctuoidea), abdomen (e.g., Pyralidae and Geometridae), and mouthparts (e.g., some Sphingidae). These sensors preadapted moths for the detection of airborne sound and the echolocation emissions of bats (49, 123). In the noctuid
Myotis bat successfully attacking a noctuid moth

Myotis bat unsuccessfully attacking Bertholdia trigona.

Figure 1

Echolocation sequences of a Myotis sp. bat (a) successfully attacking a tethered noctuid moth and (b) unsuccessfully attacking a tethered sonar-jamming Bertholdia trigona. Recordings were made in the field in southeastern Arizona with moths tethered to a 10-m pole and a miniature microphone placed 30 cm above each moth target. See text for a description of echolocation phases.

Subfamily Arctiinae, the tiger moths that are the focus of our laboratory, the tympanic membranes are located on the thorax and are typically most sensitive to frequencies between 30 and 50 kHz (38). They are directed to the side, below, and to the rear of the moth (22, 84), optimal for detecting pursuing bats. The tuning of the ears of individual species is often matched to the specific acoustic characteristics of the sympatric bat communities with which they have evolved (33, 38, 39, 41, 43, 107, 111). Moth ears are simple in neurophysiological design, with from one to four sound-sensitive cells, yet they provide their bearers with critical information about their acoustic surroundings (84). They are sufficiently sensitive to detect the echolocation cries of most bats before the bats can register their echo (52, 97). Moth species capable of detecting bats have a clear survival advantage (up to 40%) over species that lack ears (1, 2, 24, 97, 98). It is customary to divide prey defenses into two categories: Primary defenses prevent detection by the predator and secondary defenses enhance survival after detection (27, 93). Moth ears can mediate both types of defenses. If the moth hears the bat first and turns away, avoiding detection, the response would be considered a primary defense. If the moth responds after detection by the bat with more complex aerobatic maneuvers or sound production, the responses would be secondary defenses.
ANSWERING BATS

In addition to hearing ultrasound, many arctiines are also capable of producing ultrasound in the form of short, repetitive clicks in response to tactile stimulation and the ultrasonic signals of echolocating bats (4, 8, 9, 21, 23, 25, 34, 37, 44, 82). The sound-producing organs of arctiines are tymbals, modified cuticular plates (episternites) on either side of the third segment of the thorax. Located ventrolaterally, just above the third pair of legs, each tymbal is clearly visible as a translucent bubble often free of scales. Modified steering muscles beneath the cuticle move the tymbals. As the muscles contract and relax, the cuticle flexes in and out, producing clicks (46). The anterior edge of the tymbal of many species is adorned with small ridges called microtymbals. During the flexion and relaxation cycle the microtymbals produce microclicks, which add complexity to the sounds produced (Figure 2). The resulting sounds register their peak intensity in the ultrasonic frequencies ranging from 30 to 75 kHz (4, 21, 44) and have sound pressure levels as high as 119 dB measured at 2 cm (101). Sound production originated in arctiids as a survival
Figure 3

Classification of anti-bat moth sounds plotted in acoustic space along maximum duty cycle (percent of time occupied by sound) and modulation cycle complexity (number of clicks per modulation cycle) axes. Each number represents a species. The sonar-jammers cluster contains *Bertholdia trigona* (B) and the aposematic/mimetic cluster contains *Cycnia tenera* (C) and *Euchaetes egle* (E). Colored areas show proposed acoustic strategies.

Tactic against echolocating bats (40) but has been secondarily co-opted for sexual communication (16). It is important to note that ultrasound communication in nonarctiid lepidopteran lineages has evolved by different evolutionary paths (88, 106).

