Predator detection and evasion by flying insects
David D Yager

Echolocating bats detect prey using ultrasonic pulses, and many nocturnally flying insects effectively detect and evade these predators through sensitive ultrasonic hearing. Many eared insects can use the intensity of the predator-generated ultrasound and the stereotyped progression of bat echolocation pulse rate to assess risk level. Effective responses can vary from gentle turns away from the threat (low risk) to sudden random flight and dives (highest risk). Recent research with eared moths shows that males will balance immediate bat predation risk against reproductive opportunity as judged by the strength and quality of conspecific pheromones present. Ultrasound exposure may, in fact, bias such decisions for up to 24 hours through plasticity in the CNS olfactory system. However, brain processing of ultrasonic stimuli to yield adaptive prey behaviors remains largely unstudied, so possible mechanisms are not known.

Address
Department of Psychology and Neuroscience and Cognitive Science Program, University of Maryland, College Park, MD 20742, United States

Corresponding author: Yager, David D (ddyager@umd.edu)

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Introduction
Many insects have tympanate ears that provide them with sensitive hearing at frequencies from a few kHz to over 100 kHz depending on the species. There have been at least 18 independent evolutions of pressure-sensitive hearing yielding ears of diverse shapes, sizes, and locations on the body [1,2]. Having two ears is the norm, but most praying mantises have just one and a pneumotid grasshopper has six pairs. Insects including crickets, grasshoppers, water bugs, cicadas, and some butterflies and moths use hearing as part of intraspecific communication systems [3]. A few — most notably parasitoid flies that target singing male crickets as hosts — use hearing to find prey [4]. Finally, many insects, additionally or exclusively, use their hearing to detect and evade predators, which, for flying nocturnal insects means echolocating bats. This is the well-known story of the coevolutionary ‘arms race’ between hearing insects and bats [5], although ‘diffuse coevolution’ might better describe a system with many species of prey and predator [6]. An emerging theme in this story is behavioral and neural economics — balancing the benefits of hunting and evasion against the costs in terms of energetics and, especially for the prey, of the disruption of other important behaviors such as finding a mate. Thus, the assessment of risk and of potential benefit along with the mechanisms of decision-making have become key research topics.

The detection system
Insect auditory systems are based on the standard pressure-detector design with a vibrating membrane (tympanum) backed by an internal airspace for increased sensitivity, and a transducing mechanism with as few as one or as many as several thousand receptors (chordotonal sensilla) depending on the species (reviewed in [7]; Figure 1). Sensitivity and tuning are determined primarily in the periphery through bioacoustic characteristics of the tympanum and associated structures (studied most recently using scanning laser vibrometry; for instance, [8]) and/or properties of the receptor structures that are not yet fully understood. The range of frequencies to which a particular species is most sensitive is matched to the dominant echolocation frequencies used by the sympatric bat assemblage, typically 20–60 kHz, but sometimes extending beyond 100 kHz (Figure 2) [5]. Predator-generated sounds outside that range will be relatively inaudible to the insect. Sensitivity determines the response time available to the prey. The echolocation cries of aerial hawking bats are typically intense (>120 dB SPL at 10 cm), so insects with minimum thresholds of 40–60 dB SPL can detect oncoming bat at >20 m compared to detection distance for bats of <12 m [9,10]. Considering typical insect and bat flight speeds, this translates to an available response time of >1 s, more than adequate for predator recognition and evasion [11].

Neural processing
Remarkably little is known about the ‘higher’ CNS processing that controls ultrasound-based defensive behaviors. Past studies have focused primarily on the afferent side and the activities of a few key interneurons such as AN2 of crickets, 501-T3 of mantises, the T-cell of tettigoniiids, and IN533 and IN714 of locusts [12]. However, the head is necessary for evasive behavior, at least in pyraval mantis, mantises, tettigoniiids, tiger beetles, and crickets. In the last of these, there are at least 20 ultrasound-sensitive brain neurons, seven of which have descending axons [13]. Cephalic ultrasound processing is brief (<20 ms; [13,14]). Its role could simply be conditionally permissive, for
example, if the flight CPG is active AND ultrasound is present to initiate evasive behavior controlled by thoracic circuitry. Alternatively, the cephalic ganglia may play a more ‘hands on’ role. The data are not yet available to distinguish among these and other possibilities.

