

RESEARCH ARTICLE

Sonar jamming in the field: effectiveness and behavior of a unique prey defense

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SUMMARY

Bats and insects provide a model system for integrating our understanding of predator–prey ecology, animal behavior and neurophysiology. Previous field studies of bat–insect interactions have been limited by the technological challenges involved with studying nocturnal, volant animals that use ultrasound and engage in battles that frequently last a fraction of a second. We overcame these challenges using a robust field methodology that included multiple infrared cameras calibrated for three-dimensional reconstruction of bat and moth flight trajectories and four ultrasonic microphones that provided a spatial component to audio recordings. Our objectives were to document bat–moth interactions in a natural setting and to test the effectiveness of a unique prey defense – sonar jamming. We tested the effect of sonar jamming by comparing the results of interactions between bats and Grote’s tiger moth, *Bertholdia trigona*, with their sound-producing organs either intact or ablated. Jamming was highly effective, with bats capturing more than 10 times as many silenced moths as clicking moths. Moths frequently combined their acoustic defense with two separate evasive maneuvers: flying away from the bat and diving. Diving decreased bat capture success for both clicking and silenced moths, while flying away did not. The diving showed a strong directional component, a first for insect defensive maneuvers. We discuss the timing of *B. trigona* defensive maneuvers – which differs from that of other moths – in the context of moth auditory neuroethology. Studying bat–insect interactions in their natural environment provides valuable information that complements work conducted in more controlled settings.

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INTRODUCTION

The study of bats and moths has provided fundamental biological insights in areas ranging from the neurological basis of behavior (Roeder, 1967a; Yager, 2012) to the co-evolution of predator and prey (Fullard, 1998; Goerlitz et al., 2010). It has also revealed a suite of defensive behaviors that either have not previously been known to occur in the acoustic modality (aposematism and mimicry) or, in the case of sonar jamming, are unique in the natural world (reviewed by Conner and Corcoran, 2012).

Kenneth Roeder established the paradigm for moth defensive behaviors (Roeder, 1967a). Eared moths employ one of two flight behaviors depending on the intensity, and therefore proximity, of an echolocating bat (Roeder, 1962; Roeder, 1964). Quiet echolocation calls indicate a distant bat that has not yet detected the moth; these calls elicit a controlled negative phonotactic response (‘turning away’) aimed at avoiding detection (Roeder, 1962; Roeder, 1967b; Goerlitz et al., 2010). Louder echolocation calls indicate a nearby bat in pursuit and elicit a non-directional evasive maneuver such as a dive or spiral to the ground (Roeder, 1962).

Moths of the superfamily Noctuoidea have received most attention in the study of anti-bat defenses. Most noctuoids have paired metathoracic tympana that each have only two auditory receptor neurons: A1, which is sensitive to lower intensity ultrasound, and A2, which is sensitive to higher intensity ultrasound (Fullard et al., 2003; Roeder, 1967a). A1 firing is thought to initiate negative phonotactic behavior, whereas A2 firing has long been associated with late-attack defenses such as diving (Roeder, 1974).

However, recent work disputes this hypothesis, and instead proposes that late-attack defenses are stimulated by the summation of A1 and A2 firing (Fullard et al., 2003; Ratcliffe et al., 2009).

Tiger moths (Lepidoptera: Erebidae, Arctiinae; formerly Lepidoptera: Arctiidae) (Zahiri et al., 2011) respond to attacking bats by producing ultrasonic clicks through the buckling of metathoracic tymbal organs (Fullard and Heller, 1990; Barber and Conner, 2006). Depending on whether a species is chemically defended and the amount of sound it produces, moth clicks serve as acoustic aposematic (Hristov and Conner, 2005a; Hristov and Conner, 2005b; Ratcliffe and Fullard, 2005), mimetic (Barber and Conner, 2007; Barber et al., 2009) or sonar-jamming signals (Corcoran et al., 2009; Corcoran et al., 2010; Corcoran et al., 2011; Conner and Corcoran, 2012). In some cases these defenses may be combined; for example, a small degree of sonar jamming may enhance bat learning of aposematic signals (Ratcliffe and Fullard, 2005). Sonar jamming has long existed as a hypothesis for the function of moth clicks (Fullard et al., 1979; Fullard et al., 1994), but only recently has this hypothesis been confirmed in a study pitting a tiger moth with exceptional sound-producing abilities [*Bertholdia trigona* (Grote 1879)] against big brown bats [*Eptesicus fuscus* (Palisot de Beauvois 1796)] in captivity (Corcoran et al., 2009). To disrupt echolocation, moth clicks must occur in a narrow 1–2 ms window surrounding the time echoes return to the bat from the ensonified moth (Miller, 1991). These clicks then disrupt the timing of the firing of bat auditory neurons that are involved in encoding target distance (Tougaard et al., 1998). The number of

clicks that fall within this window determines the size of ranging errors (Miller, 1991) and the likelihood of bat capture (Corcoran et al., 2011). In captivity, jammed bats narrowly miss their prey by a distance predicted by psychophysical studies (Corcoran et al., 2011). Field studies of sonar-jamming moths have not previously been attempted.

Research documenting the pursuit and escape flight of bats and insects has largely been restricted to captive animals in controlled environments (Corcoran et al., 2010; Dawson et al., 2004; Ghose et al., 2006; Ghose et al., 2009; Triplehorn et al., 2008). Although these laboratory studies have yielded many novel discoveries, the limited space of a flight room prevents the animals from exhibiting the full suite of behaviors that occur in nature. Bats in captivity alter the temporal and spectral features of echolocation calls, and also the directionality and intensity of their sonar beams (Surlykke and Moss, 2000; Surlykke et al., 2009). This may substantially alter the timing of insect defensive responses, and therefore the result of encounters.

Field studies of bats and insects suffer from their own limitations. First, the species of bat and insect being observed are frequently not known (Acharya and Fenton, 1999; Roeder, 1962; Rydell, 1992). Second, echolocation calls of bats are rarely recorded (Acharya and Fenton, 1999; Agee, 1969; Roeder, 1962; Rydell, 1992), and clicks have never been recorded from free-flying tiger moths in the field (Acharya and Fenton, 1992). Third, visual observation without video documentation is the norm (e.g. Acharya and Fenton, 1999). This is especially problematic because attack sequences typically last only a fraction of a second. Fourth, observations, whether visual or photographed, are frequently made only from a single location, making assessment of directionality of movement prone to error. And fifth, the effect of artificial lights, frequently used to attract moth and bat activity to a focal observation area (Rydell, 1992; Acharya and Fenton, 1999), has rarely been considered as a factor affecting the animals' behavior (Svensson and Rydell, 1998).

