ULTRASOUND ACOUSTIC STARTLE RESPONSE IN SCARAB BEETLES

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Summary

We discovered an auditory sense in a night-flying scarab beetle, *Euetheola humilis*, the first scarab to be shown to hear airborne sounds. In the field, beetles were captured beneath speakers broadcasting ultrasound that simulated bat echolocation pulses. Apparently, the beetles took evasive action from a potential bat predator and flew into the traps. Using another behavioral assay in laboratory studies, the beetles were sensitive to frequencies ranging from 20 to 70 kHz at levels between 60 and 70 dB SPL. One component of the behavioral response, a head roll, was graded with stimulus intensity, and the number of potentials in electromyographic recordings from muscles involved in the roll increased as stimulus intensity increased. The response latency was about 40 ms at threshold, decreasing to about 30 ms at 20 dB above threshold. The beetle's short response latency is ideally suited for predator avoidance behavior and the frequency tuning of the response suggests that it could function in evasion from insectivorous bats. The beetle's acoustic sensitivity is remarkably similar to that of other night-flying insects showing ultrasound-induced startle and it should provide these scarab beetles with a similar advance warning of predation risk.

Key words: Scarabaeidae, *Euetheola humilis*, hearing, acoustic startle response, ultrasound avoidance.

Introduction

Since their appearance more than 50 million years ago, echolocating bats have probably been the most significant predatory force affecting night-flying insects (Roeder, 1967). As part of their predatory behavior, bats emit high-intensity ultrasonic pulses and use echoes to locate and track flying prey. Any night-flying insect is a potential prey, and there must be strong selection on insect sensory systems to detect foraging bats. The biosonar emitted by a hunting bat can provide a prey insect with an auditory cue about predation risk.

An acoustic startle response in insects and its relationship to bat predation was first described for moths by Roeder and Treat (1957) and was later popularized in Roeder's (1967) classic book. Since the first reports of moth audition, a considerable research effort has examined the neuroethology of the acoustic startle response in insects. Insect ears are extremely diverse (Yack and Fullard, 1993), and it is clear that predator–prey interactions between bats and insects have had a considerable impact on the evolution of insect auditory systems (Hoy, 1992).

Ultrasonic avoidance has been observed in five insect orders. For example, Miller (1970, 1971) found that green lacewings have an ultrasound-sensitive, tympanate ear at the base of their forewings. Several orthopteroid insects also respond to ultrasound. Flying field crickets (Moiseff *et al.* 1978) and katydids (Libersat and Hoy, 1991) perform negative phonotaxis when stimulated with ultrasound. Flying locusts also have a short-latency avoidance response and steer away from pulsed stimuli having carrier frequencies higher than 15 kHz (Robert, 1989). Yager and Hoy (1986) discovered that the praying mantis has an unusual ear that functions in predator detection. Flying mantids respond with evasive maneuvers that help them avoid predation by bats (Yager *et al.* 1990; Yager and May, 1990). Spangler (1988) was the first to find an ultrasound-sensitive ear located on the first abdominal segment in tiger beetles (see also Yager and Spangler, 1995). Beetles constitute a significant portion of the diets of many bats (Kunz, 1974), and many species of nocturnally active beetles must be under intense predation pressure from echolocating bats.

In this paper, we describe an ultrasound-induced startle response of a night-flying beetle, *Euetheola humilis*, the first scarab beetle to be shown to hear airborne sounds. We discovered the acoustic startle response while broadcasting ultrasound in field studies. Our subsequent laboratory studies determined the frequency tuning and response latency of the startle response.

