

**ULTRASOUND-TRIGGERED, FLIGHT-GATED EVASIVE
MANEUVERS IN THE PRAYING MANTIS
*PARASPHENDALE AGRIONINA***

I. FREE FLIGHT

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Summary

Free-flying male praying mantises *Parasphendale agrionina* (Gerst.) perform evasive maneuvers when stimulated by ultrasound and when attacked by hunting, echolocating bats. They do not, however, respond in any way when standing on a substratum. The maneuvers are graded in intensity with distance from the sound source: far from the source they are simple turns, whereas close to the source they are steep diving turns or spirals. The maneuvers are made under power, and the male's velocity doubles to almost 4 m s^{-1} by the end of a steep dive. The mantis does not show any directional preference. The behavioral threshold of 64 dB SPL and minimum latency to course change of 125 ms indicate that these mantises should have adequate time to evade bats using calls of greater than 85–90 dB SPL (at 10 cm). In field experiments with wild, hunting bats, *P. agrionina* successfully evaded capture in all five attacks to which they responded with evasive maneuvers. Out of three attacks on *P. agrionina* and three on a normally non-responding mantis, *Miomantis paykullii* Stål, in which there were no evasive maneuvers, the mantis was captured in five cases.

Introduction

Ultrasonic hearing is known to occur in species in five insect orders: Orthoptera, Neuroptera, Dictyoptera, Coleoptera and Lepidoptera (Michelsen and Larsen, 1985; Yager and Hoy, 1986a; Spangler, 1988a). It has evolved independently no fewer than eight times, at least three times in the Lepidoptera alone. In moths and green lacewings, extensive behavioral (including field studies) and neurophysiological research has established that ultrasonic hearing is used for detection and subsequent avoidance of echolocating, insectivorous bats (reviewed in Roeder,

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1967; Miller, 1984; Fullard, 1987; Surlykke, 1988). In moths, the avoidance responses consist of turns away from the sound source or erratic flight maneuvers such as dives, loops or spirals; green lacewings generally respond with passive (wings folded) dives punctuated by occasional wing flicks. The moths' response can be directional whereas that of the green lacewings is not.

Based on varying amounts of circumstantial evidence, a function of ultrasonic hearing in the avoidance of predators, particularly echolocating bats, has also been suggested in gryllids (crickets; Popov and Shuvalov, 1977; Moiseff *et al.* 1978; Moiseff and Hoy, 1983), tettigoniids (bush crickets; Kalmring *et al.* 1979; Libersat and Hoy, 1989), acridids (locusts; Wolf and von Helversen, 1986; Robert, 1989) and cicindelids (tiger beetles; Spangler, 1988a). In all but the beetles, neurophysiological data show large auditory interneurons that fire with very short latencies and are most sensitive in the ultrasonic range, a suite of characteristics suggesting a bat-related escape function. While flying tethered in the laboratory, crickets and locusts show 'steering' responses when exposed to bat-like pulses; tettigoniids briefly stop flying. Information on free-flight behavior for all these insects is lacking, however, and there has been no confirmation of the evasive nature of the responses.

Recently, we have learned that some praying mantises have sensitive ultrasonic hearing mediated by a unique and independently evolved auditory system (Yager and Hoy, 1986a, 1987). Physiological and behavioral evidence points to a function in bat avoidance in this insect as well (Yager and Hoy, 1989), and a preliminary study (Yager and Hoy, 1986b) showed that a tethered, flying mantis *Creobroter gemmatus* (Stoll) responds to pulses of ultrasound with a short-latency suite of behaviors including full foreleg extension and abdomen dorsiflexion. In free flight in the laboratory, these mantises respond with a sharp turn and dive.

Here we present the results of free-flight experiments in the laboratory and in the field that define the ultrasound-induced flight maneuvers of the mantis *Parasphendale agrionina* (Gerst.). We show that the response occurs only during flight and, most importantly, our observations with wild bats in the field establish the responses of the mantis to ultrasound as true bat-evasion maneuvers.

Materials and methods

Animals

An East African mantis, *Parasphendale agrionina* (Mantidae; Mantinae; Miomantini), was the primary species used in the experiments described below. Only males were tested since females do not fly and have reduced hearing (see Results and Yager, 1990). The age of the mantises ranged from 3 days to 6 weeks relative to the adult molt. In field experiments with wild bats, we also used males of a second African species, *Miomantis paykullii* Stål (Mantidae; Mantinae; Miomantini), which, in free flight tests, did not respond to 40 kHz pulse trains with any evasive maneuvers. All mantises were raised in our laboratory colony at

26–27°C and 40–60 % humidity. Mantises were misted with water once each day and fed flies or crickets twice a week.

Free-flight laboratory studies

Stimulus

Free-flying mantises were presented with ultrasonic stimuli lasting about 1 s produced by a portable ‘batgun’ – an ultrasonic transducer mounted on a rifle stock. The batgun produced a 40 kHz carrier frequency shaped into pulse trains of 5 ms pulses (0.5 ms rise and fall) at 60 pulses s^{-1} . This stimulus elicited strong evasive responses in flying, tethered mantises. The output of the batgun at 10 cm was 104 dB (rms) re 20 μ Pa (dB SPL). All harmonics were at least 30 dB less intense than the carrier frequency. Calibrations were carried out with a Brüel & Kjaer 2209 sound level meter fitted with a 4135 1/4" microphone (grid off) and a Nicolet 444A real time spectrum analyzer. The overall frequency response of the calibration system was flat ± 2 dB from 1 to 100 kHz.