Blest (8) was the first to attempt a serious study of the diversity of tiger moth sounds. On Barro Colorado Island in the Canal Zone, at Volcán and Santa Clara near the Panamá-Costa Rica border, and in Arima Valley of Trinidad, he monitored the sound production of some 180 species without the aid of sophisticated recording equipment. Fullard & Fenton (44) added 24 North American species to the list with detailed sound analysis, and Barber & Conner (4) recorded 84 species on the western slopes of the Andes in Ecuador. In 2010, Corcoran et al. (21) described the diversity of tiger moth sounds in multidimensional acoustic space using a principal component analysis that arrayed the variation in the characteristics of anti-bat sounds along multiple axes. They found that the sounds are not homogeneous but instead vary along a frequency axis, along a duty cycle (percent of time occupied by clicks/frequency modulation axis, and along a modulation cycle complexity axis (number of clicks produced during flexion and relaxation of the tymbal). Tiger moth species fell into two distinct clusters based on the characteristics of their sounds. One cluster comprised species that produced sound with low duty cycles (<20%) and with relatively few clicks per tymbal activation. The second cluster comprised species with high duty cycles (>20%) and many clicks per tymbal activation (Figure 3). This finding is a clue that anti-bat tiger moth sounds can function in fundamentally different ways.

CHEMICAL DEFENSES

Tiger moths are well known for the defensive chemicals that they produce de novo or sequester from their host plants (90, 121). Their chemical repertoire includes biogenic amines, lichen...
phenolics, azoxyglycosides, and iridoid glycosides (11). The pyrrolizidine alkaloids (PAs) and the cardiac glycosides (CGs) are prominent in both their potency and in the number of species that sequester or produce them (57). PAs have a variety of effects on vertebrates, ranging from bitter taste in low concentrations to tissue damage and death in high concentrations (58, 77). In the context of conditioned avoidance by predators, however, the most important factor for the defensive properties of PAs is their bitter taste. PAs are also effective feeding deterrents for invertebrate and vertebrate predators such as spiders, sucking bugs, birds, and bats (28, 29, 65). Arctiids acquire and sequester PAs in two ways: as larvae while feeding on their PA-laden host plants (57, 119) and as adults imbibing PAs from the surface of withered PA-containing plants (10, 18, 53). The pharmacological effects of cardenolides (cardiac glycosides) stem from their inhibition of the Na+/K+ ATPases and the activation of emesis (12). Arctiid larvae obtain CGs from their food plants (usually Asclepiadaceae or Apocynaceae), sequester them in body tissues, and then transfer them to the adult stage through metamorphosis (7, 118). The toxins can be stored in the integument and hemolymph of larvae and adults and are sometimes exuded via secretions from the adults’ cervical glands. Both PAs and CGs are effective in deterring bat predation (65, 94).

THE BAT-MOTH STORY

The bat-moth story is one of the most sophisticated predator-prey interactions known. The elegant system of acoustic orientation and prey detection of bats renders them extremely capable predators. Arctiid moths have evolved ears, sound-producing structures, and chemical defenses that protect them. Most researchers agree that arctiids generate ultrasonic clicks as a defensive strategy against echolocating bats (95). Several general (and not mutually exclusive) hypotheses concerning the bat-moth acoustic interaction have been proposed (21, 94). The startle hypothesis argues that the sounds elicit the mammalian startle reflex (6, 27, 67, 83). The jamming hypothesis maintains that the sounds confuse the bat by interfering with its echolocation system (45, 48, 83, 85, 94, 109). The aposematism hypothesis claims that the sounds warn the bat of the moth’s distastefulness (1, 2, 24, 25, 109). Simply put, these defense mechanisms either orient the bat by providing it with information that it uses to make an attack decision (aposematism) or disorient the bat by interrupting the normal flow of echo information required to complete a successful capture (jamming and startle) (21).

It is clear that all three hypotheses—jamming, startle, and acoustic aposematism—might function in any given interaction. However, it seems highly unlikely that the three hypotheses have the same selective value in nature. Rather, one has provided the main selective advantage driving the evolution of the tymbal and sound production in the Arctiinae. See Ratcliffe & Fullard (94) for a more synthetic view.

STARTLE

Proponents of the startle hypothesis suggest that tiger moths produce a deimatic display that exploits the mammalian startle reflex and gain a momentary advantage that may allow them to escape (27, 60, 63). However, although free-flying bats were initially startled by the low-duty-cycle moth clicks of Cynia tenera, they quickly habituated to them (from one to three presentations in a single night) (6), suggesting that the startle effect is ephemeral and unlikely to be effective under natural conditions for long periods. A more recent study with the high-duty-cycle moth Bertholdia trigona found startle-like effects that last for longer periods (up to 40 presentations over two nights) and has resurrected the possibility that they play an important role at least for naïve bats (20).
ACOUSTIC APOSEMATISM

