

Free-flight encounters between praying mantids (*Parasphendale agrionina*) and bats (*Eptesicus fuscus*)

J. D. Triplehorn^{1,*}, K. Ghose^{1,2}, K. Bohn¹, C. F. Moss^{1,2,3} and D. D. Yager^{1,2}

¹Department of Psychology, ²Neuroscience and Cognitive Science Program and ³Institute for Systems Research, University of Maryland, College Park, MD 20742, USA

*Author for correspondence at present address: Department of Biological Sciences, University of Missouri-Columbia, Columbia, MO 65211, USA (e-mail: triplehornj@missouri.edu)

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SUMMARY

Through staged free-flight encounters between echolocating bats and praying mantids, we examined the effectiveness of two potential predator-evasion behaviors mediated by different sensory modalities: (1) power dive responses triggered by bat echolocation detected by the mantis ultrasound-sensitive auditory system, and (2) 'last-ditch' maneuvers triggered by bat-generated wind detected by the mantis cercal system. Hearing mantids escaped more often than deafened mantids (76% vs 34%, respectively; hearing conveyed 42% advantage). Hearing mantis escape rates decreased when bat attack sequences contained very rapid increases in pulse repetition rates (escape rates <40% for transition slopes >16 p.p.s. 10 ms⁻¹; escape rates >60% for transition slopes <16 p.p.s. 10 ms⁻¹). This suggests that echolocation attack sequences containing very rapid transitions (>16 p.p.s. 10 ms⁻¹) could circumvent mantis/insect auditory defenses. However, echolocation attack sequences containing such transitions occurred in only 15% of the trials. Since mantis ultrasound-mediated responses are not 100% effective, cercal-mediated evasive behaviors triggered by bat-generated wind could be beneficial as a backup/secondary system. Although deafened mantids with functioning cerci did not escape more often than deafened mantids with deactivated cerci (35% vs 32%, respectively), bats dropped mantids with functioning cerci twice as frequently as mantids with deactivated cerci. This latter result was not statistically reliable due to small sample sizes, since this study was not designed to fully evaluate this result. It is an interesting observation that warrants further investigation, however, especially since these dropped mantids always survived the encounter.

Key words: escape, hearing, insect, echolocation, predator–prey.

INTRODUCTION

Insects flying at night expose themselves to potential predation by aerial foraging echolocating insectivorous bats. These bats emit ultrasonic vocalizations and listen for returning echoes from objects in their environment to navigate as well as to detect, track and capture insect prey in the dark (Kick and Simmons, 1984; Schnitzler and Kalko, 2001). However, not all insects are defenseless against attacking bats as some insects possess ultrasound-sensitive auditory systems and perform ultrasound-triggered behaviors while flying (Hoy and Robert, 1996; Miller and Surlykke, 2001). To date, ultrasound-sensitive auditory systems and in-flight evasive behaviors triggered by ultrasonic stimuli have been identified and characterized in several insects that fly at night. These insects include species within the Lepidoptera, including several moth species as well as some butterflies (Rydell et al., 1997; Yack and Fullard, 2000; Göpfert et al., 2002; Rydell et al., 2003), the Orthoptera [locusts (Robert, 1989), crickets (Moiseff et al., 1978), katydids (Libersat and Hoy, 1991; Schulze and Schul, 2001)], the Dictyoptera [praying mantids (Yager and Hoy, 1989; Yager and May, 1990; Yager et al., 1990)], the Coleoptera [tiger beetles (Yager and Spangler, 1997), scarab beetles (Forrest et al., 1995)] and the Neuroptera [green lacewings (Miller, 1971; Miller and Olesen, 1979)]. Since bat predation has been suggested to be one of the major selective forces driving auditory evolution in insects, along with intraspecific

communication and parasitism (Hoy and Robert, 1996; Conner, 1999), the coincidence of an ultrasound-sensitive auditory system and ultrasound-triggered in-flight evasive behaviors in any given nocturnal flying insect indicates that the system evolved as a defense against bat predation.

Although the conclusion that insects have evolved ultrasound hearing to avoid bat predation is widely accepted, determining the actual advantage conveyed by this auditory function is very difficult and has been attempted in only a few cases. These include noctuid moths (Roeder and Treat, 1962), arctiid moths (Acharya and Fenton, 1992; Dunning et al., 1992) and green lacewings (Miller and Olesen, 1979). These studies found that ultrasound-sensitivity and corresponding evasive maneuvers provided a 40–60% advantage over deafened individuals that did not perform evasive maneuvers.

This leads to an interesting question: what factors contribute to the success or failure of evasive responses? Insects may be able to assess the degree of danger based on the stereotyped pattern of echolocation calls during attacks. As aerial foraging bats detect, approach and attempt to capture insect prey, they increase the rate of their emissions from a low rate [10–15 pulses s⁻¹ (p.p.s.)] to very high rates (>100 p.p.s.). Triplehorn and Yager (Triplehorn and Yager, 2005) hypothesized that gradual transitions from low to high rates provide more time for the mantis to respond to the bat and escape, while rapid transitions may allow a bat to get closer to the

mantis before it can respond, providing less time for the mantis to perform an effective escape behavior.

Based on these previous findings, insects could benefit from having a 'backup' system mediated by another sensory modality to trigger 'last chance' escape responses. Wind generated by attacking bats has been proposed as a possible stimulus for mediating such 'last chance' responses (Baronetsky and Møhl, 1987; Ganihar et al., 1994). Many insects possess a wind-sensitive cercal system capable of detecting the air currents generated by an approaching bat. However, there is some question whether an insect would have enough time after initially detecting the wind generated by an approaching bat to perform an effective evasive response [around 75 ms for mantids (Triplehorn and Yager, 2006)].