Moving batgun studies

Studies in which the batgun moved along with the flying mantis provided information on the general response and directionality, and allowed controls for non-ultrasonic stimuli. All these studies were performed in the open atrium, measuring about 20 m \times 20 m, of Corson-Mudd Hall at Cornell University.

These studies incorporated five participants: one launcher/recorder, one batgunner and three observers. The launcher/recorder gently tossed the test mantises into the air to start their flight and recorded the results. The batgunner ran near the flying mantis and, when they were in straight, stable flight, ‘shot’ them (a vocal signal at the same time alerted the observers). The three observers also moved with the flying mantis. During all tests, the batgunner was 2–3 m from the mantis. With each trial, the angle of the batgunner relative to the mantis and the response of the mantis were noted. All tests were performed in a double-blind manner. Before each trial the launcher/recorder turned the batgun on or off in a randomized series; the gun was actually functional only 50 % of the time. The switch was concealed so that neither the batgunner nor the observers knew whether the gun was on in a given trial. This controlled for reactions by the mantis to non-ultrasonic stimuli.

Fixed batgun studies

Experiments in which the batgun was fixed relative to the mantis were used to determine if the response was directional or affected by intensity and to obtain stroboscopic photographs of the behavior. These studies were performed in the atrium and in the Morison room, a carpeted lecture area of Corson-Mudd Hall measuring about 12 m \times 15 m. The Morison room was more dimly lit and 2–4°C warmer than the atrium. For these experiments, the mantis was generally not tossed into the air, but rather coaxed into a voluntary take-off.

Photographs were taken with a Nikon FE2 and 55 mm lens. In most cases, we

used TMAXP3200 film exposed at ASA 6400 which allowed increased depth of field. A General Radio strobolume (type 1540; pulse duration 12 μ s) slaved to the camera shutter froze the flying mantis at successive points in the photographic frame. The interflash interval was set at 20, 22 or 30 ms using a cadmium sulfide photocell. The ultrasound at 30–60 kHz and 65 dB (at 1 m) produced by the stroboscope was attenuated to less than 60 dB by placing a sheet of glass between the stroboscope and the mantis. The onset of the ultrasonic stimulus was marked by a camera flash (Minolta auto electroflash 280) triggered simultaneously with the batgun as the flying mantis entered the camera frame. The batgun was positioned directly behind the camera, and distance markers, positioned at 1 m intervals to 12 m, were used to judge the distance from the batgun to the flying mantis. To control for possible non-batgun sources of stimuli, we also used the strobolume alone as the stimulus in 42 trials.

To assess the effect of stimulus intensity on the behavioral response, one observer noted the distance from the batgun to the mantis at the stimulus onset and assisted a second observer in describing the behavioral response. Responses were categorized as: (1) no reaction; (2) level turn; (3) slight dive; (4) moderate dive; and (5) strong dive. No reaction and level turn are self-explanatory. Slight dive meant a small downward slope in the mantis's flight path after the stimulus. When the ultrasound induced dives of roughly 0.5–1.0 m at 45°, the dives were called moderate. Only nearly vertical dives of 1.5–3 m were classified as strong. At the extreme, strong dives became spiral dives. Data are from approximately 40 males.

Data analysis

The stroboscopic photographs provided information on flight speeds (stable and evasive), latency to response, and fine details of the maneuvers. For flight speed measurements, the stroboscopic flash intervals provided a temporal marker and the body length of the mantis (Table 1) served as a distance-independent length scale.

Statistical methods were taken from Snedecor and Cochran (1967) and Sokal and Rohlf (1981). For all tests, we chose a significance level of 0.05. Means are expressed in the text as mean \pm standard deviation.

Tests with live bats

Stationary mantises

These tests, performed at York University in Ontario, Canada, were designed to examine how mantises standing on a substratum responded to approaching bats of three species. The mantises we used in these experiments were pretested to ensure that they showed evasive responses to ultrasonic pulse trains; only one male out of about 50 failed to respond at 70–75 dB SPL. *Eptesicus fuscus* (Beauvois) uses broadband (80–30 kHz) 4–8 ms long echolocation calls of high intensity (100–110 dB at 10 cm). *Phyllostomus discolor* Wagner and *Macrotus californicus*

Baird use short (≤ 1 ms), broadband (70–30 kHz and 85–62 kHz, respectively) calls of lower intensity (< 90 dB and about 60 dB) (Bell, 1985; M. B. Fenton, unpublished observations). While *E. fuscus* is known to pursue airborne prey, the other two species glean prey in the laboratory and field.

In tests with *E. fuscus*, we placed the mantis on a 1.0 m \times 0.4 m piece of screening in an upper corner of a 5 m \times 7 m room where the bats were trained to land. Once the mantis was oriented and settled, we released a bat from another corner. The bat generally circled the room one or more times and then landed on the screen less than 0.5 m from the mantis. The responses of the mantis were recorded on videotape (Panasonic Digital 5000 WV-D5000 camera and AG-2400 recorder) and a bat detector (QMC S200) was positioned near the mantis and connected to the video recorder, allowing visual documentation of the mantis and simultaneous audio documentation of the bat's echolocation calls. For the experiments with *P. discolor* and *M. californicus*, the bats were hand held at 0.25–0.5 m from the mantis and induced to call by gentle stroking. Calls produced in this situation are likely to be slightly more intense and varied in repetition rate than those produced in flight (Novick, 1977). As in the experiments with *E. fuscus*, simultaneous audio records of the bat and video records of the mantis were taped.