We aimed to overcome these limitations using a robust field methodology in our study of natural bat attacks on the only animal in nature known to jam the sonar of its predator (*B. trigona*). We set out to answer three questions: (1) how effective is sonar jamming compared with other moth defenses; (2) does *B. trigona* use evasive maneuvers in addition to jamming, and if so, do these behaviors aid in its survival; and (3) what are the acoustic stimuli that cause *B. trigona* to use its various defensive behaviors?

MATERIALS AND METHODS

Field location and equipment

Research was conducted in early August 2010 and late July 2011 at the Southwestern Research Station (operated by the American Museum of Natural History), 8 km southwest of Portal, Arizona, USA. Research was conducted in an open field surrounded primarily by Arizona cottonwood (*Populus fremontii*) and alligator juniper (*Juniperus deppeana*). Vegetation was a minimum of 25 m away from the observation area.

We recorded interactions using three Basler Scout cameras (model scA640-120gc; Ahrensburg, Germany) recording at 60 frames s⁻¹ at 640×480 resolution (Fig. 1). The cameras were hardware-synchronized by a custom-built external trigger box (Innovision Systems, Columbiaville, MI, USA). Video was acquired with MaxTraQ2D software (Innovision Systems) running on a desktop computer. Infrared illumination was provided by 12 Wildlife Engineering IR-Lamp6 lights (Tucson, AZ, USA), two Bosch UFLED20-8BD illuminators (Farmington Hills, MI, USA) and one Raytec Raymax 200 platinum illuminator (Ashington, UK).

Three-dimensional calibration of video recording

The cameras were calibrated for three-dimensional (3-D) reconstruction of bat and moth flight paths using the relative orientation method (Svoboda et al., 2005) as implemented in the MaxTraQ3D software (Dynamic Wand Method; Innovision Systems). For this method, two spherical infrared markers are anchored at a fixed distance from each other on a calibration object, or 'wand'. This wand is moved throughout the interaction volume, and the markers are later digitized in the software. A second calibration object with four calibration points along two perpendicular axes is used to set the origin of the 3-D space and the *x*-, *y*- and *z*-axes. We tested the accuracy of our calibration by moving the wand through the recorded volume a second time and determining the distance between the two points (which were set 146 cm apart) using the MaxTraQ3D software. Over 2500 frames, the points had a mean error of 3.8 mm, or 0.26%. Our calibration volume was ~6×6×5 m, or 180 m³.

Audio equipment

Audio was recorded using four Avisoft Bioacoustics CM16/CPMA ultrasonic microphones (Berlin, Germany) connected to an Avisoft Ultrasound Gate 416Hb recording interface. Each of the four microphones was placed on a stand 1.5 m off the ground, in a square-like arrangement around the calibration volume (Fig. 1). Audio was triggered to begin simultaneously with the video by a signal sent from the triggering box to the recording interface. Tests showed the error of synchronization between audio and video to be <1 ms. The four microphones allowed us to record the relatively quiet clicks of *B. trigona* and the directional echolocation calls of bats over a larger volume than would be possible with a single microphone. The arrangement of microphones also provided a spatial component to our audio recordings that was useful for assigning bat and moth sounds to individual animals captured in our video recordings.

Bat-moth field observations

One of the challenges of studying bats and moths in the field and capturing interactions on audio and video is finding a situation where attacks occur reliably within a predefined volume. To overcome this limitation we attracted moths to a focal area using two 15 W ultraviolet lights (Leptrops LLC, Georgetown, KY, USA) placed on 4 m poles, with the two poles placed ~5 m apart (Fig. 1). This arrangement allowed for varied movement of the moths as they flew between and around the lit areas.

The large numbers of moths around the lights attracted foraging bats. Between approximately sunset and midnight, the many moths around the lights interfered with our ability to isolate individual bat-moth interactions. As the night progressed (between 00:00 and 04:00 h), moth activity decreased, but the foraging bats remained. This is when we conducted our experiments. Individual *B. trigona* had previously been collected at blacklights within 100 m of the recording area. Moths were held individually in 30 ml plastic cups for up to 24 h prior to experimentation. Individuals held over from the previous night were fed a saturated sugar water solution. Moths were either left intact or had both tymbal organs ablated by puncturing the cuticle of the tymbal. No external bleeding was ever observed from the ablation. Clicking and silenced moth flight behavior was analyzed to assess whether the ablation procedure had an effect on moth flight (see below).

During experimentation, *B. trigona* were placed on a release platform consisting of a heating pad attached to a 1 m pole anchored in the ground. Individual moths flew from the heating pad to the observation area of their own volition, and bat attacks ensued within 1 to 3 min. Several methods were used to ensure that the moths

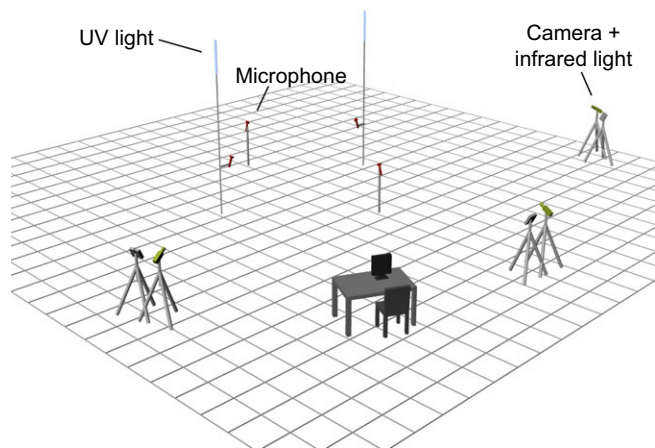


Fig. 1. Diagram of field recording setup. Two ultraviolet lights on poles were used to attract insect and bat activity to a focal observation area. Three infrared cameras with infrared lights were used to capture video, while four ultrasonic microphones recorded audio of bat–moth interactions.

being attacked were indeed *B. trigona*. In many cases an observer could track an individual moth from the release platform to an encounter with a bat. In other cases moths could be identified based on their distinctive clicks in the audio tracks. The relative timing and intensity of the clicks on the four audio channels was used to ensure that the clicks came from the moth being attacked in the video. Only attacks in which the identity of the moth could be unambiguously confirmed were used in the analysis.

Bat species identification

The species of bat in each encounter was determined using the automated acoustic species recognition algorithms (Corcoran, 2007) of Sonobat 3.0 (Arcata, CA, USA). Sonobat makes classifications by measuring numerous acoustic properties of bat echolocation calls and running them through a discriminant function analysis classifier that was created using recordings of known species. A species classification is accepted only if the discriminant probability (a measure of statistical confidence) is >0.90 . If a species cannot be determined, an individual is assigned to a species group, which consists of multiple species that make similar echolocation calls (Parsons and Jones, 2000).