Ultrasound-triggered evasion and defense

Most responses to ultrasonic pulses involve a change in flight path, and many eared insects have a repertoire of defensive strategies depending on context and level of risk [15*] (Figure 3). The strategies of: 1) getting out of
Different insect auditory frequency ranges in different ecological contexts. Physiological tuning curves for three praying mantis species. *Sphodromantis aures* is a large mantis with best sensitivity in the dominant frequency range used by many insectivorous bats with FM echolocation calls (left green bar). The *Miomantis* species are small/medium sized animals sympatric with bat species using much higher frequency CF and CF-FM echolocation calls (right green bar). Their tuning curves suggest that they could respond effectively to bats that use both low and high frequency calls (Yager, unpublished data).

The way before detection, and/or 2) disrupting the bat’s attack through some combination of startle and sudden, random flight path changes serve hearing insects well. In the few cases for which it has been measured in free-flight bat-insect encounters (noctuid moths, green lacewings, and praying mantises), sound-triggered evasion confers a 40–50% survival advantage over nonhearing conspecifics [16]. It is worth noting that dietary analysis for some bat species shows a high percentage of hearing insects (for instance [17]). However, without accompanying data about relative abundance of size-appropriate hearing and nonhearing prey or direct observations of capture success rates, it is not possible to infer the effectiveness of auditory defenses.

Tiger moths (Arctiidae) implement the unusual strategy of producing intense ultrasonic clicks when they hear pulsed ultrasound [18]. Faced with an oncoming bat, clicking arctiids do not alter their flight path and yet survive because the bats break off their attack [19]. The long-standing question of how the clicking works to deter bats has been resolved through an elegant series of experiments using naïve bats and several species of arctiids having different ecologies. In fact, all of the traditional rival hypotheses — advertising distastefulness, startling the bat, and jamming the echolocation system — are correct. Which one dominates depends on the moth species and its ecology and on the past experience of the bat [15*]. Flying tiger beetles, some of which are distasteful, also click in response to ultrasound, opening the possibility of intricate Müllerian and Batesian mimicry complexes among sympatric beetles and moths [20,21].

Bats foster false negatives in the insect defensive system. First, echolocation frequencies and intensities outside the insect’s detection capabilities could achieve this. Bats that take prey from a substrate (gleaners) often use very low intensity pulses that their insect prey cannot hear as shown by neural recordings [22,23]. An aerial insectivore, *Barbastella barbastella*, uses echolocation frequencies of 30–40 kHz, but at amplitudes 20–40 dB lower than other aerial insectivores. It is highly successful at capturing eared moths [10*]. Echolocation calls at frequencies outside an insect’s hearing range could also work [24–26]. Several studies have found a high proportion of eared moths in the diets of bat species using frequencies >70 kHz like the Old World rhinolophid and hipposiderid bats. This is above the most sensitive hearing range for most insects, although some moths and praying mantises have extended their ranges to >100 kHz (Figure 2). Secondly, at least some bats project their calls in a relatively narrow cone of sound that they sweep across the immediate environment [27]. This strategy greatly reduces their detectability. Even an insect with sensitive hearing could be surprised by the bat and have insufficient time to respond effectively.

Ultrasound serves multiple functions for bats (hunting, obstacle avoidance, intraspecific interactions; [28]), which
can make it difficult to attribute the primary driving force for particular echolocation call design features exclusively to countering evasion capabilities of prey [6,29]. Nonetheless, an ecological approach studying bat assemblages in southern Africa suggests that dealing with prey defenses is a significant contributor to bat community structure via common echolocation parameters [30]. Although less common, some insects use their ultrasonic hearing for a second function, reproductive signaling. The functions are decoded by context [31], signal characteristics [32,33] and even an analog to vertebrate ‘auditory stream segregation’ [34].