The praying mantis *Parasphendale agrionina* possesses both an ultrasound-sensitive auditory system (Yager and Hoy, 1987; Yager and Hoy, 1989; Yager, 1999) and a wind-sensitive cercal system (Triplehorn and Yager, 1999; Triplehorn, 2003). *P. agrionina*'s auditory system, located ventrally between the metathoracic legs, consists of two tympana within the midline chamber that function as a single ear. The ear is broadly tuned to ultrasonic frequencies, with greatest sensitivity (59–61 dB SPL) between 25–50 kHz. In *P. agrionina*, ultrasound triggers a multicomponent response (Yager and May, 1990) that produces a rapid power dive in free flight [172 ms latency for first change in flight path and 242 ms latency for first indication of power dive (Yager et al., 1990)]. Although the power dive can have a directional component, directionality is independent of an attacking bat's approach, since all behavioral and physiological tests indicate that the mantis ear is nondirectional (Yager and Hoy, 1989; Yager et al., 1990). The cercal system consists of the cerci (two posterior appendages) that contain approximately 100 wind-sensitive hairs each (Triplehorn, 1997). The afferents project to at least six ascending wind-sensitive interneurons (Triplehorn and Yager, 1999; Triplehorn, 2003). Stimulation of the cercal system does not evoke terrestrial escape responses, but could be involved in aerial evasive responses (Triplehorn and Yager, 1999; Triplehorn, 2003).

The current study stages free-flight encounters between *P. agrionina* and big brown bats *Eptesicus fuscus*. Here we test the efficiency of ultrasound-mediated evasive power dive responses of *P. agrionina* initiated as the bat pursues the mantis and examine whether the transition rate of the bat's echolocation emission pattern during an attack influences the mantid's probability of surviving. We also test the effectiveness of potential wind-mediated escape responses as a secondary/backup 'last ditch' response.

MATERIALS AND METHODS

Animals

This study used male *Parasphendale agrionina* [Mantidae: Miomantinae: Miomantini (Ehrmann and Roy, 2002)] raised in our colony, maintained at 25–30°C and 30–50% relative humidity with a 13 h day length. Mantids were housed individually as adults and fed flies twice a week. Testing occurred 7–21 days after their final molt to adult. Big brown bats *Eptesicus fuscus* L. were collected locally in the surrounding Maryland suburbs. Bats were housed individually in cages and fed daily on a diet of mantids (*P. agrionina*, *Creobroter pictipennis* or *Miomantis abyssinica*), crickets (*Acheta domestica*) and mealworms (*Tenebrio monitor*). Bats flew 5 days a week for 30–60 min and were fed in the flight room on those days. Otherwise, they were fed in their cages. Bats were weighed and examined on days that they flew.

Experiments were conducted between May and October across several years (1999, 2000 and 2002) using new, freshly captured

bats from the field each year. After each season, the bats were retired from the experiment. They remained in the laboratory with other bats in a cage large enough for flight and provided with food *ad libitum*. Bats were examined once a week for continued good health.

Training

At least two bats newly brought in from the field were trained and accepted for experiments each summer using the following procedure prior to data collection. First, new bats were acclimated to the flight room by allowing them to fly for at least 30 min. It typically took 2 or 3 days for the bat to fly smoothly within the flight room. Bats that did not fly continuously for several minutes after 2 or 3 days were excluded from the experiment. After acclimation, we released individual deafened mantids (*P. agrionina*, *Miomantis natalica* or *Creobroter pictipennis*) not only to determine whether the bat would pursue free-flying mantids within the flight room, but also to examine the bats' proficiency for capturing, handling and consuming the mantids. Bats that did not pursue or efficiently capture and consume mantids during the screening process were excluded after a week. Since the bats screened had been freshly caught in the field and should already be proficient aerial foragers, we avoided specifically training the bats to capture free-flying insects. The screening process ensured that these abilities remained intact, without impairment, within the flight room. However, bats were trained to capture hanging mealworm targets. This was useful for keeping bats motivated during the experimental trials as well as for feeding the bats on non-data collection days when the bats flew in the flight room. The bats that captured free-flying mantids in the flight room required very little training to capture readily hanging targets.

Eleven bats participated in the experiment. Three of the bats accounted for 70.5% of the data trials, another four for 24.9% of the trials, and the remaining four for 4.6% of the trials.

Free-flight room

All experiments were conducted in a carpeted, acoustically lined (Sonex I, Illbruck, Minneapolis, MN, USA) flight room (6.4×7.3×2.5 m, Fig. 1) at the University of Maryland, College Park. We kept the visible light at the lowest levels possible that still allowed the observers to view the encounters. Lighting conditions were the same for all trials. Although the flight room is smaller than some natural foraging sites used by *E. fuscus*, the room is large enough for the bats to maneuver vertically and horizontally and allowed 2–3 m distance between the bat and the mantis before the bat attacked its prey. Although the room has more clutter than an open space around a pond, *E. fuscus* does forage near vegetation (Simmons et al., 2001). Previous studies of tethered insect capture within this same flight room have shown that the echolocating bat's pursuit behavior in the laboratory closely resembles that observed in the field (Surlykke and Moss, 2000).