The aposematism hypothesis suggests that bats learn to associate moth clicks with the chemical defenses typical of many arctiids. Dunning (23) was the first to find evidence for acoustic aposematism. She presented two groups of moths to caged bats: live unpalatable arctiids capable of producing sound and a control group composed of silent palatable nonarctiid species. The bats avoided clicking arctiids more often than nonclicking species. In a similar study, using caged bats Eckrich & Boppré (26) found evidence for the importance of moth defensive chemistry on the efficacy of sound. Dunning and colleagues later presented arctiids with their tymbals destroyed to free-foraging bats and observed that, on average, bats captured more muted arctiids than sound-producing arctiids. After capture the bats rejected a large proportion of the muted arctiids relative to control nontoxic and nonacoustic moths (23, 24). If jamming or startle alone accounted for the interaction, the researchers should not have observed the dependence of the results on the defensive chemistry of the moths.

Stronger evidence for acoustic aposematism was obtained with a learning approach (66). It is based on the idea that the pattern of a naive (i.e., have never been exposed to moth sounds) bat’s success in capturing clicking moths over successive foraging nights should vary for each of the three proposed moth click functions (startle, jamming, and aposematism) and depend on whether the moth is chemically protected (C+) or not (C−) (Figure 4a). Acoustic aposematism would be an effective defense only for C+ moths. Naive bats must learn to associate clicks with distastefulness, so they should initially catch, taste, and drop sound-producing (S+) and distasteful (C+) moths, and then learn to avoid them. The startle response would have the opposite pattern: Bats would at first be startled but then habituate to the clicks; this response should be the same for C+ and C− moths. Jamming would be effective immediately and would remain an effective deterrent for both C+ and C− moths. Common to all the hypotheses is the assumption that bats catch silent S−C+ and S−C− moths as well as controls. The strength of this approach is in its ability to disentangle the defensive effects of clicking and chemistry and its use of naive individuals to obtain results untainted by previous experience.

By choosing moth species that naturally vary in chemistry and sound production ability, or by experimentally manipulating an individual species to vary in these properties, Hristov & Conner (66) could present all possibilities: C+S+, C+S−, C−S+, and C−S− to naive big brown bats. Moths from each of the four groups were presented on a tether to a different group of bats flying individually in a flight room. The changes in the proportions of moths caught and eaten over time were recorded in the form of learning curves (Figure 4b). The results were consistent only with the acoustic aposematism hypothesis—moth clicks were effective at deterring bats only when they were paired with defensive chemistry, and the bats first had to learn this association before the defense became effective. The same results were obtained using multiple moth species (Figure 4b) and by experimentally manipulating an individual arctiid species to fit the four defensive categories (66).

ACOUSTIC MIMICRY

The results described above strongly support the acoustic aposematism hypothesis. Given the evidence for acoustic aposematism, one would expect at least some arctiids to exploit the system through mimicry. Some palatable species should produce sounds but not back them up with defensive chemistry (Batesian mimicry), whereas some unpalatable species should benefit from hearing an acoustic resemblance to other more common unpalatable species (Müllerian mimicry). The latter species would benefit by spreading the costs of educating predators across more individuals.
Sonar jamming: a prey strategy in which the prey sounds render bat sonar less effective

The learning paradigm gave a unique opportunity to explore these relationships and see whether they function in nature as predicted (5).

Certain moth species (e.g., Euchaetes egle) produce sound but have no defensive compounds when raised on their natural host plants. Because sounds alone appear ineffective at jamming or startling bats, it was suggested that these species are acoustic mimics (66). Interestingly, the seasonal phenology of E. egle overlaps with Cycnia tenera—a common unpalatable species with a similar acoustic signature—which also suggests that E. egle may be an acoustic mimic. Dunning found a similar situation for the palatable arctiid Pyrrharctia isabella (23) but was unable to confirm her contention under natural conditions. The learning approach allowed for a test of the efficacy of mimicry in a more natural setting.