**Economics of auditory predator detection and evasion**
Predator evasion is costly. It requires the maintenance of a sensory detection and processing system, it requires energy expenditure, and it diverts effort and time from other crucial activities like eating and mating.

The costs for insects to maintain an auditory system for bat evasion have been addressed indirectly in many studies comparing auditory structure and function in morphs of a single species [35] and in closely related taxa differing in their history of exposure to bats. Some taxa of moths that have become diurnal have lost high-frequency hearing [36]. The few species of butterflies that have become nocturnal have evolved ultrasonic hearing [37]. Fullard and colleagues [38] combined genetic data with neurophysiological and behavioral results among multiple geographic populations of a single cricket species, *Teleogryllus oceanicus*, living under a range of bat predation pressures. Populations with no history of predation showed both reduction of defensive behavior and reduction in the activity of the interneuron neuron

An example of ultrasound-triggered evasive responses. (a) Ultrasound elicits a complex, multi-component behavior in the praying mantis *Parasphendale agrionina* that starts 45–85 ms after stimulation. (b) The change in flight path starts 150–250 ms after stimulation and ranges from simple turns and dives to looping power dives. The direction of the response is random relative to the bat position. (c) The types and strength of the mantis’s response varies with distance to the source (normally a bat). Data are from mantis free-flight experiments using a stationary sound source producing 40 kHz pulses at 60 pulses/s.

a, b, c: Modified from [41].
(AN2) necessary and sufficient to elicit it. In many species of praying mantis, males fly at night and have sensitive ultrasonic hearing, but the females are flightless with reduced or absent ears [39]. Although there are some counterexamples, the general picture is that the benefit of ultrasonic hearing is very high, but the cost is must be significant as well.

Because the bat auditory system is used for other purposes as well [28], the costs of echolocation specifically for hunting are primarily energetic. This can work to the prey’s advantage. For example, a mantis executing an evasive power dive from >5 m above the ground, a common flight altitude in the field, could rarely escape a bat in a prolonged chase because of the latter’s greater flight speed and adaptive targeting strategies [40]. Yet bats often break off the chase before capture [41], presumably because an extended pursuit can be costly in time, energy, and in the risk of collision with vegetation or the ground. To survive, the mantis does not have to be impossible to catch, only too expensive.

Auditory risk assessment can reduce cost for insects by minimizing false positives and by allowing the level of defensive response to be tailored to the threat. A simple version of risk assessment based on the intensity of ultrasound is well documented in moths, praying mantises, crickets, tachinid flies, and tettigoniids. Low intensity ultrasonic pulses (a distant bat) trigger low intensity behaviors, often deviations of the flight path to move away from the threat, that do not seriously interrupt the ongoing behavior. In the same animals, high intensity ultrasound triggers a ‘last ditch’ response including rapid erratic flight, steep dives, or complete flight cessation (dropping). Recently, Ratcliffe and colleagues [42] have suggested an intensity-based two-threshold mechanism in moths with low versus high intensity behavior determined by combined spike number of the A1 and the higher threshold A2 receptors. Some insects make a more nuanced risk assessment taking advantage of the stereotyped changes in echolocation pulse rate as a capture attempt progresses (Figure 4). For instance, arctiid moths can distinguish between early and late attack echolocation call patterns based on rate alone [43]. Both arctiid and pyralid moths alter their behavior (clicking rate and pheromone signaling, respectively) depending on predation risk, defined as a combination of intensity and pulse pattern of ultrasonic stimuli [43,44]. If the same threat parameters elicit spike repetition rates above a threshold level of 180/s in the cricket auditory interneuron Int-1 (=AN2) the animal initiates a evasive turn [45]. In praying mantises (Figure 4), the initiation of the full power dive corresponds to an echolocation pulse rate of 50–55 pps, which typically occurs at the transition from approach to terminal phase of the attack, 250–350 ms before potential capture [46,47]. Hartbauer and colleagues [48] have demonstrated a novel thoracic neuronal mechanism in a katydid that allows bat threat assessment based on repetition rate even in the face of intense ultrasonic background noise.