Since the individual bats used were accustomed to take food from the hand and none would spontaneously attack a mantis, unrestrained mantises were hand fed to the bats in the palatability trials.

Field experiments

Field experiments to examine the response of freely flying mantises when attacked by bats were conducted in Pinery Provincial Park near Grand Bend in southwestern Ontario, Canada, between 9 August and 12 August 1989. The tests were carried out near 6 m tall lights at the forested edges of a parking lot. Temperatures ranged from 15 to 20°C, but a temperature of at least 16°C was necessary for reliable mantis flight. All mantises were pretested for avoidance behavior, as in the stationary experiments.

Red [*Lasiurus borealis* (Beauvois)] and hoary bats [*Lasiurus cinereus* (Müller)], two species of aerial insectivores (Fenton, 1990), foraged around the lights, with red bats flying from ground level to the treetops, and hoary bats from 3 m above the ground to above the treetops. Occasionally hoary bats hunted less than 3 m above the ground. At Pinery, the echolocation calls of red bats are 5–10 ms long pulses of medium intensity with most energy around 42 kHz (Brigham *et al.* 1989), while those of hoary bats are 5–15 ms long pulses of higher intensity with most energy around 20 kHz (Obrist, 1989). The frequencies of the red bat call fall in the most sensitive range for the *P. agrionina* male's ear, but the mantis is 10 times less sensitive to the hoary bat call frequencies (Yager and May, 1990). At Pinery, both species typically hunt at flight speeds of 5–7 m s⁻¹ and attack large saturniid, e.g. *Antheraea polyphemus* (Cramer), and sphingid moths (L. Acharya and M. B. C. Hickey, personal communication).

The tests involved 3–6 participants, all well experienced in observing bat–insect

interactions. The minimum team of three workers included a launcher, a spotlihter and a chaser. The launcher threw the mantises into the air from a 3 m stepladder to a starting height of about 6 m off the ground. This placed the flying mantis in the airspace where many of the bats foraged. The spotlihter tracked the flying mantis with a spotlight if it flew into poorly lit areas. The spotlight had been shown to have no effect on either bat species. The chaser followed the flying mantis to its landing spot. Each of these people doubled as observers, and other observers were added as available. Seven of the 11 attacks (below) were described by four or more people; three people saw three of the attacks; one attack was seen by a single observer.

Results

Anatomy

Because of the relevance of mantis size to any discussion of its suitability as bat prey, we present measurements of the *P. agrionina* males (Table 1). Females weigh 8–10 times more than males, their wings are shortened to about half the abdominal length, and they do not fly. Ultrasonic hearing in the females is also markedly reduced (Yager, 1990).

General description of behavior

Normal flight

P. agrionina flies moderately slowly, but strongly. The males fly readily and, both in the atrium and in the field, made long flights that included both increases and decreases in elevation. Once in stable flight, they most often proceed in a straight line until they encounter an obstacle. We observed three general patterns of flight. (1) Stable flight, the most common type, is characterized by: a very shallow body angle relative to the horizontal; high flight speeds; and long, straight flights (Fig. 1A). The male is in a streamlined posture with all legs tucked in close

Table 1. *Anatomical measurements for adult male Parasphendale agrionina*

	Body length (mm)	Mass (g)	Forewing length (mm)	Mesothorax width (mm)	Total wingspan (mm)
Mean	41.66	0.317	27.82	3.56	59.20
s.d.	1.24	0.037	0.68	0.36	1.55
Range	39–43	0.243–0.387	26.5–29	3–4	56–62

Forewing length is measured from wing tip to wing base. The fore- and hindwings are approximately the same length.

Mesothorax width is measured at the base of the forewings.

Sample size for all measurements is 25.