To determine the distance between the bat and the mantis in selected trials, two synchronized high-speed video recorders (Kodak MotionCorders) recorded the encounters at 240 frames s⁻¹. In addition to the low visible light levels, long wavelength lighting was also used and the cameras were adjusted to increase their sensitivity to red/infrared light. A 25-point calibration frame (2.2×1.9×1.6 m; Peak Performance Technologies, Centennial, CO, USA) placed within the room was filmed in both camera views. Since the most relevant portions of the pursuit and capture/escape sequences occurred away from the release point, the calibration frame was placed off-center, favoring the half of the

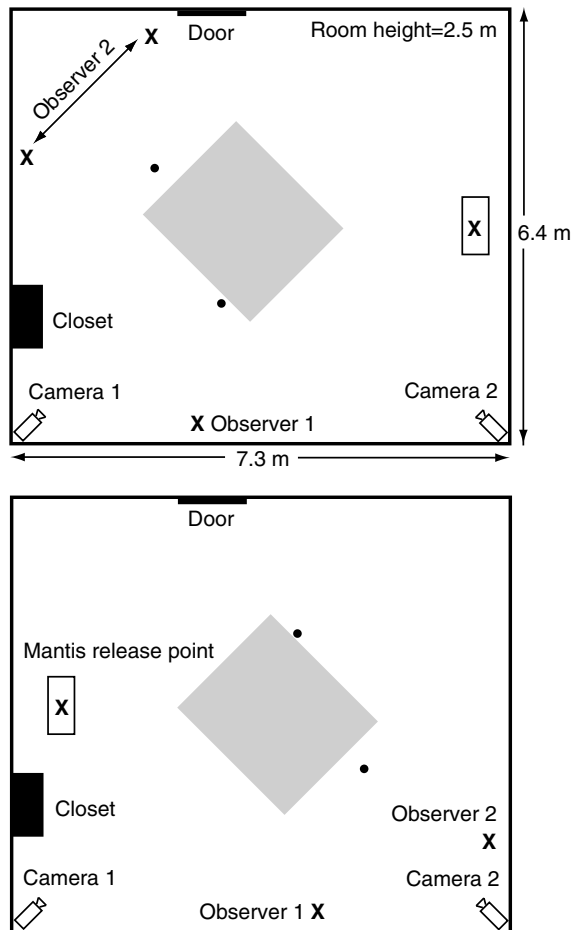


Fig. 1. Arrangement of the flight room, with two different release locations and the positions of the two other observers for each release location. Gray box represents the calibrated space for video analysis. Black circles are the approximate positions of the two microphones.

flight room opposite where the mantis was released (see Fig. 1). Video data were analyzed using these images and commercial motion analysis software (Motus, Peak Performance Technologies). In most trials, two microphones (Ultrasound Advice, London, UK) recorded bat vocalizations. The microphone output was bandpass-filtered (10–100 kHz) and amplified using a Stewart Electronics (model VBF 44; Columbia, CA, USA) filter (–110 dB at 1.5fc). An IoTech 512 Wavebook controlled by a Dell Inspiron laptop computer directly digitized the signals at 250 kHz per channel. We used a custom MATLAB-based program (developed by Aaron Schurger and Amaya Perez) to analyze bat vocalizations. Measurements were taken of the start and stop time of the bat vocalizations.

Experimental groups

Mantids were divided into four different experimental groups: (1) hearing and cercal hairs functional (control group); (2) hearing, but cercal hairs deactivated; (3) deafened, but cercal hairs functional; (4) deafened and cercal hairs deactivated.

Mantids were deafened by filling the ear with vaseline, essentially deactivating the ear without adding any significant mass. This method was preferable to other deafening procedures (i.e. puncturing the tympana) since it prevented possible

collateral damage. We estimated the volume of the auditory chamber in five mantids by measuring the dimensions of a cast of the chamber made with Mercor (Ladd Industries, Kettering, OH, USA), an ultra-low viscosity casting medium. This was 2.2×10^{-4} ml. Considering the density of vaseline (0.935 g ml^{-1}), the mass of the vaseline was 2.1×10^{-4} g at most (very unlikely that the chamber was completely filled). The mass of a male *P. agrionina* is 0.281 ± 0.008 g ($N=10$). Therefore, the mass of the vaseline was about 0.1% of the mantis mass. The mantis ear is located at the mantid's center of mass, so any added weight would have no effect on maneuverability.

Mantis ears were filled 1 day prior to testing to avoid stressing the animal immediately before the experiment. Physiological recordings from two mantids before and after filling the ear demonstrated that the vaseline conveyed a hearing loss of at least 40 dB for frequencies between 20 and 60 kHz (no response to 70 ms tones <100 dB SPL). In two other mantids, the ear was filled with vaseline and tested the following day (following the procedure used in preparing mantids for the free-flight experiments). Physiological recordings confirmed that the vaseline plug eliminated responses to frequencies between 20 and 60 kHz (no responses to 70 ms tones <100 dB SPL). Vaseline plugs were inspected in deafened mantids that escaped and the trial was excluded if a hole existed.

Burning the filiform hairs using a fine soldering iron deactivated the cercal wind response. The procedure left the cerci otherwise intact (compared to cercal ablation) without significantly altering the load on the cerci (compared to covering the cerci with vaseline).