Barber & Conner (5) first presented the toxic and sound-producing model moth C. tenera to naive big brown (Eptesicus fuscus) or red bats (Lasiuris borealis) for five nights (Figure 4c). The bats quickly learned to associate the clicking moths with bad taste and stopped catching them, again illustrating acoustic aposematism. On nights 6 through 10 they presented a second clicking species. This was the critical test of mimicry. They found that the experienced bats generalized clicking species and treated the mimic much like the model, i.e., they did not attempt to catch them (Figure 4c) (3, 5). On the final night of the experiment they disabled the tymbals of the mimics. The bats immediately began to catch the mimics. This clearly illustrated that the tymbal sound (and not any other sensory modality) was the cue that the bats were using to discern the relationship between the first and second moth species. The results showed that Euchaetes egle is a Batesian mimic of C. tenera (Figure 4c) and that Syntomeida epilais is an effective Müllerian mimic of C. tenera and vice versa. Acoustic mimics were most effective against big brown bats (beetle specialists that occasionally include moths in their diet) but were still significantly effective against many red bats (moth specialists) (5).

Later work (3) based on the three-dimensional reconstruction of bat flight tracks as they approached model and mimic suggested that the bats can actually distinguish between moths on the basis of their sounds but choose to generalize the warning signal and avoid both model and mimic. Perhaps this is because of the severity of the punishment associated with mistakenly tasting a model.

SONAR JAMMING

Sonar jamming has been a popular hypothesis for anti-bat moth sounds for many years (45, 48), and until recently no hard evidence for it existed in natural bat-moth interactions. Field studies in the cloud forests of western Ecuador identified moth species that have acoustic signals one order of magnitude more complex than those previously described (4). Members of the genus Bertholdia stood out because they produce acoustic signals in response to bat cries that are far more complex than would appear to be necessary to advertise distastefulness (Figure 2). They have a very high

Figure 4

Predicted and observed success of naive bats attacking arctiid and control moths over successive nights. (a) The success of bats attacking chemically defended (C+S+) and palatable (C−S+) clicking moths should vary according to three proposed moth click functions. (b) Acoustic aposematism experiment. Naive big brown bat success attacking toxic, clicking Cycnia tenera and palatable, clicking Euchaetes egle matches predictions of the aposematism hypothesis. (c) Batesian mimicry experiment. Red bats (Lasiuris borealis) and big brown bats (Eptesicus fuscus) learned to avoid C. tenera but then avoid subsequently presented E. egle due to Batesian mimicry. Intermediate red bat success on days 6–10 reflect three bats that discovered the mimics and four bats that were fooled. (d) Jamming experiment. Big brown bats attacking the abundantly clicking and palatable Bertholdia trigona demonstrate a response consistent only with the sonar-jamming hypothesis. Adapted from References 3, 4, 19, and 66.
duty cycle, a high degree of frequency modulation, and larger numbers of clicks per tymbal activation cycle, and the clicks are produced during the final moments of a bat’s attack—just when jamming should be most effective. These characteristics suggest that they may have evolved to jam the echolocation system of a bat. Feeding experiments showed that *Bertholdia trigona* is palatable to big brown bats; this provided the opportunity to experimentally separate warning sound from jamming again using the learning approach (19). The *Bertholdia* clicks were extremely effective at deterring attacking bats right away (as opposed to the aposematic moths, which require an initial learning period to be effective), and the effect persisted over seven foraging nights. This was the response predicted to be the hallmark of sonar jamming (Figure 4d). Furthermore, bioacoustics analysis of sonar cries during bat attacks on *Bertholdia* revealed changes in echolocation behavior consistent with the jamming hypothesis (19, 20). This was the first conclusive evidence that moth clicks, or any other defensive animal sounds, jam the echolocation system of a predator.

**JAMMING MECHANISM**

Three mechanisms have been proposed to explain how moth clicks might jam bat sonar. Fullard and colleagues (45, 48) suggested that because some moth clicks and echolocation calls have similar temporal and spectral properties, bats could mistake clicks for echoes returning from nonexistent objects and become thoroughly confused. This hypothesis, the phantom echo hypothesis, has received little empirical support (20, 21, 83, 109, 114, 115). A second possibility, the ranging hypothesis, raised by Miller (83), is that the clicks disrupt the neural mechanism that encodes the time of arrival of the moth’s echo and thus gives the bat the distance (or range) of the moth. Miller (83) found that moth clicks can degrade bats’ ranging ability by up to 400%, but only when clicks occur in a narrow 2-ms time window preceding the arrival of echoes. Tougaard et al. (114, 115) demonstrated that moth clicks interfere with the neural responses of single units in the lateral lemniscus of big brown bats—a nucleus implicated in target ranging—but again only when they fall within a 2-ms window preceding the test signal (or simulated echo). They concluded that because moths cannot time their clicks to precede echoes, only moth clicks produced at a very high rate, or duty cycle, would effectively interfere with bat sonar. Finally, it is conceivable that moths clicks mask the presence of echoes, much like white noise would, rendering the moth invisible (85, 117).