Based on 19 years of mist-netting capture data, 18 insectivorous bat species are known to occur at our field site (J. Tyburec, Bat Conservation International, personal communication). Twelve of these 18 species were used in our acoustic classifier. Two species (*Lasiurus xanthinus* and *N. femorosaccus*) were excluded from our analysis because of their rarity (fewer than one bat per 387 net hours each). Four species – *Idionycteris phylottis*, *Myotis auriculus*, *M. velifer* and *Nyctinomops macrotus* – lacked a sufficient number of known recordings to be included. *Idionycteris phylottis* and *N. macrotus* produce characteristically low-frequency calls (12–17 kHz) that were not recorded during the experiments. *Myotis auriculus* and *M. velifer* both produce calls with peak frequency in the 40 kHz range (J. Szewczak, personal communication). Therefore, any calls identified to the genus *Myotis* in the 40-kHz range are reported only to the species-group level (referred to as 40 kHz *Myotis*).

Analysis of bat and moth flight trajectories

The flight trajectories of bats and moths were manually digitized using Maxtraq2D. A single point representing the ‘center of mass’

for each animal was used. The digitized values were then imported into MaxTraq3D, which generated 3-D coordinates for the bat and moth for each frame of each attack. These values were then imported into a custom MATLAB (Natick, MA, USA) program (BATracker; coded by B. Chadwell). A smoothing spline function (MATLAB spaps routine) was fit to each flight trajectory, and this function was used to estimate various flight parameters.

A 3-D plot of the bat and moth for each encounter was analyzed. The moth’s flight response was first described qualitatively, and discrete behaviors were then confirmed using quantitative metrics. Two categories of behaviors were observed: flying away and diving. Fly-aways were designated by a rapid decrease in the angular deviation between the moth’s flight vector and the bat–moth vector (β) combined with a rapid rise in tangential acceleration. Alternatively, a fly-away could also be designated by the moth rapidly increasing translational acceleration while β remained low. Diving involved a rapid vertical acceleration toward the ground. The number of attacks where bats aborted pursuit in response to moth clicks was determined using previously established criteria (Corcoran et al., 2011); these include lengthening pulse intervals and bats veering away from the moth soon (100–300 ms) after clicking began. The duration of each attack was taken as the total time when the angular deviation between the bat’s instantaneous flight vector and the vector from the bat to the moth (ϕ) was less than 45 deg.

In order to visualize moth evasive behavior with greater detail than that possible in the field, high-speed video of big brown bats attacking free-flying *B. trigona* in captivity was taken using a RedLake N3 camera (Tallahassee, FL, USA) shooting at $1000 \text{ frames s}^{-1}$. In order to restrain the moths’ flight to an area within the camera’s view, two ultraviolet LEDs were suspended 1.5 m from the ceiling of an outdoor flight cage ($6 \times 4 \times 3 \text{ m}$) and approximately 1 m from each other. This effectively replicated our outdoor recording setup, but on a much smaller scale. The moths were attracted to the area around the suspended LEDs and bats released into the flight cage attacked the freely flying moths.

Statistical analysis

Statistical analysis was conducted in SPSS version 19 (IBM, Armonk, NY, USA) and R version 2.12.1 (R Foundation for Statistical Computing, Vienna, Austria). The *G*-test was used to test for independence between categorical variables (Sokal and Rohlf, 1995). The Williams correction was applied when expected cell values in the *G*-test were less than five (Sokal and Rohlf, 1995). In such cases, the *G*-statistic is labeled ‘*G*-adjusted’. For continuous variables normality was assessed visually using normal quantile plots (Sokal and Rohlf, 1995) and quantitatively using the Shapiro–Wilk test of normality. Alpha was set at 0.05.

RESULTS

Effectiveness of the sonar-jamming defense

The presence of moth clicks had a strong effect on the result of bat–moth encounters (*G*-adjusted=56.1, d.f.=3, $P < 0.0001$; Fig. 2). Nearly all of the clicking moths avoided capture from attacking bats (supplementary material Movies 1, 2), and the few moths that were captured were released unharmed. In contrast, bats captured a large majority of the silenced moths, and ate two-thirds of those they captured (Fig. 2). In order to later compare the effectiveness of different defenses, we will use a measure we call the ‘defense ratio’, which equals the capture success when a defense is absent divided by the capture success when the defense is present. In this case the defense ratio for sonar jamming is 10.4 (71% divided by 6.8%).

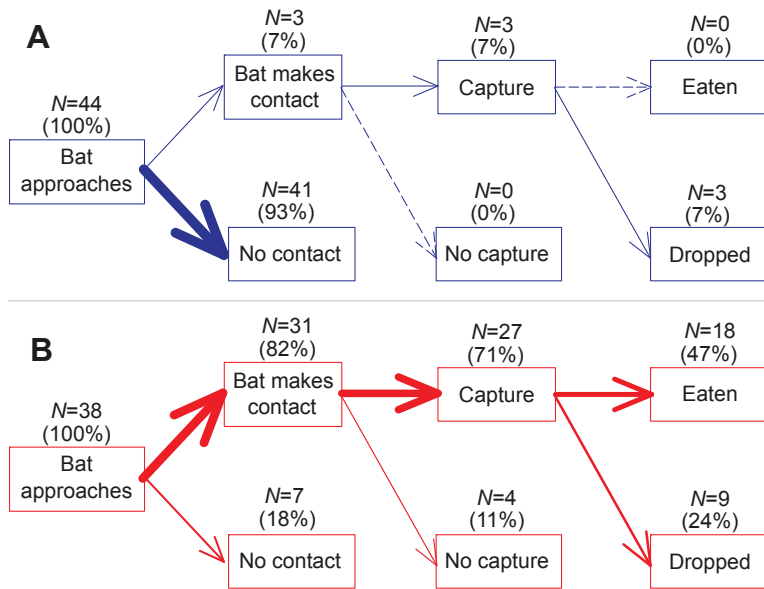


Fig. 2. Ethogram showing results of bats attacking (A) clicking and (B) silenced *Bertholdia trigona*. Line widths are proportional to the percentage of encounters that include a particular transition.

Bertholdia trigona evasive maneuvers

Moths employed two distinct evasive maneuvers: fly-aways and dives (Fig. 3). Fly-aways involved a sharp turn or acceleration away from an oncoming bat. We prefer this term over ‘turn-away’ as turning is not necessarily required if the moth accelerates away from a bat approaching from the rear. Dives involved a rapid acceleration toward the ground with vertical speed of 1.5 to 4 ms⁻¹. The resolution of our cameras did not allow us to determine visually whether these dives were passive or active. However, the rate of maximum vertical acceleration during dives (18.8±7.0 ms⁻¹) well exceeded the rate of gravitational acceleration (9.8 ms⁻¹), indicating that the dives were active. A high-resolution video of the diving behavior obtained in captivity confirms this finding (supplementary material Movie2).