Experimental procedure

Each trial consisted of a single free-flight encounter between one bat and one mantis. Since only one bat was in the flight room at any time, other bats could not eavesdrop on the echolocation calls emitted by the bat pursuing the mantids. Three observers, blind to the condition of the mantis, scored each encounter. A code on the housing cup designated its condition and these codes were not checked until all trials were collected for the day. The releaser stood on a stepladder while the other two observers sat on the floor against the wall in two different configurations, depending on the release point (see Fig. 1). One observer monitored bat echolocation vocalizations using a bat detector and headphones. Increases in the bat's pulse repetition rate (PRR) confirmed that the bat detected and pursued the mantis using echolocation under the low light level conditions.

The bat circled the room continuously before mantis release. Release occurred when the bat was at a point in its flight path that would likely give the mantids enough time to fly away from the release location yet give the bat enough time to detect, track and possibly capture the mantis. Using a conservative approach, the experimenters accepted an encounter as a data trial only if the following conditions were met:

(1) The bat detected and pursued the mantis (indicated by a change in the bat's flight behavior).

(2) During pursuit, the bat increased its vocalization repetition rate. However, a terminal buzz (determined by the experimenter monitoring the echolocation calls *via* a bat detector and headphones) was not necessary for a trial to be accepted, especially for trials in which the mantis entered a power dive. During power dives, bats sometimes increased their repetition rate but broke off pursuit before the terminal buzz.

(3) The mantis flew more than 1 m from the release point before being captured (ensuring the mantis achieved a stable flight condition and had a reasonable chance to produce an evasive response).

(4) The encounters occurred away from other obstructions, such as the walls and the observers (about 30–60 cm away, based on observer judgment). In trials where a bat had the opportunity to make multiple attacks, this rule only applied to the bat's first capture attempt in a trial. Interference with subsequent capture attempts counted as misses (mantis escaped).

The experimenters observed and scored each trial as a successful escape (bat did not capture the mantis), a capture (bat captured the mantis) or a dropped mantis (bat made contact with the mantis, but the mantis immediately dropped to the ground). Mantids dropped in this manner that survived for 24 h counted as successful escapes while those that died during this period counted as unsuccessful escapes (i.e. captures from the mantis point of view). Experimenters also noted the behavior of the mantis (evasion vs no evasion).

After an encounter, the bat was caught to prevent it from tiring or becoming unmotivated while recording the results, downloading video data to tape, and setting up for the next trial. Repeatedly landing on the walls and showing a reluctance to fly was characteristic of a fatigued or unmotivated bat. Bats exhibiting such behavior were first given a tethered mealworm to renew their motivation. If this failed to encourage the bat, we switched to another trained bat. To avoid satiation effects, we limited bats to four captures a day. Bats continued to pursue flying mantids under this procedure and four mantids was sufficient to sustain the bat's body weight.

Transition periods

As described previously (Triplehorn and Yager, 2005), the transition period was defined as the period of increasing PRRs from 20 to 100 p.p.s. and the slope of the transition period (p.p.s. 10 ms^{-1}) provides a measure of how quickly the bat switches from low to high PRRs during an attack (Triplehorn and Yager, 2005). Increasing transition slopes indicate more rapid transitions. In the free-flight encounters, bats circling the room in the absence of a mantis echolocated with PRRs under 20 p.p.s. During capture attempts, PRRs increased over 20 p.p.s. and exceeded 100 p.p.s. PRRs under 20 p.p.s. or over 100 p.p.s. do not elicit evasive responses in tethered flying *P. agrionina* (Triplehorn and Yager, 2005). In some trials, bats increased their PRRs to over 20 p.p.s. during pursuit but broke off their attack before reaching 100 p.p.s. (due to the mantis diving response). In those cases, the transition slopes were calculated using the maximum PRR the bat reached during the pursuit.

RESULTS

Bat echolocation and pursuit behavior

Typical bat pulse repetition rates (PRRs) emitted during free-flight encounters for three different outcomes (escape, capture and drop) are displayed in Fig. 2. In these examples, transition periods between the low to high pulse repetition rates can stretch over long periods. During these transitions, bats can abort a possible attack or attempt a capture as they proceed to produce the terminal buzz. *P. agrionina* auditory sensitivity broadly overlaps with the frequencies emitted by the bat during the attack sequence (Yager et al., 1990).

In a typical pursuit, the bat first positioned itself behind the mantis and pursued it at a level equal to or slightly above the elevation of the mantis. Mantids usually flew about 1–2 m above the floor while circling bats typically flew >2 m above the floor. When a bat captured a mantis, it collected the insect in its tail membrane and quickly transferred the mantis to the mouth. Due to the size of the mantids, portions of the mantis (usually the abdomen) dangled out of the bat's mouth during consumption. The