Distinguishing among the hypotheses for how moth clicks jam bat sonar is not an easy proposition. But the phantom echo hypothesis, the ranging interference hypothesis, and the masking hypothesis should leave telltale clues in the flight tracks and acoustic emissions of bats as they approach a jamming moth. Corcoran et al. (20) again took advantage of *B. trigona* and the way in which naive big brown bats approach them. They found that bats approach control noctuid moths directly. Bats gradually increase their echolocation rate, refreshing their “sonar screens” more rapidly as they approach the target. In the last moments before contact they produce a terminal buzz to get an accurate fix of the exact location of the moth and then cup the moth in their tail membrane for capture. This stereotyped choreography takes place in less than 600 ms. How they approach a clicking *Bertholdia* is another matter. If the moth clicks function as phantom targets, the bats would be expected to veer toward the phantoms to pursue them or perhaps perceive them as clutter (like the echoes from the twigs of a bush) and move quickly away. If the moth clicks interfere with the ability of the bat to determine the exact range of the target, the bats might be expected to miss their target by an amount characteristic of the degree of range interference and to make repeated capture attempts. And last, if the clicks are masking the echo, you might expect the bats to lose the ability to track their target completely. When the experiment was carried out, the bats were first startled by the avid sound producer. After a period of habituation, the bats
continued pursuing the moths as they clicked but narrowly missed by a distance predicted by the ranging interference hypothesis. The bats did not make capture attempts either on the moths or on the locations of phantom targets. These results are most consistent with the hypothesis that clicks interfere with the bats’ ranging program. *Bertholdia* appears to be able to confuse the bat about its exact location (20).

**TAKING THE BAT-MOTH STORY BACK TO THE FIELD**

Much of the research described above was done in dark, sound-attenuated rooms viewed with infrared-sensitive video cameras and monitored using one or an array of high-frequency microphones. Although this has allowed researchers to gather evidence for acoustic aposematism, mimicry, and sonar jamming, it falls short of the ultimate goal to decipher what bats and moths actually do in the night sky. The methods and equipment can be made field portable (59, 64), allowing researchers to return to the field. Throughout the world, unfettered bats and moths are battling under the watchful eyes of modern technology. It is here that new strategies and counterstrategies of the bat-moth arms race will be revealed.

**A DIVERSITY OF EARS AND ANTI-BAT STRATEGIES**

Moths are not the only insects to evolve bat detectors (84). Insect ears have evolved in at least 7 of 27 insect orders (62). The proprioreceptor precursors are found throughout the bodies of insects and so too are ears (62, 122).

**Beetles**

Tiger beetles (Cicindelidae) possess ultrasound-sensitive ears (107, 125, 129, 130). Their ears are tucked neatly away under the fore of their elytra; thus they only hear when they are in flight, when their elytra are elevated. Hearing appears to be a shared primitive trait in the family. Many tiger beetles respond to bat sonar with head roles, elytra swings, and changes in wingbeat frequency that should result in altered flight trajectories and render them a more difficult target for bats. Much like tiger moths, several North American genera answer the sonar signals of feeding bats with trains of ultrasonic clicks. The sounds are produced by swinging the elytra down into the path of the flapping hindwings. The function of the tiger moth clicks, whether warning, startle, mimicry, or jamming, are not yet known.

Some night-flying dynastine scarab beetles (Scarabaeidae) also have ultrasound-sensitive ears (34, 36). They are located on the cervical membranes and represent an independent evolution of auditory organs in the Coleoptera. In response to simulated bat cries (20–80 kHz) beetles executed a head role characteristic of in-flight turning and dropped to the ground, classic anti-bat maneuvers (35). Because some bat species are beetle specialists (14), it seems likely that many more beetles will prove sensitive to ultrasound and display anti-bat behaviors.