Diving occurred in more than half of all bat–moth encounters, and at similar rates for both clicking and silenced moths ($G=0.279$, d.f.=1, $P=0.60$); fly-aways and no evasive maneuvering were less common (Fig. 4A). Fly-aways occurred twice as often in silenced

moths, whereas attacks where moths exhibited no evasive maneuvers were twice as common in clicking moths (Fig. 4A); however, these differences were not statistically significant (fly-aways: $G=3.09$, d.f.=1, $P=0.08$; no maneuvers: $G=1.648$, d.f.=1, $P=0.20$). Bats captured more silenced than clicking moths regardless of whether the moths were diving ($G=22.0$, d.f.=1, $P<0.0001$), flying away ($G=24.7$, d.f.=1, $P<0.0001$) or exhibiting no evasive maneuvers ($G=12.2$, d.f.=1, $P<0.001$; Fig. 4B). Both clicking (G -adjusted=4.78, d.f.=1, $P=0.03$) and silenced (G -adjusted=5.37, d.f.=1, $P=0.02$) moths that dove were caught less often than moths that either flew away or exhibited no evasive maneuver (Fig. 4B). In both the clicking ($P=0.30$) and silenced treatments ($P=0.37$), bats caught moths that flew away and moths that exhibited no evasive maneuver at similar rates (Fig. 4B).

Clicking caused bats to rapidly abort their attacks (as evidenced by increasing pulse intervals and bats veering away from the moth soon after clicking began) in 61% (27 of 44) of bat–moth encounters. This behavior was never observed in 38 attacks on silenced *B*.

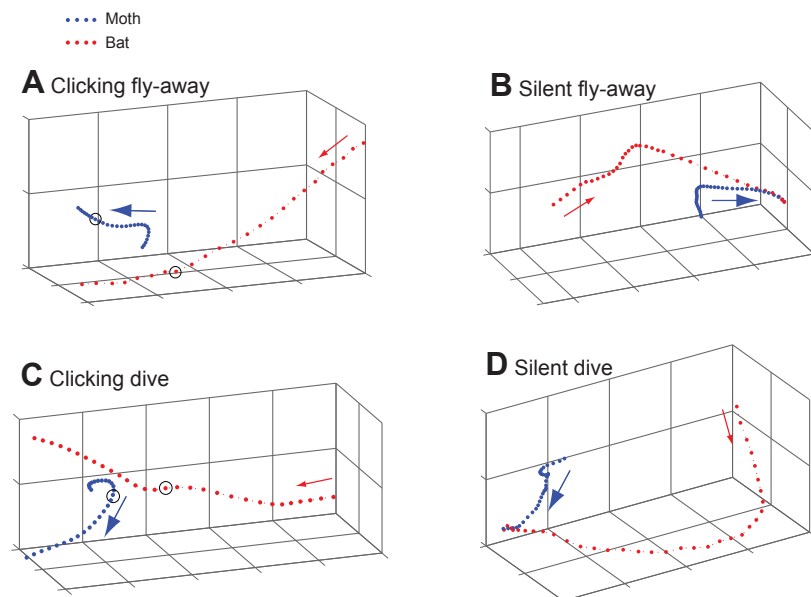


Fig. 3. Three-dimensional flight trajectories of bats (red) attacking (A,C) clicking and (B,D) silenced *Bertholdia trigona* (blue) exhibiting defensive maneuvers. Moths are seen flying away (A,B) and diving (C,D). Both interactions with silenced moths resulted in capture. Arrows show the direction of flight. In A and C, circles indicate the positions of bats and moths when the moth began clicking. Gridlines are each 1 m apart.

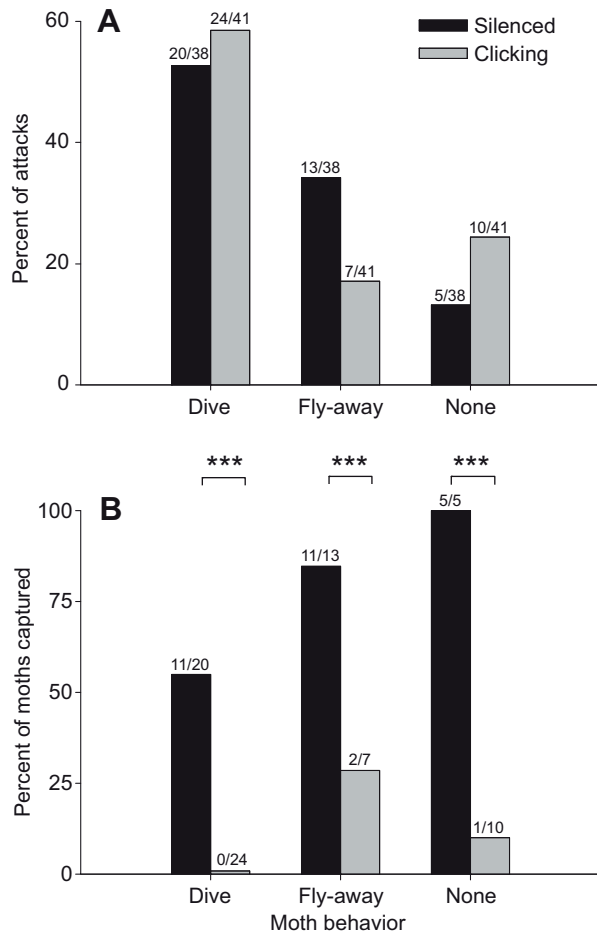


Fig. 4. (A) Percentage of bat attacks in which *Bertholdia trigona* exhibited defensive behaviors, and (B) bat capture success of moths exhibiting different combinations of behaviors. Numbers over bars show the proportion of total attacks where a behavior was exhibited (A) or capture was made (B). ***Significantly different capture success ($P < 0.001$).

trigona, a significantly different margin ($G=45.2$, d.f.=1, $P < 0.0001$). The duration of attacks on silenced moths (median 1.4 s; interquartile range 1.0–1.5 s) was twice that of attacks on clicking moths (median 0.7 s; interquartile range 0.6–1.0 s), a significant difference (Mann–Whitney U -test, $U=1012.5$, d.f.=1, $P < 0.0001$). The distance silenced moths flew during attacks (median 2.2 m; interquartile range 1.7–3.4 m) was 47% greater than that of clicking moths (median 1.5 m; interquartile range 1.1–2.2 m); this difference was statistically significant ($U=882.0$, d.f.=1, $P=0.002$), and may be an underestimate as some silenced moths were chased out of the calibrated volume during attacks. Finally, of moths that were not captured in attacks, 64% (7 of 11) of silenced moths, but only 7% (3 of 41) of clicking moths, flew to the ground, a significantly significant margin (G -adjusted=13.8, d.f.=1, $P=0.0002$).