Materials and methods

Preliminary field observations

The discovery that flying *Euetheola humilis* detect and respond to ultrasound was made during a field experiment (Farris, 1994). In that experiment, two 1.25 m diameter funnel
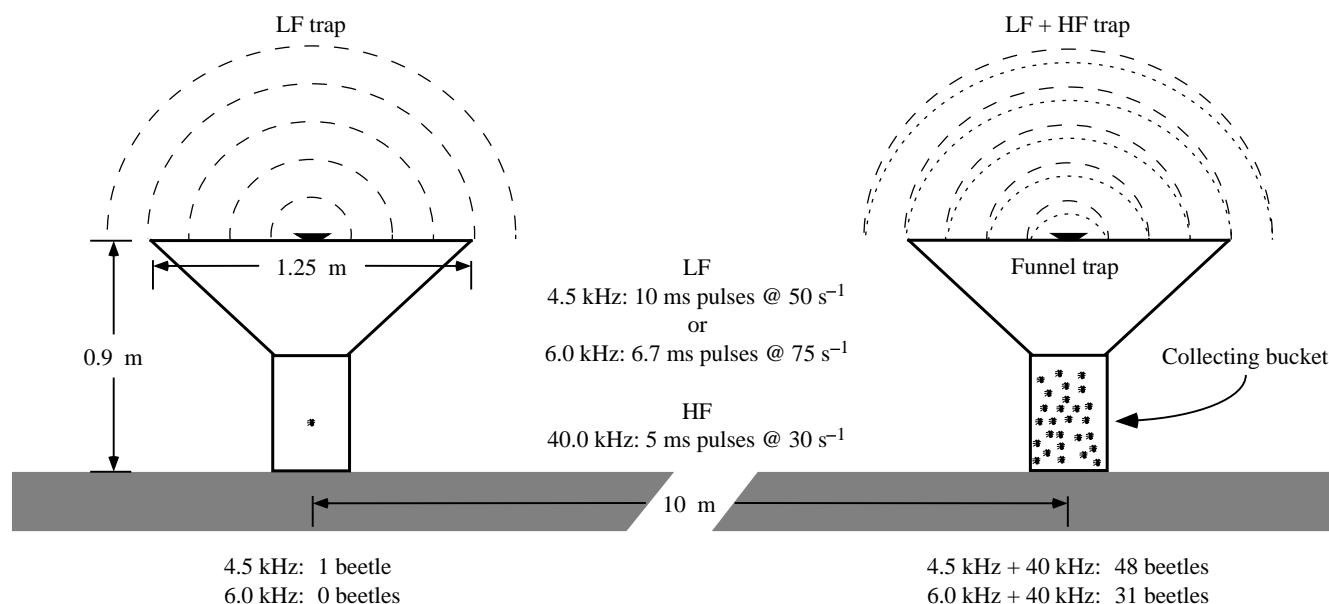
Fig. 1. Summary of the field experiment. During October 1992 and from April to September 1993, two sound traps separated by 10 m were operated in a field on the campus of the University of Mississippi, USA. The traps were 1.25 m diameter funnels that emptied into plastic collecting buckets. Speakers in the center of each funnel broadcast computer-generated stimuli. Both traps broadcast the same low-frequency signal (LF), either a 4.5 kHz carrier modulated at 50 pulses s^{-1} or a 6.0 kHz carrier modulated at 75 pulses s^{-1} (50 % duty cycle). The output level of one trap was 6 dB higher than that of the other; 105 *versus* 99 dB SPL. A high-frequency (HF) ultrasonic stimulus (5 ms pulses of 40 kHz at 30 pulses s^{-1}) was also broadcast from the high-intensity trap. During the experiments, 79 beetles were caught in the trap broadcasting ultrasound (LF+HF), while only one beetle was caught in the trap without ultrasound (LF). The ratios of beetles caught in LF+HF:LF traps were 48:1 for the 4.5 kHz LF treatment and 31:0 for the 6.0 kHz LF treatment.

traps were placed 10 m apart in a large field on the campus of the University of Mississippi, USA (Fig. 1). In the center of each funnel trap, a Motorola piezoelectric speaker continuously broadcast either a 4.5 kHz carrier modulated at 50 pulses s^{-1} (50 % duty cycle, with 2.0 ms raised-cosine ramps) or a 6.0 kHz carrier modulated at 75 pulses s^{-1} (50 % duty cycle, with 1.3 ms ramps). The two traps differed in the playback intensity of the 4.5 kHz (or 6.0 kHz) signals. The high-intensity trap broadcast at a sound pressure level (SPL) of 105 dB (re 20 μPa at 15 cm), whereas the low-intensity trap was set to 99 dB SPL. From the high-intensity trap, we simultaneously broadcast an ultrasonic stimulus composed of 5 ms pulses of a 40 kHz carrier at a rate of 30 pulses s^{-1}. The intensity of the ultrasound was varied over several nights from 95 to 115 dB SPL at 15 cm. The traps captured flying insects responding to the sounds in collecting buckets below the funnels (Fig. 1). Over 29 nights during the course of the experiments, 79 beetles were collected in the trap broadcasting pulsed ultrasound (31 for 6.0 kHz treatments, 48 for 4.5 kHz treatments), whereas only one beetle was collected in the trap without ultrasound (Fig. 1). The results indicated that these night-flying beetles detected and responded to ultrasound, but they did not distinguish whether the response was negative or positive (see below). We carried out the following laboratory studies to determine the frequency-sensitivity and latency of the response in these scarab beetles.