**Mantids**

Yager & Hoy (126) discovered a median cyclopean ear in praying mantids (Mantodea). Although the ear is composed of two tympanic membranes on the ventral midline of the thorax, it functions as a single unit, hence the term cyclopean. Sixty-five percent of all mantids have them and they are generally sensitive to sounds between 25 and 50 kHz (124). In *Paraspindle agrionina* (Mantidae), the ears mediate a suite of defensive behaviors that include extension of the forelegs, rolling the
head to the side, changes in wingbeat and excursion, and curling of the abdomen upward (127). The behaviors result in clear evasive maneuvers—dives, turns, and spirals—that thwart capture by echolocating bats (128).

**Lacewings**

One of the most interesting insect bat detectors is the ear found on the wings of green lacewings (Chrysopidae). The ear is a swelling located on the radial vein of the forewings (80). When a green lacewing detects the sonar signals of a bat, it folds its wings and drops rapidly. To render its trajectory less predictable, it extends its wings, i.e., puts on its air breaks, at random intervals (81). Interestingly, bats may counter dropping strategies by approaching targets from underneath (see Bat Countermeasures to Insect Defenses: The Arms Race, below).

**Crickets**

Female true crickets (Gryllidae) including Australian oceanic field crickets, *Teleogryllus oceanicus*, use their ears to localize the low-frequency calling song of potential mates. A second high-frequency peak in the sensitivity of their hearing (86) allows them to detect and steer away from bats while searching for mates (78, 79, 86, 91). Similar responses have been noted in members of the genus *Gryllus* (30, 63). Cricket ears are located just below the “knee” (tibia-femur joint) on the forelegs in the location of the proprioreceptive subgenal organ in other insects.

**Mole Crickets**

As their name implies, male mole crickets (Gryllotalpidae) dig burrows. They position themselves in a trumpet-shaped burrow and project their mating call with great intensity. Females fly to the males guided by the calling song. Like true crickets, gryllotalpids define their acoustic world by frequency. Low-carrier frequencies define mates and high-carrier frequencies define predators, bats (76).

**Katydid**

Recent studies indicate that some katydids (Tettigoniidae) can detect the bat sonar signal of gleaning bats (31, 113). In response to the echolocation calls of sympatric bats, they shut down their own acoustic courtship displays to avoid passive detection by gleaners. Flying *Neoconocephalus ensiger* shows classic bat avoidance in the presence of bat-like ultrasound. Within 50 ms of receiving a sound pulse, they close all four wings and begin a free fall (75).

**Locusts**

Adult migratory locusts (*Locusta migratoria*: Acrididae) speed up their flight and turn away from ultrasonic pulses that mimic bat echolocation calls. This response is mediated by paired abdominal tympana (96) and is considered an early warning system for bats. Interestingly, African tribes take advantage of the high-frequency hearing of locusts by rapping a metallic pot to deflect medium-sized swarms of locusts from their property (96).

**Earless Insects**

Insects without ears are not totally at the mercy of echolocating predators. Nocturnal moths that lack bat-detecting ears should fly particularly fast or fly erratically (74). Another option is
to fly close to vegetation in what bioacousticians refer to as the clutter zone, an area in which the echoes of the prey are lost in the myriad echoes from nearby vegetation (73). Lekking ghost moths (*Hepialus humuli*) appear to use this strategy. They carry out their sexual flight displays within 0.5 m of the surrounding vegetation and gain protection by exploiting the clutter zone (99). Water striders may employ a similar strategy against gleaning bats by staying near the edges of water during times of peak bat activity (112). Earless moths have also been shown to avoid the peak foraging times of bats (47, 74), to decrease the total time in flight, or both (13, 87). Taking this to the extreme, some groups (including eared species) have become increasingly diurnal and thus avoid bat predation to a great extent (40, 43).