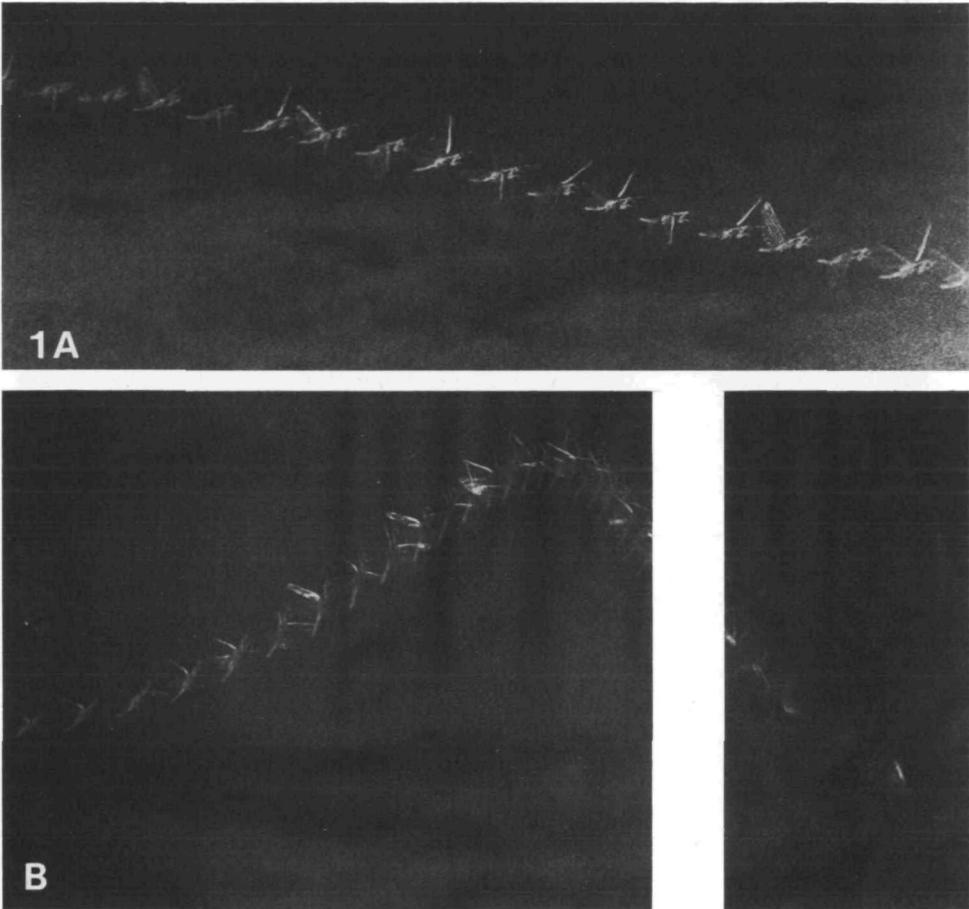


Fig. 1. Normal flight behavior of *Parasphendale agrionina* males. Interflash intervals are 22 ms. (A) Stable flight. The flight path is typically straight, the body angle low, and the legs tucked against the body. (B) Goldfinch flight. Stable flight is interrupted by upward deviation of the flight path and a marked slowing, followed by a dive back into stable flight. In this example, the stable flight speed is 2.1 m s^{-1} and the minimum is 0.62 m s^{-1} . The vertical white bar is a meterstick in the foreground. Note also the change in body angle.

to the body. (2) 'Goldfinch' flight combines stable flight and short periods of very slow flight always accompanied by an upward deflection in flight path (Fig. 1B). During the slow periods, the body angle is high, and the legs are kept close to the body. Flight durations can be quite long. We observe this flight pattern primarily under low-light conditions when the male was 'exploring', but did not see it in the outdoor trials. (3) Landing flight is a pattern seen in short flights, when the mantis seems to be searching for a suitable landing sight. Flight speed is low, body angle is very high, and the forelegs are held widely outstretched.

Evasive maneuvers

The in-flight responses of *P. agrionina* males to bursts of ultrasound fall into three categories reflecting the intensity of the response.

(1) *Level turns*. The least dramatic of the responses to ultrasound is a simple turn without a change in elevation or obvious change in flight speed. The turn is either towards or away from the sound source (see below), and commonly approaches 180°; mantises shot by the batgun as they flew out of the study area often return directly to the release point. Some of these turns, especially at greater distances from the batgun, could be quite leisurely with latencies obviously longer than for diving turns and without the subjective impression of 'snapping into' the turn.

(2) *Diving turns*. In the most common reaction to ultrasound in our experiments, a change in elevation accompanies the turn (Figs 2,3). Normally this is simply a sharp dive, but the stroboscopic traces indicate that the dive can be preceded by a brief rise. The distance the mantis dives, the dive angle and the magnitude of the accompanying turn are all quite variable, and occasionally the turn is absent. The mantis resumes normal flight after the dive, sometimes skimming along very close to the ground after a strong dive. It is clear from the stroboscopic photographs that the dives are not passive; the wings continue to beat, and the mantis accelerates during the dive (Fig. 3). Also, while yaw and pitch changes are clearly present, the roll component of the turn is particularly prominent (Fig. 2). In many of the photographs, it is 60° or more. These responses are very abrupt, especially close to the batgun.

(3) *Spiral dives*. This most extreme dive is seen primarily when the mantis is close to the ultrasound source (Fig. 3). Full spiral dives were not common in the laboratory, but it was the behavior seen in response to three of the attacks by wild bats. In most cases, the mantis very abruptly goes into a steep, spiral power dive that takes it to the ground. In some other cases, the spiral component is partly or completely absent, yielding a power dive straight to the ground.

Control experiments

The results of the control experiments demonstrate that ultrasound, and not visual or other disturbance stimuli, triggers the evasive maneuvers. In the 62 trials (using 10 mantises) constituting the moving gun controls, the three observers unanimously agreed about the response in 55 cases. The mantis responded in 27 trials, none with the gun off. There was no response in 28 trials, three with the gun on and 25 with the gun off. In five other trials, one of the three observers reported a slight response when the gun was off. The distribution of responses is not random (binomial test).