Figure 4

Basis for risk assessment during bat attacks. Simultaneous recordings of bat echolocation pulses (lower trace) and a mantis ultrasound-sensitive ascending interneuron (501-T3) during a free-flight bat attack. Contact is the time of capture with no evasion. The stereotyped pattern of bat pulses progresses from ca. 20 pps during early approach phase (early attack) through 55 pps when 501-T3 stops tracking the pulses to the terminal buzz with >100 pps. The mantis’ evasive dive begins at 200–300 ms before contact when the echolocation pulse rate is 50–60 pps. The interneuron may be involved in triggering the dive. Modified from [46].
Increasing evidence, especially from eared moths, shows that insects can use auditory risk assessment in a cost/benefit ‘decision’ balancing predator evasion against a reproductive opportunity. Male moths flying toward a pheromone source (a female in the wild or an artificial source in a wind tunnel) respond less vigorously or less often to ultrasonic pulses than controls without the pheromone. Svensson and colleagues [49] showed that not only the presence but the quality of the pheromone matters in determining the reduction of ultrasound-triggered evasive dives by flying males. Skals et al. [50] were able to titrate the intensity of ultrasound against the concentration of pheromone to determine production of defensive behavior. In fact, it can be a dual system because some pyralid moth females regulate pheromone production based on level of bat predation risk [44]. In a recent field study [51] pheromone trap catch rates of a nocuid moth were not affected by ultrasound broadcast continuously over a crop field. This could imply cost/benefit favoring immediate mating, but could also indicate habituation to the constant ultrasound. For ultrasound-producing tettigonids and lekking pyralid moth males, determining the balance is even more complex because they are surrounded by other calling conspecifics [34,52]. The interaction of reproductive and evasive demands is taken to an ironic extreme by male corn borer moths. They emit ultrasonic clicks at intensities sufficient to elicit defensive behavior (immobility) in receptive walking females, which increases the male’s copulation success [53,54]. Svensson et al. [55] noted that disruption of pheromone tracking by ultrasound could considerably outlast the stimulus, and some males failed to resume tracking at all. This suggests that in addition to an immediate mechanism based in rapid neural processing, ultrasound can induce longer term plasticity in the nervous system. Using naïve male nocuid moths, Anton and colleagues [56] found that a single 10-min exposure to bat-like ultrasound or to nonpulsed ultrasound induced changes in sensitivity to pheromone of neurons in the primary olfactory processing area of the brain measured 24 hours postexposure. However, only the bat-like ultrasound caused changes in a walking assay of pheromone tracking behavior the next day. The implication is that the exposure to ‘bats’ created a bias affecting later decisions between following a pheromone plume and a defensive response, thus shifting the titration point toward reproduction.

Conclusions
We continue to uncover intricacies and adaptations in the special predator–prey relationship between eared insects and echolocating bats. Emerging lines of research combine bioacoustic, neural, behavioral, and ecological strands and show that the relationship is far more complicated than just capture or escape. We are seeing risk assessment and cost–benefit analyses and beginning to glimpse some of their neural underpinnings. In particular, the results of cross-modal studies linking olfactory and hearing point us toward lines of research into the least studied aspects of hearing in insects — processing and plasticity in the brain control systems for bat evasive behaviors.

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References and recommended reading
Papers of particular interest, published within the period of review, have been highlighted as:

- of special interest
- of outstanding interest


54. One of a series of three papers showing much broader use of ultrasound in moth intraspecific communication than previously thought. This is the first report of male moths mimicking bats to elicit defensive behavior in conspecific females.


This study provides the first neural evidence of brain plasticity induced by ultrasound that could bias cost-benefit decisions at a much later time.