Animals

All beetles were collected at the National Center for Physical Acoustics on the campus of the University of Mississippi, USA. After shipment to Cornell University, we housed 10–30 beetles at room temperature (20–24 °C) in 18 cm×15 cm×9 cm plastic boxes containing moistened paper towels. Apple slices were supplied as food twice weekly. This housing proved adequate for maintaining beetles; most beetles survived more than 6 months and mating was observed on several occasions.

Stimulus generation

We generated 5 ms duration pulsed sinusoids (5–80 kHz) using a Tektronix FG501 function generator and a PG505 pulse generator. A 1 ms linear ramp was applied to the onset and the offset of all pulses using a custom-built pulse shaper. The output of the shaper was amplified using a Harman/Kardon HK 6150 integrating amplifier and the stimuli were broadcast from an ESS AMT-1 tweeter, located 30 cm from the insect preparation. Stimulus level was adjusted using a TDT PA-4 programmable attenuator. Sound pressure level at the preparation was calibrated using a Bruel and Kjaer (B&K) model 4138 microphone (90 ° angle of incidence) at the location of the beetle's head (insect removed). The microphone was connected to a B&K model 2209 sound level meter (fast, linear weighting) or to a model 5935 microphone power supply and a Nicolet spectrum analyzer. The calibration systems were

standardized with a B&K model 4220 pistonphone calibrator. For frequencies below 30 kHz calibration levels never differed by more than 1 dB (typically 0.5 dB) for frequencies between 30 and 60 kHz calibration levels never differed by more than 2.5 dB (typically 1.5 dB) and for frequencies above 70 kHz calibration levels never differed by more than 3.5 dB (typically 3.0 dB). We used linear weighting for measuring sound pressure levels (SPL) and we report these levels in decibels referenced to 20 μPa.

Behavioral tuning curve

Our studies concentrated on one component of the beetle's behavioral response elicited by an ultrasonic stimulus, a head roll. This rotation of the head around the longitudinal axis of the body is performed during both walking and flying startle responses. We tethered beetles using wax with a low melting temperature and suspended them in a 130 cm×70 cm×60 cm foam-lined Faraday cage that reduced acoustic reflections and electrical interference. We measured the behavioral tuning of the head roll by presenting tethered (non-flying) beetles with 300–500 ms trains of 5 ms pulses at a rate of 50 pulses s^{-1}. For different carrier frequencies, we determined the minimum sound pressure level (to the nearest 1 dB) required to elicit a noticeable rotation of the head in three out of five presentations. We monitored the beetle's behavior through a stereomicroscope. For each beetle, the presentation order of stimulus frequency was randomized.

Latency measurements

Electromyographic recordings were made from muscles responsible for the head roll. We recorded electrical potentials from muscle M7 [M. dorsoventralis primus, Larsen (1966)], which originates on the anterior part of the pronotum and inserts on the cervical sclerite. Contraction of M7 causes the head to be extended slightly forwards and to rotate upwards on the side of the contracted muscle. A 20 μm stainless-steel electrode was pushed through a small puncture in the beetle's pronotum and inserted into the muscle near its origin. The output of the electrode was amplified using a model 1700 AM Systems differential amplifier filtered between 300 and 1000 Hz. The electromyograms (EMGs) were amplified by 60 dB before being recorded on one channel of a Vetter model 400 PCM recorder. The electrical stimulus was recorded simultaneously on a second channel of the recorder. The indifferent electrode was placed in the prothorax and served as a ground. For some beetles, we recorded simultaneously from M7 on each side.

Because the behavioral audiograms of the beetles had their lowest thresholds at 45 kHz, we used 5 ms pulses of 45 kHz sinusoids having 1 ms linear ramps at the beginning and end of each pulse. Five beetles were presented with five or 10 trials at different intensities above threshold, defined as the stimulus level eliciting a noticeable behavioral response in at least 60 % of the presentations. We measured response latency and counted the number of spikes during the first 250 ms of the stimulus for each presentation where a positive response was

noted. For any individual, we included only those responses where the head rolled in the same direction. Afterwards, each beetle was fixed in alcohol and electrode placement was confirmed through dissection.