Similarly, there is no apparent effect of the stroboscope used in the fixed gun experiments in triggering the evasive maneuvers. The stroboscope alone was used as the stimulus in 42 trials with flights 0.5–4.5 m away from it. We saw responses in

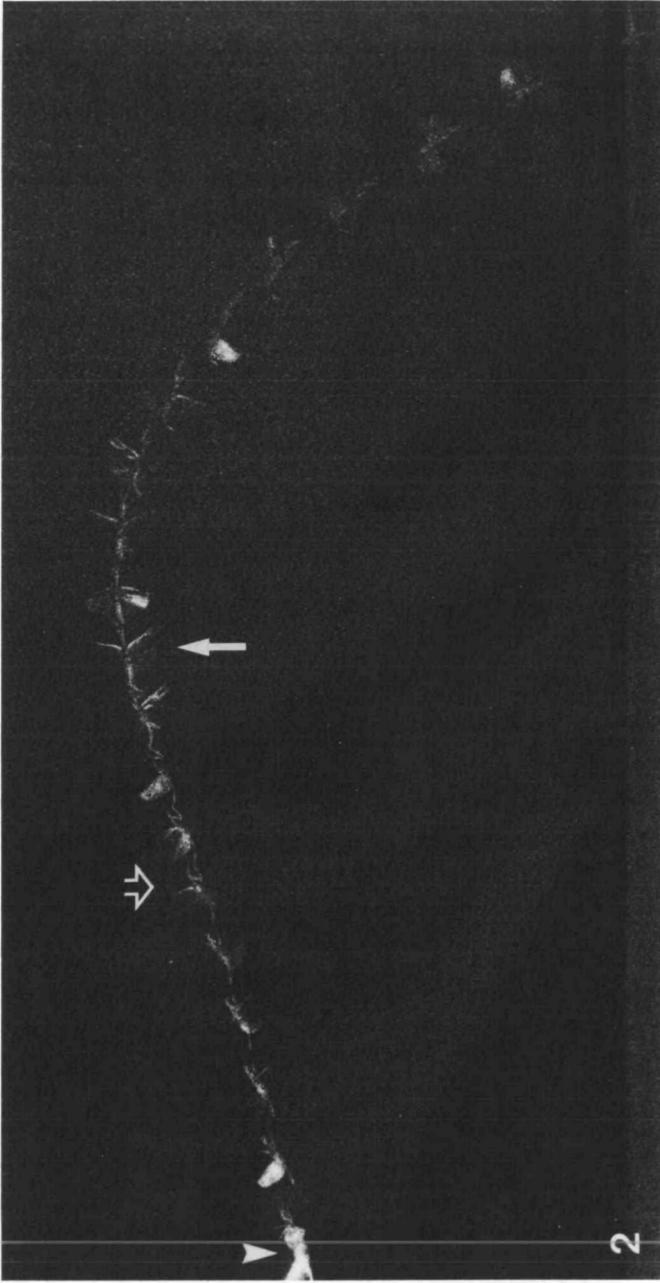


Fig. 2. A moderate diving turn in response to ultrasound triggered at the arrowhead. Interflash intervals are 30 ms. The extension of the forelegs (open arrow) occurs well before the first clear indication of a roll (arrow). The turn was towards the batgun and camera in this case.

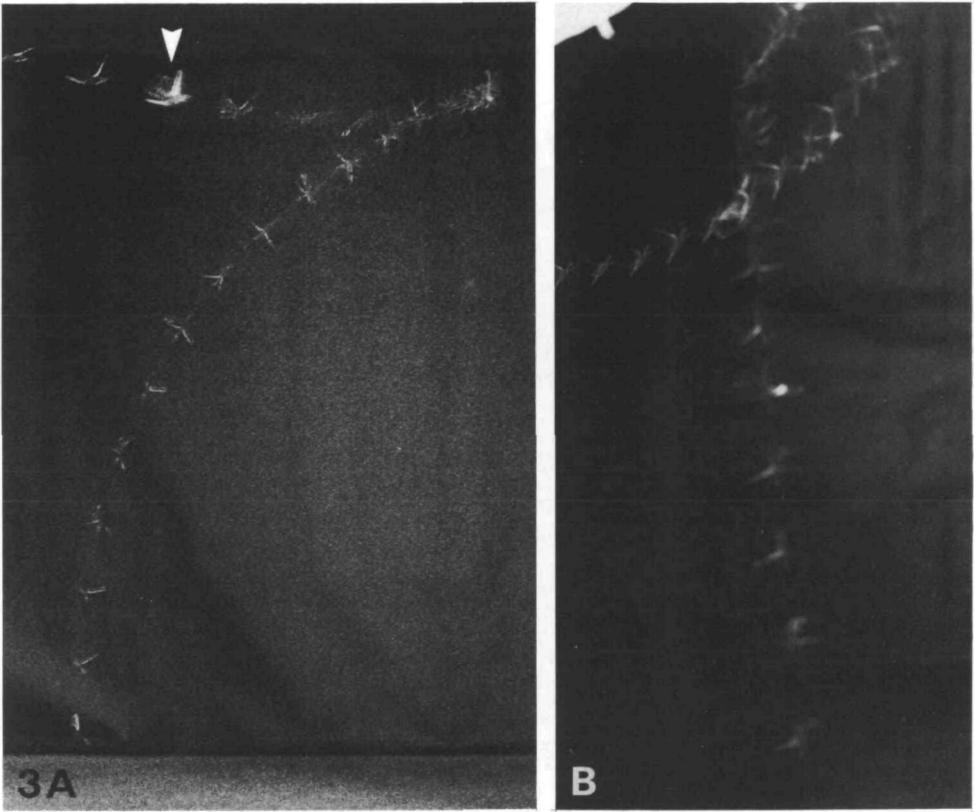


Fig. 3. Strong dives with spiral components. Note that the wings are extended and flapping during evasion. (A) An approximately level turn followed by a gradual spiral away from the camera. The arrowhead marks the stimulus onset. The final speed of the mantis was 4.1 m s^{-1} . Interflash intervals are 30 ms. (B) An initial upturn in flightpath followed by a looping dive towards the camera. Stimulus onset is just out of the camera frame to the left. Interflash intervals are 22 ms.

only four trials. All occurred between 0.5 and 2 m from the light and were low-intensity behaviors: three level turns and one slight diving turn.