**BAT COUNTERMEASURES TO INSECT DEFENSES: THE ARMS RACE**

For the predator-prey interactions described above to be called an arms race, the two players must be locked in an evolutionary struggle with sequential adaptations and counteradaptions (100). The current frequency sensitivity of moth ears is clearly the result of the selective pressures of bats. The question is, Have bats countered? Fullard was the first to address this issue with the allotonic frequency hypothesis. He argued that some bats have lowered the frequency of their echolocation sonar, rendering them difficult for the moths to detect (40). Other bat species may have countered by moving to ultrahigh frequencies above the frequency sensitivity of their moth targets. Although both patterns have been seen in various bat species, each can be argued to have additional advantages such as high resolution at high frequencies and greater echolocation range at lower frequency (100), making counteradaptation less clear.

The recent discovery of stealth echolocation has provided the strongest evidence for a counteradaptation on the part of a bat (52). *Barbastella barbastellus*, a vespertilionid bat that specializes on eared moth prey, has countered moth hearing by producing echolocation calls 10 to 100 times lower in intensity than related aerial hawking bats (also see 42). This decreases the distance at which the moth can detect the bat by one order of magnitude and gives the bat a distinct advantage when approaching eared prey. Stealth echolocation does come at a cost. The maximum distance at which the bat detects the moth decreases three- to fourfold. This suggests that the adaptation is solely a counteradaptation to moth hearing and bears no further advantage in echolocation strategy.

The nervous systems of insects key not only on the frequency of bat calls but also on the timing of the calls that clue the insect of an impending attack. One example is the call repetition rate of approach-phase echolocation. It has been suggested that big brown bats can omit the critical timing parameters as they approach a target, depriving the insect of the information that it needs to trigger evasive action. This may also be construed as a counteradaptation (116).

Researchers are becoming more sophisticated in their study and understanding of pursuit strategies in bats (50, 51). It appears that specific maneuvers employed by red bats, such as approaching prey from below and using their tail membranes to anticipate and thwart dropping behavior, may represent counteradaptations to predictable prey evasion tactics. Additional research is needed here.

**THE FUTURE**

As efficient nocturnal predators, bats have been shown to limit arthropod abundance in some habitats (70). New molecular methods applied to bat guano provide a summary of the insects eaten by bats (14, 15) and point out how little we know about the details of this important predator-prey interaction. Following in the footsteps of Roeder, most researchers have concentrated on bat-moth...
interactions, but there is much more to learn. Countless species of insects representing at least nine orders are known to be active at night and are eaten by bats. We know about the workings of only a handful of insect ears and even fewer animals that answer echolocation. Like the deepest ocean trench or the most isolated rainforest valley, the night sky remains largely unexplored. Using the beautiful analogy of Donald Griffin (55): The magic well remains full.

SUMMARY POINTS
1. Echolocating bats have been a major selective force on nocturnal insects, resulting in an escalating arms race of bat sonar adaptations and insect anti-bat counteradaptations.
2. Some insects produce anti-bat sounds when they detect the sonar signals of attacking bats.
3. Anti-bat sounds function in acoustic aposematism, startle, Batesian mimicry, Müllerian mimicry, and sonar jamming.
4. Sonar jamming appears to function by interfering with the target-ranging program of bats.
5. Moths, beetles, mantids, lacewings, crickets, mole crickets, katydids, and locusts can detect the sonar emissions of bats and exhibit various forms of anti-bat behavior.
6. Researchers are beginning to use sophisticated high-speed infrared videography and high-frequency microphone arrays to study bat-insect interactions under natural conditions.
7. The nocturnal sky remains a largely unexplored habitat that will yield a multitude of exciting predator-prey interactions in the future.

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LITERATURE CITED


5. Conducts first test of acoustic mimicry in a predator-prey system.
Contents

Insect Responses to Major Landscape-Level Disturbance
   T.D. Schowalter ......................................................... 1

Sound Strategies: The 65-Million-Year-Old Battle Between Bats and Insects
   William E. Conner and Aaron J. Corcoran .......................... 21

Approaches and Incentives to Implement Integrated Pest Management that Addresses Regional and Environmental Issues
   Michael J. Brewer and Peter B. Goodell .......................... 41

Transmission of Flea-Borne Zoonotic Agents
   Rebecca J. Eisen and Kenneth L. Gage ............................ 61

Insect Nuclear Receptors
   Susan E. Fahrbach, Guy Smagghe, and Rodrigo A. Velarde .... 83