Results

Behavioral tuning curve

The threshold tuning curve of the head roll behavioral response was broad, and beetles were sensitive to frequencies between 15 and 80 kHz (Fig. 2). Average thresholds were between 60 and 70 dB SPL for frequencies ranging from 20 to 70 kHz. The lowest average threshold was 56 dB SPL at 45 kHz. Nine out of 11 beetles showed no response to the 5 kHz stimulus at the maximum level of 101 dB (Fig. 2). Both sexes responded in the same way to pulsed ultrasound.

EMG recordings

The muscle potentials we recorded from M7 correlated with behavioral observations of the head roll elicited by ultrasound (Fig. 3A). When simultaneously recording from M7 on both sides, EMG activity was always greatest on the side on which the head was rotated upwards. The behavioral response was graded, as was the EMG activity, in that the number of muscle potentials increased with stimulus intensity (Fig. 3B). All individuals showed approximately the same increase in spike number from an average of 3–5 spikes near threshold to 10–15 spikes at 20 dB above threshold (Fig. 3B). The recordings are multi-unit, and the increase in the number of spikes with intensity probably represents recruitment at higher intensities. Response latency was short, 30–60 ms, and decreased with
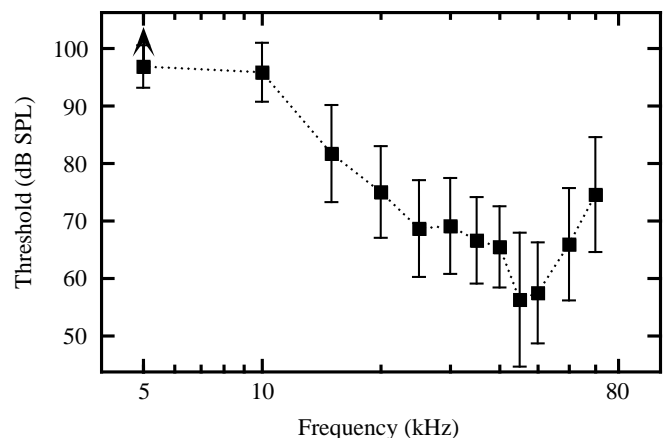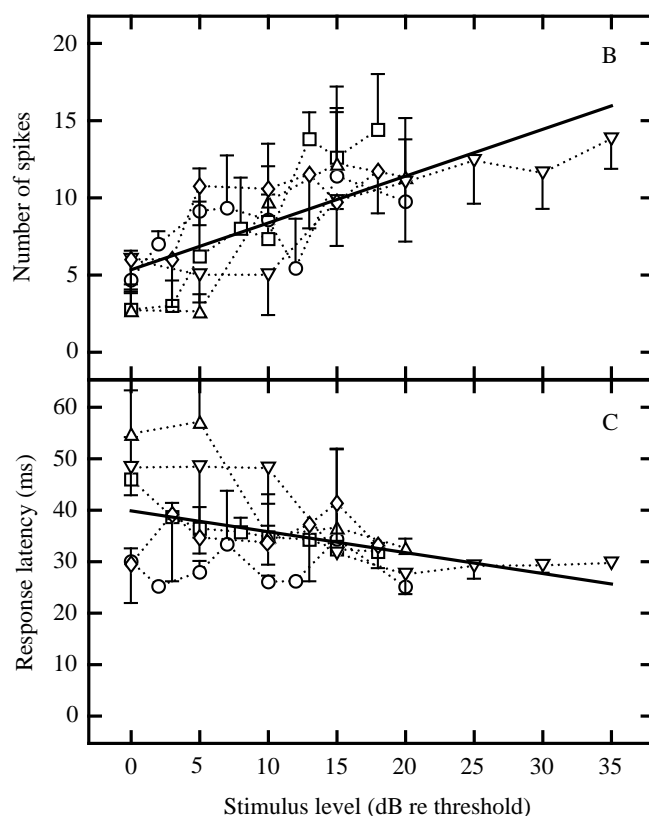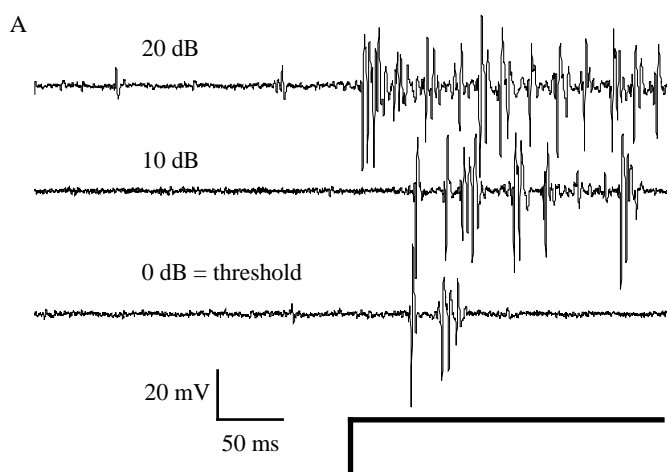