Effect of light on moth evasive maneuvers and bat capture success

The moth's distance from a light did not affect the moth's likelihood of diving (G -adjusted=1.67, d.f.=3, $P=0.64$; Fig. 5A) or of being captured (silenced moths: G -adjusted=2.55, d.f.=3, $P=0.46$; clicking moths; G -adjusted=3.34, d.f.=3, $P=0.34$; Fig. 5B). Silenced moths within 1 m of a light appeared to be captured less often than moths

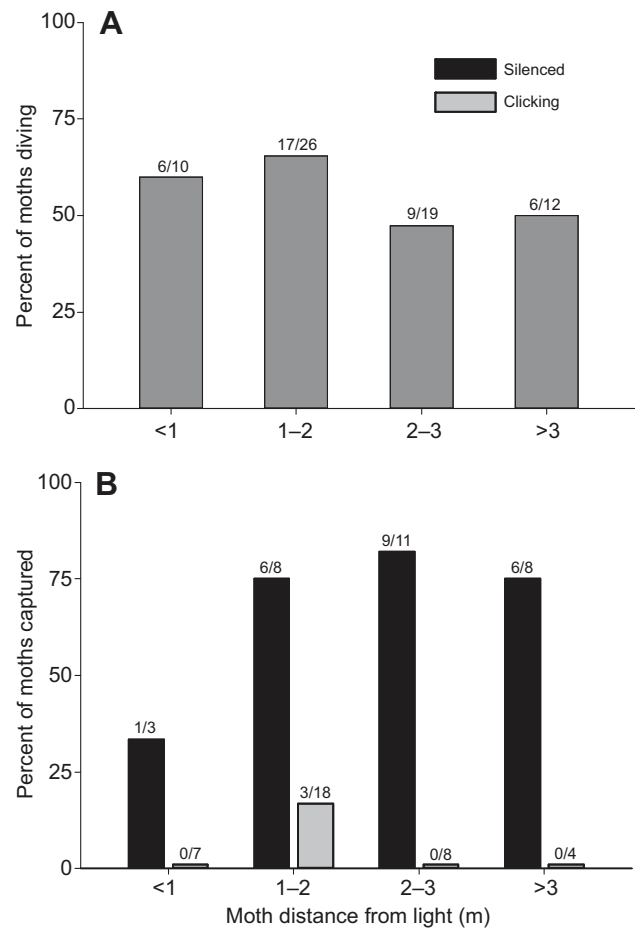


Fig. 5. Percentage of moths (A) diving and (B) captured by bats relative to moth distance from a light source. Numbers above bars indicate the proportion of attacks resulting in a dive or capture. Frequency of moth diving and bat capture success did not differ significantly with moth distance from a light (see Results for statistics).

flying farther from a light (Fig. 5B), although this may be a result of the small sample size of moths flying within 1 m of a light ($N=3$).

Timing of moth defenses

Moth clicking, diving and flying away were all initiated after the bat detected the moth and began its approach (Fig. 6). Moth defenses occurred within a similar range of bat–moth distances and bat pulse intervals. The one exception to this was that fly-aways for silenced moths occurred when the bat was particularly close (Fig. 6). This late response may not have been observed for clicking moths because bats frequently aborted their attacks earlier in the sequence, not providing the moths an opportunity to evade at such a close distance.

Directionality of moth diving

An additional analysis was conducted on the directionality of moth flight prior to and during diving (Fig. 7). Prior to dives, the horizontal component of moth flight was random with respect to the oncoming bat (Rayleigh test, $z=0.207$, $P=0.86$; Fig. 7A). However, during dives the horizontal component of the moths' flight showed a significant directional trend away from the oncoming bat ($z=4.77$, $P=0.007$; Fig. 7B). Moths flew slightly upward ($z=5.03$,

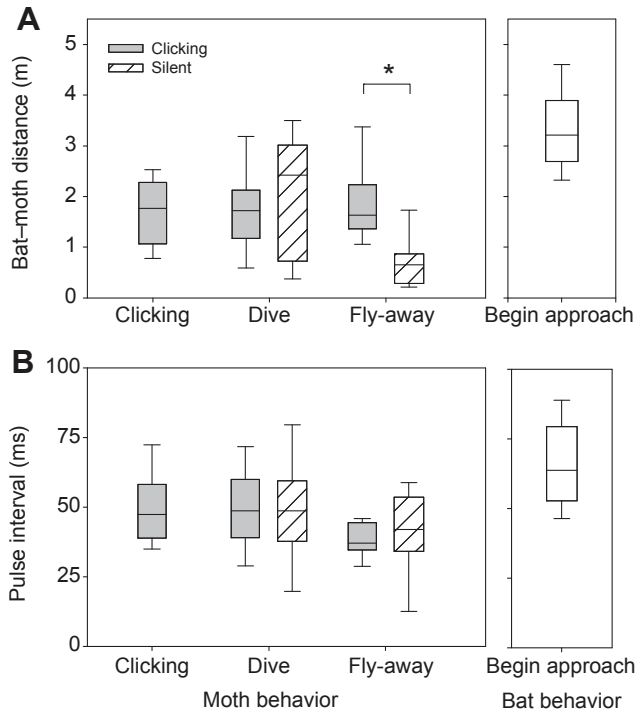


Fig. 6. Box plots of (A) bat-moth distances and (B) bat echolocation pulse intervals at the initiation of *Bertholdia trigona* defenses and bat approaching behavior. Moth defenses were initiated at a similar range of bat-moth distances and pulse intervals, with the exception of fly-aways for silenced moths. Note that all moth defenses were initiated after bats began their approach. Box plots show 5th, 25th, 50th, 75th and 95th percentiles of distributions. *Significantly different distributions ($P < 0.05$).

$P = 0.006$; Fig. 7C) prior to diving at a sharp angle away from the approaching bat ($z = 27.4.03$, $P < 0.0001$; Fig. 7D).

Bat species identification and capture success rates

Ninety percent of bats attacking clicking *B. trigona* and 79% of bats attacking silenced *B. trigona* were classified in the 40 kHz *Myotis* group (Table 1). Three other bat species were identified in one to nine attacks. Although sample sizes for species other than 40 kHz *Myotis* were small, capture success for both clicking and silenced moths was fairly consistent between species (0–8.3% for clicking moths, 70–100% for silenced moths; Table 1).

DISCUSSION

Sonar jamming is highly effective against a range of bat species

Bats captured over 10 times more silenced moths than clicking moths, indicating that sonar jamming is a highly effective defense (Fig. 2). Sonar jamming's defense ratio (10.4) compares favorably with that of insect evasive flight maneuvers (2.1–4.9; Fig. 8). Aposematic clicking in *Hypoprepia fucosa* has a defense ratio of 9.6. Clicking therefore appears to be more effective than evasive flight maneuvers regardless of whether it is used to warn bats of toxicity or jam their sonar. *Bertholdia trigona* clicking also appears to increase survival after capture, as none of the three clicking *B. trigona* that were captured were eaten, whereas two-thirds of silenced *B. trigona* that were captured were eaten (Fig. 2). Clicking itself may therefore have an aversive effect on bats, either because of the high intensity of the clicks at close range or possibly through

tactile stimulation (Masters, 1979). This effect could be important against gleaning bats, whose relatively quiet echolocation calls do not elicit a clicking response prior to capture (Ratcliffe and Fullard, 2005).