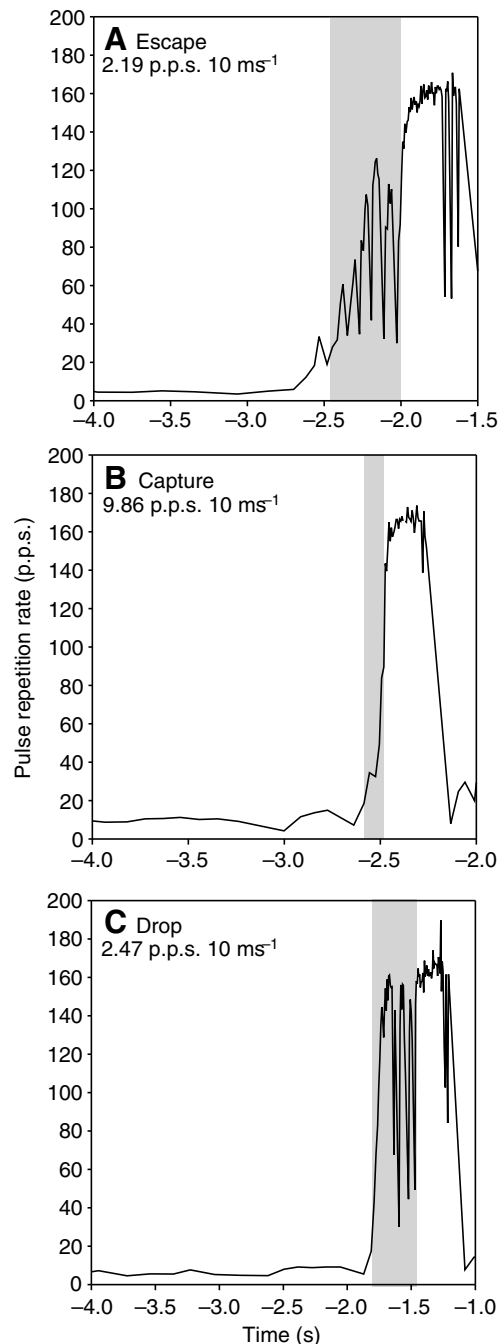


Fig. 2. Three examples of bat pulse repetition rates (PRRs) emitted during attack sequences from the free-flight encounters as bats attacked free-flying mantids. An example is included from an escape (A), capture (B) and a trial where the bat dropped the mantis (C). The transition period (gray area) and slope (number) are indicated in each graph.

echolocation and pursuit behavior of the bats catching mantids in the flight room will be addressed in a future paper.

Effectiveness of mantis ultrasound-triggered evasive responses

The results for all 173 free-flight encounters are shown in Fig. 3 (137 individual mantids: 119 single-trial individuals, 28 multi-trial individuals, each trial occurring on a different day). Hearing

mantids successfully escaped bats in 76% of the trials (55 out of 72 trials) whereas deafened mantids only escaped in 34% of the trials (34 out of 101 trials; Fig. 3A, combining active and deactivated cercal groups for hearing and deaf conditions). These results were statistically significant (two-tailed Fisher's Exact Test, $P < 0.0001$). For hearing mantids, 91% of the escape trials (50 out of 55) involved the mantis performing a power dive. In the other 9% of the trials, the bat made contact with the mantis, but immediately mishandled the insect and dropped it. Deafened mantids never performed power dives in response to bat attacks. For trials resulting in a deafened mantis escape, 41% of the trials (14 out of 34 escapes) involved the bat contacting the mantis and the mantis immediately tumbling to the ground.

Effect of transition rate on mantis escape responses

We performed two analyses to examine the effect of the transition rate in the attacking bat's echolocation sequence on mantis escape responses. The first analysis examined how the transition rate affected the success of the mantis ultrasound-triggered power dive response by comparing the percentages of escapes and captures across transition slopes for 53 encounters involving hearing mantids (Fig. 4). Mantids were very successful at escaping bats when the transition slopes were less than 16 p.p.s. 10 ms^{-1} (84% when transition slopes were between 0–4 p.p.s. 10 ms^{-1} ; 64% when 4–8 p.p.s. 10 ms^{-1} ; 90% when 8–12 p.p.s. 10 ms^{-1} ; 100% when 12–16 p.p.s. 10 ms^{-1}). The pattern switched when transition rates were over 16 p.p.s. 10 ms^{-1} , however, as the majority of mantids were caught (33% escaped when transition slopes were between 16–20 p.p.s. 10 ms^{-1} ; 40% when over 20 p.p.s. 10 ms^{-1}). Sequences containing transitions over 16 p.p.s. 10 ms^{-1} accounted for only 15% of the total trials (8 out of 53). On the other hand, sequences containing transitions between 0–4 p.p.s. 10 ms^{-1} accounted for 36% of the trials (19 out of 53) and sequences containing transitions between 0–12 p.p.s. 10 ms^{-1} accounted for 81% of the trials (43 out of 53).

Echolocation sequences with faster transitions cause mantids to perform dives closer to the time of capture compared to sequences with slower transitions (Triblehorn and Yager, 2005). To determine whether attack sequences with faster transitions allowed bats to get closer to hearing mantids that successfully escaped, we performed a second analysis. Fig. 5 compares the slope of the transition period and the closest distance between the bat and the mantis during the transition period for 15 trials involving hearing mantids that escaped. No relationship was found between the closest distance and transition slope (Pearson's correlation coefficient: $r = 0.059$; t -test: $t(13) = 0.213$; $P = 0.8346$).

Effect of cercal hair deactivation on mantis ultrasound-mediated evasive response

Research on cockroaches indicates that the cerci provide sensory feedback to the thoracic flight motor circuitry once per wing-beat cycle (Libersat et al., 1989). Removing the cercal hairs can affect flight performance, primarily in the yaw direction (Altman, 1983). Results from the free-flight studies indicate that cercal hair removal does not, however, affect the performance or effectiveness of the mantis power dive. Mantids without their cercal hairs were just as successful at escaping from bats (79% success, 27 out of 34) as mantids with cercal hairs (74% success, 28 out of 38; two-tailed Fisher's Exact Test, $P = 0.5926$; Fig. 3A). For hearing mantids with functioning cerci, 93% of the escapes were due to power dives (26 out of 28) while 89% of escapes were due to power dives in hearing mantids with deactivated cerci (24 out of 27; see Fig. 3B).