Fig. 2. Threshold tuning curve for the head roll behavioral component of the acoustic startle response of the scarab beetle *Euetheola humilis*. Stimuli were 300–500 ms trains of 5 ms duration pulses each with 1 ms linear ramps at the onset and offset. Pulses were presented at a repetition rate of 50 pulses s^{-1}. Thresholds are mean (±1 S.D.) sound pressure level (dB re 20 μPa) required to elicit a noticeable rotation of the head in three out of five stimulus presentations (N=11 individuals). The arrow indicates that nine out of 11 beetles showed no response to the 5 kHz stimulus presented at the maximum level of 101 dB.

A

Fig. 3. (A) Electromyographic recordings from muscle M7 (Larsen, 1966) responsible for the head roll behavior in *Euetheola humilis*. Stimuli were 300–500 ms trains of 5 ms pulses of a 45 kHz carrier frequency presented at 50 pulses s^{-1}. EMG records are 250 ms before and after the stimulus onset (thick line at the bottom of figure) for one animal at three intensity levels relative to threshold, 0 dB. Note the decrease in response latency and the increase in the number of muscle potentials with increasing intensity above threshold. Scale bars apply to all three traces. (B,C) Effect of stimulus intensity on EMG potentials for *Euetheola humilis* (*N*=5). Each symbol represents the mean (error bars show 1 S.D.) for one individual at several intensities relative to that individual's threshold. Means are based on 3–10 responses at each level. Lines are linear fits to averaged data for all individuals. The mean number of EMG spikes increased with increased stimulus intensity (B). The mean response latency decreased at higher stimulus intensities (C).

Discussion

We have shown that the scarab beetle *Euetheola humilis* responds to ultrasound in free flight and when tethered. In the laboratory, when two beetles attempted flight while on a tether and were stimulated with a pulse train of ultrasound resembling the echolocation signals of insectivorous bats, the beetles increased their wingbeat amplitude and frequency. At least four other nocturnally active insects respond to bat-like ultrasound by making power dives or by dropping to the ground (Roeder and Treat, 1962; Miller and Olesen, 1979; Yager *et al.* 1990; Libersat and Hoy, 1991). We believe that scarab beetles flying over the trap detected the ultrasound and were captured when they tried to avoid predation by the simulated bat. In addition, the beetles express acoustic startle responses in a context other than flight (Farris, 1994, in preparation). When stimulated with ultrasonic pulses, freely walking beetles showed a robust and stereotyped negative phonotactic response: the beetles ceased walking, they raised their legs from the substratum and they rolled their heads; sometimes they turned and walked away from the sound source.

Several characteristics of this response suggest that the acoustic startle response might function in predator avoidance, primarily from night-flying bats. First, flying beetles fell or flew towards the ground near a broadcast of pulsed ultrasound. Second, the beetles are sensitive to ultrasound in the range produced by sympatric, echolocating bats (e.g. *Eptesicus fuscus*, *Nycticeius humeralis* and *Tadarida brasiliensis*). Third, both sexes of the scarab beetles respond in an identical negative fashion. Finally, the response has a short latency that will provide an excellent early warning response for the beetle.