Can *B. trigona* clicks jam the sonar of a variety of bat species? As the moth's tymbal buckles, it produces a burst of broadband microclicks covering frequencies of 25–89 kHz and with peaks of energy that sweep from 85 kHz down to 50 kHz and back again (Corcoran et al., 2009). It is not clear what role, if any, these acoustic properties play in enhancing the jamming function. The most common predators in this study were *Myotis* bats that use peak echolocation frequencies between 40 and 45 kHz (Table 1). The most frequent prey of these bats (which at our field site could include *M. volans*, *M. auriculatus*, *M. ciliolabrum* and *M. velifer*) are lepidopterans (Fenton and Bell, 1979; Fitch et al., 1981; Warner, 1985) and they only overcame the jamming defense in 8.3% of attacks. *Myotis californicus* (which uses echolocation above 50 kHz) (Gannon et al., 2001) and *Lasiurus blossevillei* (a highly agile flyer) (Norberg and Rayner, 1987) were also each defeated by sonar jamming in two of two encounters in the present study (Table 1). Previous laboratory work found that sonar jamming is also effective against *E. fuscus* (Corcoran et al., 2009; Corcoran et al., 2011), whose peak echolocation frequency is near 30 kHz. Therefore, the current data suggest that sonar jamming by *B. trigona* is effective against bats that use a range of echolocation frequencies (30–50 kHz) and flight behaviors. This is impressive considering that moths do not dynamically alter their jamming defense to the bat predator, as moths are tone deaf (Roeder, 1967a) and largely lack the ability to alter the frequency and temporal composition of sounds they produce (Barber and Conner, 2006; Corcoran et al., 2010; Fullard, 1992).

Bertholdia trigona combine sonar jamming with evasive maneuvering

To our knowledge, this study represents the first 3-D analysis of moth flight patterns in response to attacking bats in the natural environment. We found that *B. trigona* use the same evasive maneuvers employed by other moths: (1) flying away and (2) diving. Diving behavior in silenced *B. trigona* had a defense ratio of 1.8, a value only slightly less than that of other insects' diving behaviors (Fig. 8). Diving and clicking proved the most effective defense, with none of the 24 moths exhibiting both behaviors being captured (Fig. 4B). Diving may therefore serve two potential functions in *B. trigona*: (1) enhancing the effectiveness of sonar jamming and (2) serving as a 'backup' defense in cases where their tymbal organs are not functioning. In captivity, *B. trigona* did not click in 22% of attacks (Corcoran et al., 2009). Because these moths were tethered it is not possible to know whether they would have exhibited diving behavior, but if they had they would have increased their chances of survival. These results demonstrate that evasive flight maneuvers in *B. trigona* are not vestigial traits, such as the auditory systems of certain noctuid moths that inhabit remote, bat-free islands (Fullard et al., 2004; Fullard et al., 2007a), or have diurnal activity periods (Fullard et al., 1997).

Jamming occurs by interfering with the bat's neural processing of prey echoes (Tougaard et al., 1998). This diminishes the bat's precision in determining target distance and prevents it from coordinating its capture maneuver (Miller, 1991; Corcoran et al., 2011). By simultaneously diving and clicking, *B. trigona* presents a dual challenge to the attacking bat, which must simultaneously overcome its errors in echo processing and adjust its flight path to intercept the diving moth (Ghose et al., 2006). This proves to be

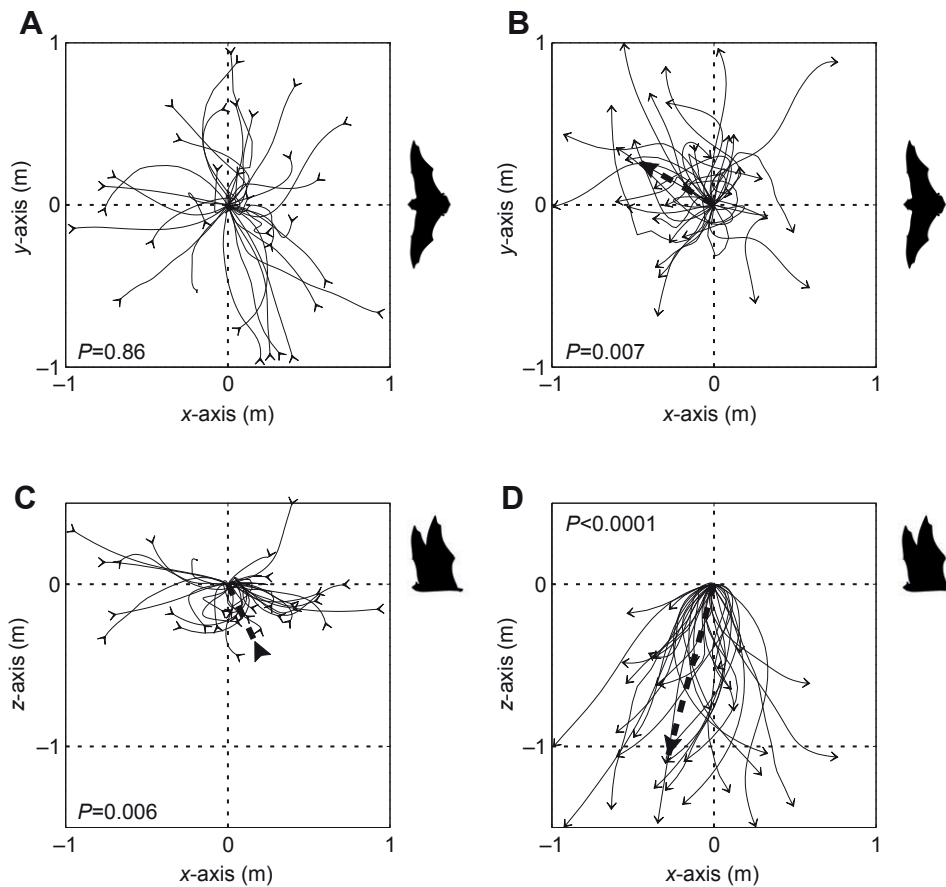


Fig. 7. Directionality of *Bertholdia trigona* diving behavior in response to bat attack: (A) overhead before dive, (B) overhead of dive, (C) profile before dive and (D) profile of dive. Prior to diving (A,C), moths flew randomly with respect to the direction of the oncoming bat. However, the diving behavior (B,D) had a strong directional bias away from the oncoming bat. Moths often flew slightly upwards (C) prior to diving (D). Arrowheads mark the starting (A,C) and ending (B,D) positions of moth flight. Moth flight trajectories were rotated and translated such that the bat approaches from the right (black bat symbols) and the initiation of the moth dive is at the plot's origin. Dashed black arrows indicate the median distance and direction of moth flight when the direction of flight was not randomly distributed. *P*-values indicate results of the Rayleigh test.

too great a challenge, and the bat is unable to capture the moth. Based on visual observations, some researchers have reported that tiger moths use diving or spiraling evasive maneuvers in addition to clicking (Agee, 1969; Roeder, 1974; Fullard et al., 1979); others have reported that evasive maneuvers were absent during bat attacks (Dunning, 1968; Acharya and Fenton, 1992). It is not clear why some tiger moths use evasive flight maneuvers while others do not.