Temporal parameters

Table 2 summarizes the temporal parameters of the normal and evasive flight of *P. agrionina* males. In stable flight, the males travel at an average of 1.90 m s^{-1} , while in the slow periods of the goldfinch flight pattern the velocity can be as low as 0.62 m s^{-1} . By contrast, measurements at the end of evasive dives show a mean velocity of 3.76 m s^{-1} . In the 10 photographs allowing calculation of both stable and evasive speed, the mean increase was $100.0 \pm 0.41\%$. This value, however, is an underestimate because, in some cases, measurement was only possible early in the evasive maneuver, i.e. early in the acceleration phase. Males diving from greater heights will also have longer to accelerate and may attain higher speeds.

Table 2. *Flight temporal parameters*

	Stable speed (m s^{-1})	Evasive speed (m s^{-1})	Latency I (ms)	Latency II (ms)
Mean	1.90	3.76	172.5	242.2
s.d.	0.31	0.58	38.9	47.2
<i>N</i>	30	20	10	16
Range	1.53–2.60	3.08–4.92	125–230	140–290

Flight speeds are measured during stable flight before or just after a stimulus and also as late as possible in the evasive dive.

Latencies are measured from the beginning of the ultrasound burst to two events: (I) the first clearly discernible upturn in the flight path or the first indication from wing position of a significant roll; (II) the first visible indication of a dive. All latencies include a 10 ms correction for travel time of the sound to the mantis.

The sound pressure level of the stimulus at the mantis was approximately 72–78 dB SPL, i.e. 8–14 dB over the threshold for response.

In the stroboscopic photographs, the first sign of a discrete upturn in the flight path of the mantis or a clear indication of the onset of roll occurs on average 172.5 ms after the ultrasonic stimulus, with shortest latencies of 125 ms. In the few photographs where it is clearly visible, extension of the forelegs occurs earlier, but it is not associated with any obvious change in flight path. The dive begins considerably later (242 ms after the stimulus), but the range of latencies to the dive is almost the same as for the upturn or roll. Our latency values must be overestimates since the roll had to be fairly well established before it was visible in many of the photographs, because the strobe measurement technique allows errors in that direction, and because motion in the yaw plane is difficult to assess given our angle of view.

Directionality

We find no consistent evidence, either in the moving or fixed gun experiments, that the evasive maneuvers are directional.

In the moving gun trials when the sound source was clearly to one side of the flying mantis, i.e. not behind or in front, and when all three observers agreed on the direction of the turn, the mantises turned towards the sound source nine times and away eight times (random; binomial test). The results of the fixed gun studies give differing results under two conditions. During the first series of trials (154 trials with 22 animals) we saw 49 turns away from and 105 towards the sound source. This result is significantly different from the hypothesized 50:50 distribution (G -test statistic=20.84; d.f.=1), but in the unexpected direction. In the second series of fixed gun trials (63 trials with 16 males) there was no stroboscopic lighting for photography and there were more trials at distances greater than 5 m from the batgun. In this series, 33 trials included turns away from the ultrasound and 30 towards it, not significantly different from our prediction of non-directional responses (G -test statistic=0.14; d.f.=1).

Response variation with intensity

The intensity of the male mantis's response to bat-like ultrasound is graded with distance from the sound source and, hence, sound pressure level (Fig. 4). In the ranges 1–3 and 3–5 m from the source, strong and moderately strong dives predominate. The frequency distributions for these two distance ranges do not differ significantly (chi-square=3.41; d.f.=4). In contrast, at 5–7 and 7–9 m slight dives and level turns are most common. Even with the complete disappearance of strong dives between 7 and 9 m, the frequency distributions in these two ranges are also not different (chi-square=7.22; d.f.=4), although a chi-square test (chi-square=26.04; d.f.=4) confirms that the frequencies of the various behaviors differ between the 3–5 and 5–7 m ranges. A clear transition occurs between 9 and 10 m as strong and moderate dives disappear completely and the number of no responses increases dramatically. At 10–12 m we saw one level turn and 11 no responses. While the distributions at 1–3 and 3–5 m as well as those at 5–7 and 7–9 m are not statistically different, Fig. 4 suggests a continuous grading of the types of responses with distance. Statistical substantiation comes from regressions on the percentages of behavior types with distance for strong dives and no responses; the slopes in both cases differ from zero ($t=4.05$ and 8.68 , respectively; d.f. values >200). The moderate dives, slight dives and level turns each increase in prominence with distance, each becoming predominant at a different range from the source, and then decline at greater distances. The data in Fig. 4 show that the