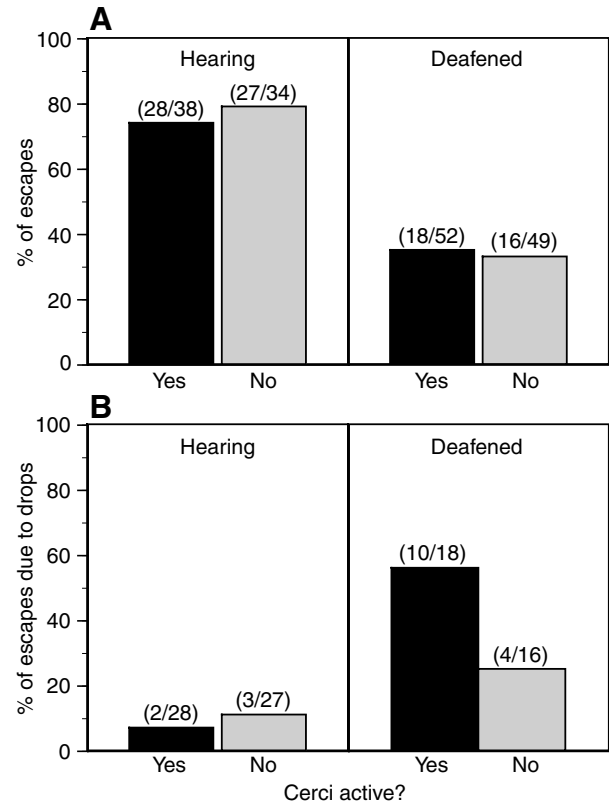


Fig. 3. (A) Percentage of escapes for all four experimental groups (within parentheses: number of escapes/number of trials). (B) Percentage of escapes due to drops for all four experimental groups (number of escapes due to drops/number of total escapes).

Effects of cercal hair deactivation on wind-mediated evasive responses

For deafened mantids, those with functioning cerci escaped in only 35% of the trials (18 out of 52) while those with deactivated cerci escaped in 33% of the trials (16 out of 49; see Fig. 3A). This difference was not statistically significant (two-tailed Fisher's Exact Test, $P = 1$). Deafened mantids never exhibited power dives. Bats mishandling and dropping the mantids accounted for 56% of the survivors in the deafened mantids with functioning cerci group (10 out of 18) and for 25% survivors in the deafened mantids group with deactivated cerci (4 out of 16; see Fig. 3B). However, this difference in survivals due to drops between the two deafened groups was not statistically significant (two-tailed Fisher's Exact Test, $P = 0.0921$). The failure to find a statistically significant difference in the escape percentages between the two hearing groups as well as the two deafened groups justifies combining the four groups into two in the previous section. In these cases, one dropped mantis appeared 'frozen' or in a thanatotic state, but the rest appeared unharmed. All dropped mantids (including the 'frozen' mantis) survived for at least 24 h.

DISCUSSION

Advantage conveyed by the mantis ultrasound-sensitive auditory system

Two previous studies have examined the effectiveness of mantis ultrasound-mediated responses. First, Yager et al. (Yager et al., 1990) demonstrated that mantids performing dives eluded capture (100% success, five total encounters), while those that did not dive

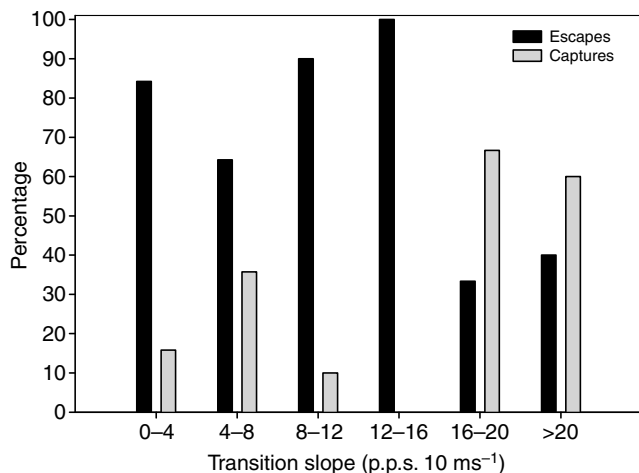


Fig. 4. Percentage of successful mantis escapes vs captures as a function of the transition rate slope in the echolocation attack sequence.

escaped in only 17% of the trials (1 out of 6 trials). These results indicate the power dive response conveyed an 83% advantage. Utilizing a larger data set, the current results confirmed that mantids entering power dives always escaped from the bats (100% effective).

In the other study, Cumming (Cumming, 1996) found that *Miomantis natalica* also performed evasive maneuvers when attacked by the bat *Rhinolophus clivosus*. Instead of measuring escape rate, Cumming counted how many attempts the bats made before capturing the mantis. Bats had a more difficult time capturing *M. natalica* that could hear compared to those that were deafened (three times as many passes for hearing vs deafened mantids) and determined that hearing conveyed a 32% advantage to mantids.

The current study (using different methods, bat species and mantis species) gave similar results, as hearing conveyed a 42% advantage to mantids (hearing mantids survived 76% of all encounters vs 34% for deafened mantids). The effectiveness of the mantis power dive response is similar to that found in moths [40% advantage (Roeder and Treat, 1962), 48% (Acharya and Fenton, 1992), 50% (Dunning et al., 1992); latter two studies were conducted under bright light conditions] but less than green lacewings [60% advantage (Miller and Olesen, 1979)].