Frequency tuning and sensitivity

Euetheola humilis respond to frequencies ranging from 20 to 80 kHz and are sensitive to levels above 70 dB across most of this range (Fig. 2). This sensitivity should provide the beetles with enough advance warning to decrease the probability of predation (see Nolen and Hoy, 1986; Robert, 1989). The behavioral audiogram of *E. humilis* is similar to

stimulus intensity (Fig. 3C). Mean latency was 42 ms near threshold and dropped to approximately 30 ms at 20 dB above threshold (Fig. 3C). Two individuals showed very little change in latency at different presentation levels (see circles and diamonds, Fig. 3C).

During these experiments, two individuals attempted to fly while tethered. When stimulated with high-intensity ultrasound, these tethered individuals appeared to increase the amplitude and frequency of their wingbeats. Because the beetles were on a fixed tether, it was impossible to determine the effect that this behavioral change would have had on flight.

that of the praying mantis (Yager and May, 1990). The scarab beetles and the praying mantis have averaged thresholds of about 90 dB SPL at 10 kHz and a minimum threshold of 55–60 dB near 45–50 kHz. Like the mantis, the beetles showed almost no response to frequencies below 10 kHz. Our field data are consistent with this in that all but one of the beetles fell into the traps broadcasting ultrasound (Fig. 1).

E. humilis also show a negative stop response to ultrasound while walking (H. E. Farris, in preparation). Walking beetles were never attracted to an ultrasonic stimulus. Instead, they usually stopped walking, raised their legs from the substratum and rolled their heads (Farris, 1994, in preparation). H. E. Farris (in preparation) found that the probability of this stop response increased with stimulus frequency from 0.0 at 5 kHz to 1.0 at frequencies above 20 kHz. The stop response also depended on the intensity of the 40 kHz stimulus; a level of 80 dB SPL was required to elicit the stop response in more than 70 % of the animals.

Many beetles, including scarabs, are known to produce acoustic signals. As far as we can determine, there are no records of acoustic signals produced by adult *E. humilis*. However, larvae do have stridulatory organs on their mandibles and it is possible that the auditory structures in adults function in communication. It will be interesting to determine whether larvae also possess ears.

Latency

Short-latency responses are typical for escape behavior. The response latency for the *E. humilis* head roll behavior is short, in some cases less than 30 ms. These latencies are comparable to the acoustic startle responses measured using EMGs for the katydid *Neoconocephalus ensiger* (31 ms; Libersat and Hoy, 1991) and the cricket *Teleogryllus oceanicus* (25–35 ms; Nolen and Hoy, 1986). Changes in flight behavior often have a longer latency than changes in other behavioral components associated with an acoustic startle. Yager and May (1990) showed that the latency for foreleg extension (66 ms) preceded changes in forewing swing angle by approximately 30 ms and preceded steering component changes (yaw) by more than 100 ms. A decrease in response latency with increased intensity of ultrasound is characteristic of acoustic startle responses for locusts (Robert, 1989), katydids (Libersat and Hoy, 1991), crickets (Nolen and Hoy, 1986) and mantids (Yager and May, 1990). The response latency of the *E. humilis* head roll was negatively correlated with stimulus intensity and decreased by 10 ms for a 20 dB increase in stimulus level (Fig. 3C).

Opportunity for bat predation on Euetheola humilis

Euetheola humilis are night-flying insects. In the southeastern United States, large numbers of these scarabs are attracted to and land at lights at night (White, 1990). As an indication of prey availability, on one occasion we trapped 38 beetles in the 1.25 m funnel during the first 2 h after sunset, a time when many bats are actively foraging (Kunz, 1973). Seven or more species of bats occur in the southeastern United States that are potential predators of scarab beetles (Harvey,

1992), and beetles make up a significant proportion of the diets of many bats. Kunz (1974) found that 37 % of the total food items taken by *Myotis velifer* in Kansas, USA, was beetles and 16 % of the total was scarabs. Beetles may constitute 16–80 % of the prey volume consumed by some of the large bats that occur in the southeastern United States (e.g. *Eptesicus fuscus*, *Nycticeius humeralis* and *Tadarida brasiliensis*; see Freeman, 1981, and references therein). Given that *E. humilis* fly in large numbers at a time when bats are actively foraging, it is likely that these scarabs are under intense predation pressure from echolocating bats.