Plasmodium knowlesi: A Malaria Parasite of Monkeys and Humans
   William E. Collins .................................................. 107

Group Size and Its Effects on Collective Organization
   Anna Dornhaus, Scott Powell, and Sarah Bengston ............ 123

Mosquito Genomics: Progress and Challenges
   David W. Severson and Susanta K. Behura ....................... 143

Reevaluating the Arthropod Tree of Life
   Gonzalo Giribet and Gregory D. Edgecombe ....................... 167

Morphology and Diversity of Exocrine Glands in Lepidopteran Larvae
   Francesca Vegliante and Ivar Hasenfuss .......................... 187

Insects as Weapons of War, Terror, and Torture
   Jeffrey A. Lockwood ................................................ 205

Mites (Acari) as a Factor in Greenhouse Management
   Uri Gerson and Phyllis G. Weintraub ................................ 229

Evolutionary Ecology of Odonata: A Complex Life Cycle Perspective
   Robby Stoks and Alex Córdoba-Aguilar ......................... 249
Insect Transgenesis: Current Applications and Future Prospects
Malcolm J. Fraser Jr. ................................................................. 267

The Ecology of Nest Movement in Social Insects
Terrence P. McGlynn ................................................................. 291

Molecular Bases of Plant Resistance to Arthropods
C. Michael Smith and Stephen L. Clement .................................. 309

Prospects for Managing Turfgrass Pests with Reduced Chemical Inputs
David W. Held and Daniel A. Potter ........................................... 329

Managing Social Insects of Urban Importance
Michael K. Rust and Nan-Yao Su .............................................. 355

Systematics, Biodiversity, Biogeography, and Host Associations of the
Miridae (Insecta: Hemiptera: Heteroptera: Cimicomorpha)
G. Cassis and R.T. Schub ............................................................ 377

Essential Oils in Insect Control: Low-Risk Products in a High-Stakes
World
Catherine Regnault-Roger, Charles Vincent, and John Thor Arnason .................. 405

Key Aspects of the Biology of Snail-Killing Sciomyzidae Flies
William L. Murphy, Lloyd V. Knutson, Eric G. Chapman, Rory J. McDonnell,
Christopher D. Williams, Benjamin A. Foote, and Jean-Claude Vala .............. 425

Advances in Insect Phylogeny at the Dawn of the Postgenomic Era
Michelle D. Trautwein, Brian M. Wiegmann, Rolf Beutel, Karl M. Kjer,
and David K. Yeates ................................................................. 449

Indexes

Cumulative Index of Contributing Authors, Volumes 48–57 ......................... 469
Cumulative Index of Chapter Titles, Volumes 48–57 .................................. 474

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**TABLE OF CONTENTS:**

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- **Probabilistic Forecasting**, Tilmann Gneiting, Matthias Katzfuss
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- **Bayesian Computation Via Markov Chain Monte Carlo**, Radu V. Craiu, Jeffrey S. Rosenthal
- **Build, Compute, Critique, Repeat: Data Analysis with Latent Variable Models**, David M. Blei
- **Structured Regularizers for High-Dimensional Problems: Statistical and Computational Issues**, Martin J. Wainwright
- **High-Dimensional Statistics with a View Toward Applications in Biology**, Peter Bühlmann, Markus Kalisch, Lukas Meier
- **Next-Generation Statistical Genetics: Modeling, Penalization, and Optimization in High-Dimensional Data**, Kenneth Lange, Jeanette C. Papp, Janet S. Sinsheimer, Eric M. Sobel
- **Breaking Bad: Two Decades of Life-Course Data Analysis in Criminology, Developmental Psychology, and Beyond**, Elena A. Erosheva, Ross L. Matsueda, Donatello Telesca
- **Event History Analysis**, Niels Keiding
- **Statistical Evaluation of Forensic DNA Profile Evidence**, Christopher D. Steele, David J. Balding
- **Using League Table Rankings in Public Policy Formation: Statistical Issues**, Harvey Goldstein
- **Statistical Ecology**, Ruth King
- **Estimating the Number of Species in Microbial Diversity Studies**, John Bunge, Amy Willis, Fiona Walsh
- **Dynamic Treatment Regimes**, Bibhas Chakraborty, Susan A. Murphy
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