The 42% advantage accounts for the effectiveness of ultrasound-sensitivity and the power dive response, the primary foci of this study. However, mantids also exhibit an 'early' evasive turning behavior when detecting a bat that is far away (Yager et al., 1990), which can prevent a bat from detecting and pursuing the mantis. Therefore, this 42% advantage is likely a minimum estimation of the actual advantage conveyed by hearing in the field.

Although the experimental conditions included low-level visible light, the light conditions were the same for both hearing and deafened mantids, as well as the bats hunting them. Therefore, any additional advantage using vision by the bats or mantids would be equivalent across all experimental conditions designed to test the effectiveness of either the ultrasound- or the wind-mediated responses discussed below.

Effect of transition rate on mantis escape responses

The transition rate hypothesis proposed (Triplehorn and Yager, 2005) suggests one potential explanation why insect ultrasound-

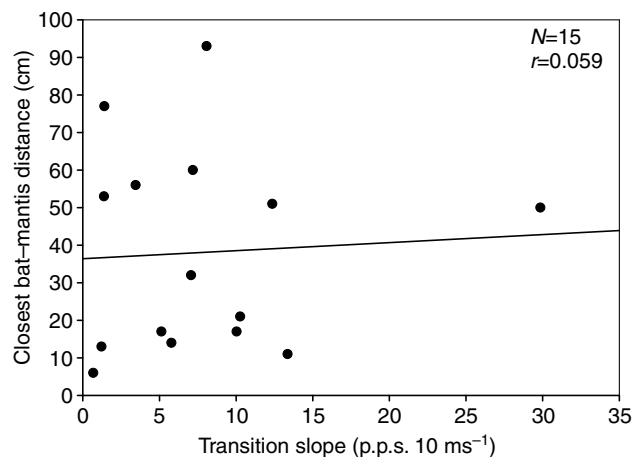


Fig. 5. The relationship between how close a bat came to the mantis and the slope of the transition period the bat emitted during the bat attack sequence. Faster transition rates from low to high PRRs did not allow bats to get closer to capturing the mantis.

mediated evasive behaviors are not 100% effective. Using pulse trains simulating the PRRs and pulse durations of several actual bat attack sequences, they found sequences with rapid transitions elicited escape responses closer to the time of 'contact' compared to sequences containing gradual sequences. Therefore, a bat could potentially circumvent the mantis (or other insect) auditory defense by rapidly increasing from low to high PRRs during an attack echolocation sequence. The results of Triplehorn and Yager (Triplehorn and Yager, 2005) indicated that attack sequences containing gradual transitions would provide mantids with more time to escape while sequences with rapid transitions would provide less time. However, they did not directly test whether the bat's sonar signal transition rate actually reduced the mantid's chance of escaping or what transition rates decrease the number of successful escapes.

The results from this study showed that mantids escaped from bats 80% of the time when transition rates were less than 16 p.p.s. 10 ms⁻¹ (84% for 0-4 p.p.s. 10 ms⁻¹; 64% for 4-8 p.p.s. 10 ms⁻¹; 90% for 8-12 p.p.s. 10 ms⁻¹; 100% for 12-16 p.p.s. 10 ms⁻¹), but fell to 37.5% for transition rates over 16 p.p.s. 10 ms⁻¹ (Fig. 4). The simulated sequences in the previous study (Triplehorn and Yager, 2005) contained transitions between 1-14 p.p.s. 10 ms⁻¹, all of which fall within the range where mantids escaped 80% of the time. These results support both hypotheses that mantids can successfully escape from bats producing echolocation sequences containing gradual transitions and that bats can improve their chances of capturing mantids (and possibly other insects with ultrasound-sensitive auditory systems) by employing faster transitions in their attack sequences. Based on these results, the advantage switches to the bats when their attack sequences contain transitions over 16 p.p.s. 10 ms⁻¹. In our study, however, bats produced attack sequences containing rapid transitions in only 15% of the trials. In fact, bat attack sequences contained gradual transitions with slopes <4 p.p.s. 10 ms⁻¹ in one-third of the encounters.

Attack sequences containing gradual transitions typically did not include a continuous increase in PRR, but rather incorporated clusters of sonar sound groups with stable PRRs. Bats would emit two or three vocalizations at a stable PRR (known as a sonar strobe group) (Moss and Surlykke, 2001), followed by a gap (indicated

by the alternating high and low PRRs in Fig. 2, escape example). Although the function of sonar strobe groups is still unclear, they may facilitate analysis of sonar scenes by the bat during complicated acoustic tasks such as capture attempts (Moss and Surlykke, 2001; Moss et al., 2006). However, the fact that bats produce these strobe groups, and not how bats utilize them, is what is relevant from the mantis point of the view for three reasons. First, echolocation attack sequences containing strobe groups had longer transition periods, which provide the mantis with more time to escape. Second, these echolocation sequences provide more information (*via* the auditory system) that the mantid's nervous system can use to determine the appropriate time to initiate a power dive response. Third, the production of strobe groups could strongly activate the mantis auditory system through temporal integration at the level of auditory interneurons and/or higher centers.