The relationship between size and behavioral threshold

There have now been several studies measuring the behavioral threshold of insects startled by ultrasound. Because ultrasound-induced startle responses of insects are probably involved in evading bat predation, it could be predicted that lower thresholds would provide the insects with more time to escape a bat predator. However, if there is some cost to lowering threshold, then there might be a trade-off to an insect between costs due to predation risk and benefits accrued by lowering the threshold for detecting predators. If such a trade-off exists, one would expect a negative relationship between response threshold and size (larger insects should have lower thresholds than smaller insects) for the following reasoning. The acoustic power echoed from an insect target will be directly related to its size. Larger insects can, therefore, be detected by a bat at a greater distance, and larger insects should be at greater risk from predation. We used empirical data from
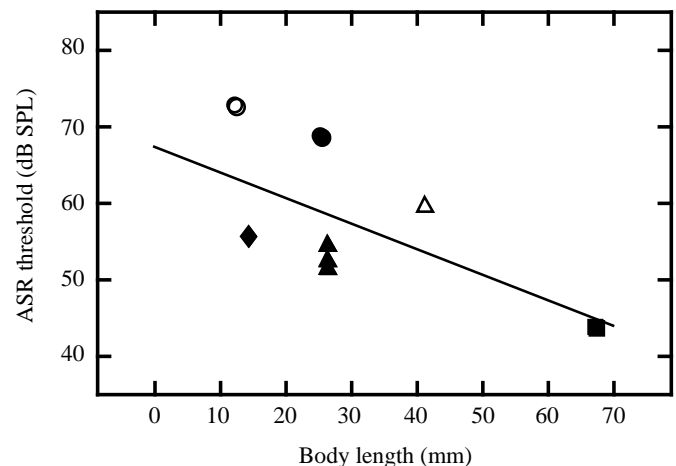

Fig. 4. Plot of the behavioral thresholds of the acoustic startle response (ASR) in a number of insect species as a function of the size of the insect (body length). The least-squares fit to the data using a linear model is shown ($T=-0.34L+67.9$, $P=0.09$, $r=0.64$), where T is the ASR threshold (in dB SPL) and L is the body length (in mm). Square, *Locusta migratoria* (Robert, 1989); open circle, *Cicindela lemniscata* (Spangler, 1988); filled circle, *Neoconocephalus ensiger* (Libersat and Hoy, 1991); filled triangles, *Teleogryllus oceanicus*, *Teleogryllus commodus*, *Gryllus bimaculatus* (Nolen and Hoy, 1986); open triangle, *Parasphendale agrionina* (Yager and May, 1990); diamond, *Euetheola humilis* (present study).

several studies to test the prediction that larger insects should have lower response thresholds. In each case, we used the minimum threshold from the behavioral audiogram (Fig. 4). The relationship is nearly significant (linear regression, $P=0.09$, $r=0.64$), and a linear model with a negative slope explains about 40 % of the variation in the data. Locusts, the largest insect for which behavioral thresholds of the acoustic startle response have been measured (Robert, 1989), have the lowest thresholds. Tiger beetles, the smallest insect in the sample, have the highest thresholds (Spangler, 1988). We excluded the data from moths that generate acoustic signals when stimulated with ultrasound because their behavioral responses may function in a different manner (to startle the predator or to jam the bat's echolocation) from those strictly involved in predator detection and avoidance. However, Morril and Fullard (1992) found that larger moths with ears (Notodontidae and Arctiidae) were less likely to fly than smaller moths with ears, as would be expected if the larger moths were under a greater risk of predation.

We have shown that, in the field under natural conditions, flying scarab beetles respond to ultrasound by flying towards the ground, they respond to stimuli in the frequency range commonly produced by sympatric bats and the response has the short latency necessary for an escape response. We are currently investigating the sensory structures used by the beetles to detect ultrasound. Our preliminary findings indicate that the scarab ear is typical of insect ears in having paired tympanal membranes covering tracheal air-sacs. However, the scarab ears appear to be quite different from those of tiger beetles (Spangler, 1988; Yager and Spangler, 1995) and, therefore, may represent an independently evolved auditory system within the Coleoptera. Two aspects of the scarab beetle's auditory system and response should be further investigated to show that the response functions in predator avoidance. First, we need to measure the sensory basis of the acoustic startle and to characterize how various parameters of bat cries are coded in the nervous system. Second, we need to show that flying beetles take evasive action upon hearing bat cries and that the evasive maneuvers result in an increased probability of escape from predation.

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