A number of differences in flight were observed between silenced and clicking moths. Silenced moths appeared to more frequently exhibit fly-aways (and they did so with bats at a closer distance) and less frequently exhibit no evasive maneuvers compared with clicking moths. Attacks on silenced moths lasted longer and silenced moths flew longer distances evading capture. Silenced moths also flew to the ground nearly 10 times as often as clicking moths. It is unlikely that these differences are due to the ablation procedure, as manipulated animals would not be expected to exhibit evasive maneuvers more frequently than unaltered animals. Instead, they are likely a result of bats behaving differently when attacking

clicking and silenced moths. Bats frequently (61%) aborted attacks on clicking moths after hearing clicks, but never aborted attacks on silenced moths prior to making a capture attempt.

These findings are the first evidence that moths dynamically alter their evasive flight pattern depending on the behavior of an attacking bat. They also demonstrate that moths are capable of processing bat echolocation call information in the very late stages of attack. This contradicts a hypothesis made by Fullard and colleagues (Fullard et al., 2003), which stated that moth tympanic receptors are not capable of encoding bat calls in the final stage of attack, as these calls have reduced intensity, duration and time intervals between calls. Finally, these results demonstrate that combining jamming and diving provides maximum defensive advantage with minimum costs in time spent avoiding predators.

Timing and directionality of *B. trigona* evasive maneuvers

Bertholdia trigona exhibited the same two categories of defenses – flying away and diving – as was first described in the pioneering

Table 1. Capture success of clicking and silenced *Bertholdia trigona* by bat species

Bat species	Clicking <i>B. trigona</i>			Silenced <i>B. trigona</i>		
	<i>N</i>	No. caught	% Caught	<i>N</i>	No. caught	% Caught
40 kHz <i>Myotis</i> ^a	36	3	8.3	30	21	70.0
<i>M. californicus</i>	2	0	0.0	7	5	71.4
<i>Lasiurus blossevilli</i>	2	0	0.0	–	–	–
<i>M. auriculus</i>	–	–	–	1	1	100.0
Total	40	3	7.5	38	27	71.1

^aIncludes *M. auriculus*, *M. ciliolabrum*, *M. velifer* and *M. volans*.

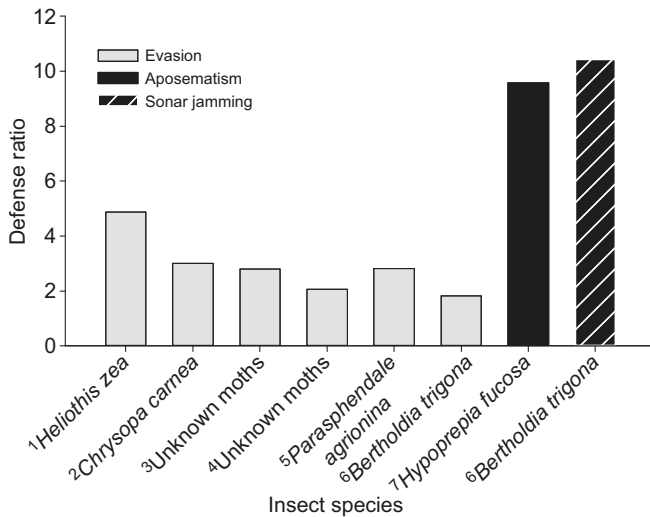


Fig. 8. Cross-species comparison of the effectiveness of insect defenses at preventing capture by bats. The defense ratio equals the percent of insects captured when the defense is absent divided by the percent captured when the defense is present, and is used to control for varying environmental conditions between studies. Gray bars indicate insect evasive flight maneuvers, and black bars indicate moth clicking defenses of acoustic aposematism and sonar jamming. All insects are in the order Lepidoptera, except *Chrysopa carnea* (Neuroptera) and *Parasphendale agrionina* (Mantodea). Data were taken from: ¹Agee (Agee, 1969); ²Miller and Oleson (Miller and Oleson, 1979); ³Rydell (Rydell, 1992); ⁴Acharya and Fenton (Acharya and Fenton, 1999); ⁵Tribblehorn (Tribblehorn et al., 2008); ⁶present study; and ⁷Acharya and Fenton (Acharya and Fenton, 1992).

experiments of Kenneth Roeder (Roeder, 1962; Roeder, 1967a). However, two key differences exist between our results and the paradigm established by Roeder some 50 years ago. First, Roeder found that moths exhibited negative phonotaxis in response to relatively quiet ultrasound pulses that simulated distant bats (Roeder, 1962). In contrast, *B. trigona* exhibited negative phonotaxis after bats had already begun their approach and locked their intense sonar beams on the moth (Ghose and Moss, 2003). This finding supports prior evidence that clicking tiger moths do not alter their flight activity in response to search-phase echolocation, whereas silent noctuid moths do (Ratcliffe et al., 2008). This finding is also supported by evidence that some tiger moths have reduced sensitivity of the A1 auditory neuron (Fullard et al., 2003), the sensory cell implicated in the moth negative phonotactic response. However, we cannot exclude the possibility that the lights used in our experiment prevent the moths from exhibiting negative phonotactic behavior earlier in attacks, or that the moths have habituated to the relatively low-danger threat of quiet bat search calls (Ratcliffe et al., 2011).

Second, Roeder argued that the intense calls of bats late in an attack saturate the moth's tympanic receptors and eliminate its ability to determine the directionality of the sound (Roeder, 1967b). Diving behavior elicited late in the attack should therefore be non-directional, as Roeder observed from unidentified moths using stroboscopic flash photography (Roeder, 1962). In contrast, *B. trigona* diving has a clear directional component, indicating that their tympanic receptors are not saturated by approach-phase echolocation. When a bat echolocation attack sequence was broadcast to preparations of five species of noctuid moths while recording the auditory receptor cells, the dogbane tiger moth (*Cycnia tenera*) demonstrated the highest thresholds for both the A1 and A2 receptors. Tiger moths may be less susceptible to

saturation of auditory receptor cells, and directional diving responses may be limited to this group. Alternatively, directional diving responses may be more common than has previously been documented. The only other insect that has been systematically tested for this behavior is the praying mantis *Parasphendale agrionina*, whose single functional ear precludes directional behavioral responses (Ghose et al., 2009).