The results from this study did not support the hypothesis that using faster transition rates would allow bats to get closer to the mantids (Fig. 5). This indicates that other factors in the bat's echolocation behavior, such as sound frequency or intensity, likely contribute to how close the bat can get before the mantis dives. The simulated sequences in Triblehorn and Yager (Triblehorn and Yager, 2005) did not vary in frequency or intensity, as occurs in actual bat attack sequences (Griffin, 1958; Simmons et al., 1979; Kick, 1982; Surlykke and Moss, 2000; Boonman and Jones, 2002). Of these two parameters, intensity is likely to have a greater influence over triggering the mantis power dive response. The mantis auditory system is broadly tuned and lacks frequency discrimination (Yager and Hoy, 1989; Triblehorn and Yager, 2001). On the other hand, emission intensity, the distance between the bat and mantis, and the bat's head position relative to the mantis (Ghose and Moss, 2003) all affect the intensity of the sound reaching the mantid's ear. We could not determine the intensity of the echolocation the mantis received during attack sequences or across attack sequences and cannot account for this effect. However, it is an area that warrants future investigation.

Since pulse trains with single PRRs can trigger mantis power dive responses (Yager and May, 1990; Yager et al., 1990), it is clear that mantids do not require a rate of change in the echolocation pulses to perform a response. However, it is equally clear that the transition period in bat echolocation sequences contains rapid changes in the intervals between successive vocalizations. Other phases of the echolocation sequence do contain relatively consistent PRRs, such as the low PRRs (<15 p.p.s.) emitted prior to the transitions period and the high PRRs (>100 p.p.s.) after the transition period. However PRRs <15 p.p.s. and >100 p.p.s. do not evoke mantis power dive responses while the changing PRRs during the transition period do (Triblehorn and Yager, 2005). Therefore, changing PRRs are the reality that the mantis nervous system (*via* auditory input) must respond to in the natural predator-prey situation. This not only affects when power dive responses occur, but also could influence the magnitude (*i.e.* increase in flight speed, steepness of dive) of the response. Future experiments will examine how the mantis nervous system incorporates this variable incoming information and produces a subsequent power dive response.

Effectiveness of the mantis wind-evoked response

Previous studies by two of the current authors (Triblehorn and Yager, 2002; Triblehorn and Yager, 2005) have provided reasons why mantids could benefit from a backup escape system. The current finding that hearing mantids sometimes failed to perform power dives effective at evading capture supports this idea. Wind-

evoked aerial evasive responses, mediated by bat-generated wind acting on the cercal system, could potentially serve as this backup system. For flying insects unable to hear echolocating bats (*i.e.* cockroaches), these responses may serve as the only protection against bat predation. However, the current study shows that deafened mantids with functioning cerci were not better at evading capture than deafened mantids with deactivated cerci. This finding indicates that wind-evoked evasive responses in mantids do not serve as a beneficial backup system in the event that the auditory system fails, possibly because the wind-evoked in-flight responses observed under experimental simulation conditions (Triblehorn, 2003) either do not occur or are ineffective in the free-flight situation.

One interesting observation does warrant further investigation, however. Quantitatively, bats dropped twice as many deafened mantids with functioning cercal systems compared to deafened mantids with deactivated systems. Mantids have, on average, 75 ms between detection of bat-generated wind and capture to escape from a bat (Triblehorn and Yager, 2006). It is unlikely that this is enough time for the mantis to perform a maneuver that will cause the bat to completely miss its target, but may allow the mantis to alter its flight path sufficiently to cause the bat to drop the mantis without damage, resulting in a successful escape. Bat wing stretch receptors, sensitive to membrane deformations, overlap to form regions of high sensitivity where bats prefer to capture insects on the wing (Zook, 2005). Last-ditch wind-mediated responses could cause the mantis to move away from these regions of high sensitivity as the bat attempts a capture, causing the bat to contact, but not capture, the mantis. Based on this hypothesis, deafened mantids with functioning cercal systems should be dropped more often. This was the trend, but it was not statistically reliable, most likely due to the small sample size (deafened mantids only escaped capture 29 times). The larger sample size required to properly address the issue of dropped mantids was beyond the scope of the current study. The finding that most dropped mantids appeared unharmed immediately after the encounter and that they all survived for at least 24 h demonstrates that being dropped is an effective escape strategy. Even if a larger sample size revealed that some dropped mantids do not survive 24 h 100% of the time, it is possible that these mantids could mate prior to dying and being dropped would still be an effective strategy.

Other insects, such as crickets and cockroaches, have more developed cercal systems than *P. agrionina*. These insects possess more wind-sensitive hairs on their cerci, the hairs are longer (and, thus, more sensitive), and they have larger ascending wind-sensitive neurons, resulting in faster neural conduction velocities (reviewed in Boyan and Ball, 1990). Wind-mediated in-flight evasive responses could be more effective in crickets and cockroaches since these factors allow these insects to detect bats earlier (*via* wind cues) alone and respond faster. The dropping phenomenon observed in this study may also occur more often in these insects and may be a general escape strategy for flying insects possessing cercal systems.

In summary, the results from this study demonstrate that the mantis ultrasound-triggered evasive response is very effective for eluding bat predators. However, the response was not 100% effective. Incorporating very rapid transition rates in attack sequences increased the bat's probability of capturing a mantis with functional hearing. Mantids did not gain a significant advantage from the wind-sensitive cercal system serving as a secondary 'backup' evasive system, but bats dropped deafened mantids with active cercal systems twice as often as deafened mantids with

deactivated cercal systems. Although this difference was not statistically significant, this latter observation was an unexpected result that this study was not specifically designed to evaluate fully, and failure to find a statistical difference was likely due to small sample sizes. As such, this interesting observation warrants further investigation to sufficiently evaluate this result, especially since dropped mantids always survived the encounter.

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