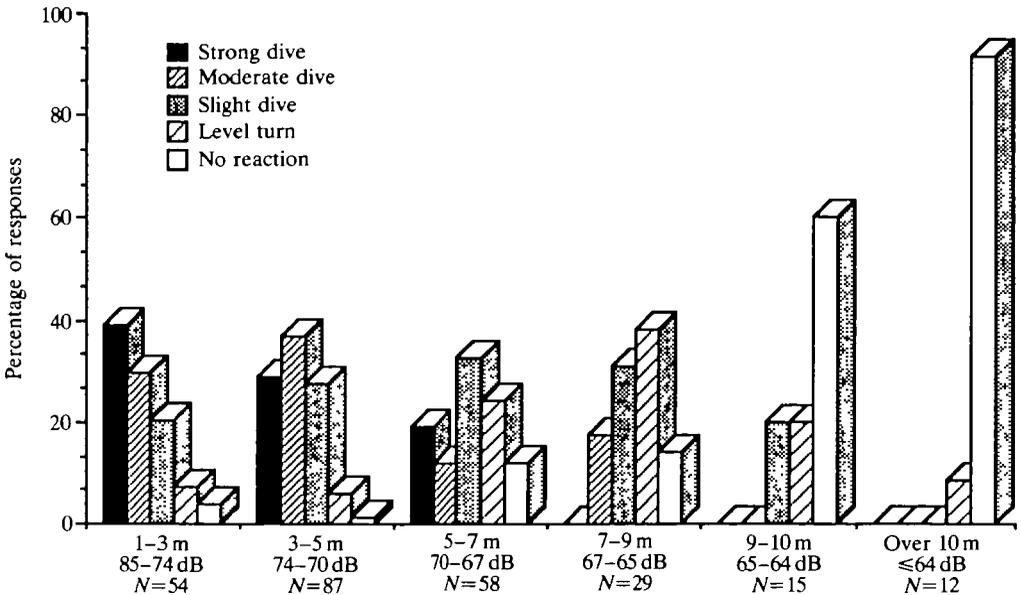


Fig. 4. Variation in response type with increasing distance (decreasing sound intensity) from the ultrasound source. Spiral dives are combined with strong dives. The greatest distance tested was 12 m.

behavioral threshold distance is approximately 10 m. Since the output of the batgun at 10 cm is 104 dB SPL (rms), the behavioral threshold for evasive maneuvers in *P. agrionina* is 64 dB SPL.

Tests with live bats

Stationary mantises

Our results with three species of bats indicate that male *P. agrionina* standing on a substratum do not respond in any way to ultrasound. In the tests with *M. californicus* (16 trials with four mantises) and *P. discolor* (15 trials with four mantises), we saw no motion of any kind in response to the bat cries. Furthermore, if the mantis was grooming, it continued grooming, and if it was walking, it continued walking while exposed to the echolocation calls.

The tests with *E. fuscus* (23 trials with six mantises and two bats) gave slightly more complicated results. The mantis never responded in any way to the ultrasonic pulses produced as the bat passed or came in for a landing nearby on the screen. This was particularly surprising since from about 1–5 m from the screening, the bats accelerated their pulse rates in an approach buzz. However, immediately after the bat landed, the mantis almost always assumed a rigid posture with forelegs extended, head oriented towards the bat, and sometimes crouched slightly. We observed this response as readily when the bat landed facing away from the mantis as when facing towards it. The foreleg extension was very slow, taking 1–2 s to develop fully, but even then, the tibia was not extended and remained flexed, along with the tarsus, against the femur.

Although these normally hand-fed bats did not directly attack the mantises, they ate them with relish. The two *E. fuscus* each ate three males; the *M. californicus* also readily ate three males.

Field experiments

The two mantis species we challenged in the field with attack by wild bats showed substantially different patterns of response.

We performed over 200 trials using 37 *P. agrionina* males and observed seven attacks and one close approach on this species, six by *L. borealis*, one by *L. cinereus* and one by a bat that was probably *L. borealis*. In four of the attacks by red bats the observers unanimously agreed that the mantis performed evasive responses. In three of those cases, the response of the mantis was a steep, spiral power dive to the ground; in the fourth case (the probable red bat), the mantis dived straight down then levelled off and continued flying. In the close approach by a red bat, the mantis also dived without turning and then levelled off. The bat did not capture or contact the mantis in any of these five encounters. In the three remaining cases none of the observers saw any evasive maneuvers. In the hoary bat attack, the bat missed the mantis. In the two red bat attacks, the mantis was captured or at least hit by the bat, but held only momentarily and released

unharméd. All the eight bat attacks/approaches originated from above and to the side or from above and behind the mantis.

M. paykullii males are excellent fliers and readily presented themselves for attack by the wild bats. In approximately 50 trials with 10 mantises we observed three attacks by red bats on this species. None involved any evasive maneuvers, and in all cases the mantis was captured by the bat. In one case, the bat released the mantis, and it escaped unharméd.

Discussion

Based solely on indirect evidence, ultrasonic hearing in praying mantises had been hypothesized to be the sensory component of a defensive system allowing escape from echolocating bats (Yager and Hoy, 1989). The direct evidence presented in this paper confirms that flying *Parasphendale agrionina* (Gerst.) uses ultrasonic hearing to help it evade capture by hunting bats. The mantis now joins the moths and the green lacewings as insects known to have responded to the considerable predation pressure exerted by echolocating bats with the independent evolution of ultrasonic hearing and an associated set of effective evasive maneuvers.