***Bertholdia trigona* begins clicking earlier in attacks in the field compared with in captivity**

Data on the defensive responses of *B. trigona* in the field (present study) and in captivity (Corcoran et al., 2009; Corcoran et al., 2011) allow us to compare the stimuli that provoke clicking under the two environmental conditions. Clicking by tiger moths is triggered primarily by the intensity and pulse intervals (the inverse of pulse rate) of echolocation calls (Fullard et al., 2007b). In the field, bats triggered *B. trigona* to click in response to longer pulse intervals (47 versus 25 ms) and at a greater distance (170 versus 76 cm). This cannot be explained by the studies using different bat species as the larger-bodied *E. fuscus* used in captivity should have echolocated more loudly and elicited clicking earlier than the smaller *Myotis* used in the field (Holderied and von Helversen, 2003). Bats in the field echolocate approximately 20 dB louder than bats in captivity (Surlykke and Kalko, 2008; Holderied and von Helversen, 2003; Waters and Jones, 1995), because they are typically further from background objects (Surlykke and Kalko, 2008). However, the intensity of bat calls used during attack has not been measured in the field (Fullard et al., 2007b). Studies that broadcast calls of attacking bats while recording moth auditory nerve cell and behavioral responses have employed echolocation attack sequences recorded in captivity (Fullard et al., 1994; Fullard et al., 2003; Barber and Conner, 2006; Corcoran et al., 2010). Results of such studies may therefore differ from what occurs in open habitats in nature. Further work is needed to characterize the acoustic field moths are exposed to when being attacked by bats under natural conditions, and to apply this information to our understanding of moth neuroethology.

Moth proximity to ultraviolet lights does not inhibit defenses or affect capture success

Man-made lights provide a useful tool in the study of bat–insect interactions by drawing the animal participants into a focal observation area (Acharya and Fenton, 1992; Acharya and Fenton, 1999; Roeder, 1962; Rydell, 1992). These lights, however, undoubtedly affect the behavior of moths, and likely bats, under study. Geometrid winter moths flying within 4 m of a 125 W mercury vapor lamp exhibit fewer evasive flight maneuvers in response to pulsed ultrasound compared with moths flying in a dark woodland (Svenssen and Rydell, 1998). Studies of bats attacking insects around lights have typically not quantified the effects of lights on moth behavior and on the outcome of interactions (Acharya and Fenton, 1992; Acharya and Fenton, 1999; Rydell, 1992). In the present study (where 15 W ultraviolet lights were used) we found no such effect, as the percentages of moths diving and being captured were independent of moth distance to ultraviolet lights (Fig. 5). The one difference that appeared to stand out (albeit not statistically significant and with the small sample size of $N=3$) was a decrease in capture success of silenced moths within 1 m of lights. This result is the opposite of what would be expected if lights reduced the effectiveness of moth defenses. Instead, this more likely demonstrates the difficulty aerial hawking bats have when trying to capture prey close to background objects (Siemers and Schnitzler,

2004). We conclude that the use of low-wattage ultraviolet lights appears to be a valid method for attracting naturally behaving bats and moths for study. This finding also demonstrates that the insect species and the type of light may be crucial for understanding the environmental impacts of light pollution. There may be effects of lights on moth and bat behavior that we cannot observe, and further work is required to confirm these findings using conditions that do not require light.

Ecological benefits of sonar jamming

Sonar jamming provides many benefits to a nocturnal, volant insect. It is more effective than evasive maneuvering, and as effective as acoustic aposematism (Fig. 8), without the costs of sequestering toxins and having a limited number of available host plants (Nishida, 2002). In environments where toxic, clicking moths are present (including our field site), palatable, jamming moths may gain additional protection through acoustic Batesian mimicry (Barber and Conner, 2007; Barber et al., 2009), whereby bats misperceive the clicks as aposematic messages. However, the large differences in the acoustic signals of aposematic moths and jamming moths (Corcoran et al., 2010; Conner and Corcoran, 2012) would facilitate predators' ability to differentiate the two (Barber et al., 2009). Given that jamming moths far outnumber aposematic moths at our field site (A.J.C. and W.E.C., unpublished), Batesian mimicry would be predicted to be ineffective (Harper and Pfennig, 2007; Pfennig et al., 2001). *Bertholdia trigona* clicks may sometimes also serve as a legitimate aposematic signal, as 33% of silenced *B. trigona* that were captured were rejected (Fig. 2B), a number similar to what was found in palatability assays conducted using big brown bats in captivity (Corcoran et al., 2009). Therefore, jamming would be expected to be the predominant defense in approximately two-thirds of attacks.

Bertholdia trigona clicks frequently turned away bat predators without a chase, thus preventing lengthy and energetically expensive escape sequences. Clicking moths also less frequently flew to the ground during bat attacks, avoiding encounters with other predators (Guignon and Fullard, 2004) and time lost foraging and looking for mates. Having the security of a clicking defense may also allow moths to continue their normal activities when echolocating bats are present but not yet attacking (Ratcliffe et al., 2008). The question thus arises, why is jamming not more common if it confers so many advantages over other defenses? One possible answer is that jamming defenses are more common than we realize, especially in the tropics, where tiger moth diversity is high and most species remain unstudied (Corcoran et al., 2010). Selection on anti-bat defenses may be stronger in the tropics, where bat species richness is high (Stevens and Willig, 2002). Costs of clicking for jamming and other purposes – be they energetic, developmental or other – have not been investigated.

CONCLUSIONS

We have demonstrated a reliable and robust method for studying 3-D flight trajectories and acoustic behavior of bats attacking insects in their natural environment. This approach allows researchers to determine the effectiveness of defense and attack strategies, document and describe flight behaviors, and measure the effect of the environment (such as proximity to lights or background vegetation) on bat–insect interactions. The primary limitation of the present method is the use of lights for confining moth activity within a pre-defined observation area. Further field studies are needed to complement the existing literature on bat–insect interactions, which consists largely of dietary analyses of fecal pellets (Clare et al., 2009;

Whitaker et al., 2009), bioacoustic and physiological studies of sound production in bats and sound reception in moths (e.g. Goerlitz et al., 2010), and laboratory experiments using captive animals (Corcoran et al., 2009; Ghose et al., 2006; Ghose et al., 2009). Field studies also provide an opportunity to generate and test hypotheses in neuroethology, such as the relationship between insect hearing sensitivity and initiation of defensive behaviors.

The present study focused on a few species of bat and one species of moth with a unique defensive ability. We found that sonar jamming is a highly effective defense against a variety of bat predators, particularly when used in conjunction with diving behaviors. Future work will highlight the similarities and differences in behaviors of different predator and prey species. When combined with our understanding of insect auditory systems, we will finally understand the connections between physiology and behavior that Kenneth Roeder began to unravel decades ago.

LIST OF SYMBOLS AND ABBREVIATIONS

3-D	three-dimensional
β	angular difference between the bat–moth vector and the moth flight vector
ϕ	angular difference between the bat–moth vector and the bat flight vector

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