Behavioral comparisons

Insects have many different modes of flight. For example, dragonflies readily switch from synchronized to alternating wingbeat patterns (Rüppel, 1985) and locusts combine bouts of powered flight with intervals of gliding (Baker and Cooter, 1979). In *P. agrionina*, we have described three contrasting flight patterns: stable, goldfinch and landing. One characteristic that distinguishes the three flight patterns is body angle relative to the horizontal. Larger body angles correlate with lower flight speeds and smaller body angles with higher flight speeds, a relationship noted in several other insects, such as the locust (Weis-Fogh, 1956). The average speed of *P. agrionina* during normal flight, 1.90 m s^{-1} , is moderate for flying insects, appreciably faster than green lacewings, $0.5\text{--}1.0 \text{ m s}^{-1}$ (Miller and Olesen, 1979), and slower than the migratory locust, 4.6 m s^{-1} (Baker *et al.* 1981). Although *P. agrionina* is a versatile and competent flier, it should be no match for maneuverable insectivorous bats cruising at $3\text{--}7 \text{ m s}^{-1}$ (Hayward and Davis, 1964). As in moths and green lacewings, the mantis appears to use as one of its strategies sudden, unpredictable changes in flight path to avoid the attacks of bats.

Evasive maneuvers performed by insects in response to bat cries can be placed in two general categories: active and passive (Miller, 1984). Green lacewings (Miller and Olesen, 1979) perform passive dives simply by folding their wings, and add unpredictability to their trajectory by occasional wing flicks. The response is non-directional and has a behavioral latency of 50–100 ms to intense feeding buzzes. Moths (Roeder, 1962, 1964) may dive passively, but more often perform powered dives, spirals and turns. Their responses vary with the intensity of the

ultrasound, and they are directional far from the bat, but non-directional close to it. The response latency in free flight is 200–1000 ms.

Except for the lack of directionality imposed by the cyclopean ear (Yager and Hoy, 1986a), the mantis evasive behaviors resemble those of moths (Figs 2, 3). They are power maneuvers coarsely graded with sound pressure level. At distances of less than 7 m, the male mantis unpredictably chooses an angle of turn and degree of dive, and spirals are part of their repertoire, whereas at greater distances, level turns are common. Mantises and moths both skim along the ground after a dive and later resume their usual flight (Roeder, 1962). The categorization is not absolute for any of these insects: moths occasionally dive passively (Roeder, 1962), green lacewings perform active flight maneuvers up to 25 % of the time with certain stimuli (Miller and Olesen, 1979), and mantises may also occasionally use passive dives.

All three insects detect bats at distances much greater than those at which they actually respond to them. Detection distances of 30–40 m for moths have been determined neurophysiologically under natural or semi-natural conditions (Roeder, 1966), and calculations suggest detection distances for both mantises and green lacewings of 15–30 m. Moths first actually respond to a bat-like ultrasound at more than 6 m (maximum distance not measured; Roeder, 1964; but to real bats at less than 4 m; Roeder and Treat, 1960), mantises first respond at 10 m, and lacewings at only about 2 m (Miller and Olesen, 1979). Clearly, a substantially suprathreshold level of neural activity is required to trigger the behavior, and the results of Nolen and Hoy (1984) demonstrate this phenomenon in the cricket.

Most of the insects suspected also to use ultrasonic hearing for bat avoidance can be placed in one of the two response categories. It appears, for instance, that crickets and locusts perform powered maneuvers that involve directional turns and dives (May *et al.* 1988; Robert, 1989), while tettigoniids simply fold their wings in response to ultrasound, which should produce a passive dive (Libersat and Hoy, 1989). It is intriguing that there has been convergence over broad phylogenetic lines onto each of the two categories of response, and that the two most closely allied groups, the gryllids and the tettigoniids, show different behaviors. Phylogeny cannot have been of great importance in determining which behavioral avenue to follow, and the evasive behaviors must have evolved independently even within the Orthoptera. There is not yet sufficient information on the ultrasound-induced behavior of the tiger beetles to put them into either category.

Do bats pose a threat to mantises?

Opportunity

Like bats, mantises are primarily tropical in their distribution and are found in virtually every habitat type in the tropics (Roy, 1987). Mantises reach their greatest numbers and diversity in eastern and western Africa and Malaysia, but are also common throughout the warmer regions of the New World. Like virtually all mantises, *P. agrionina* is sympatric with insectivorous bats utilizing intense,

30–60 kHz echolocation cries such as those produced by red bats. Among the more than 90 species of insectivorous bats found in East Africa (Kingdon, 1974), at least 60 belong to taxa commonly using this acoustic hunting strategy, the dominant one in all regions where bats have been studied (Fenton and Fullard, 1979; Fenton and Bell, 1981; Fullard, 1988; Obrist *et al.* 1989). We know of no other aerial predator producing sounds which would trigger the mantis evasive maneuvers.

Most insectivorous bats hunt after dark and, although mantises are well known as diurnal hunters, they also are active at night. Many mantises are caught at lights at night, and the sex ratio of these samples is strongly skewed towards males (Edmunds, 1986; Roy and Leston, 1975). This is in keeping with evidence suggesting that females produce pheromone plumes at night, or just as the light level begins to increase at dawn, to attract males flying in the area (Edmunds, 1975; Robinson and Robinson, 1979).

Suitability as prey

Animal-eating bats range in size from less than 10 g to more than 100 g and can handle a correspondingly large range of prey sizes (Fenton, 1990). Most mantises are less than 40 mm long, weigh less than 0.5 g (D. D. Yager, unpublished data), and would be appropriate prey for many bats. In laboratory experiments (D. D. Yager and M. B. Fenton, unpublished observations) a flying *E. fuscus* (approx. 16 g) captured a male *Mantis religiosa* L. (>45 mm) and ate it on the wing without difficulty, and in the field experiments two *M. paykullii* (>40 mm) were captured and carried off by red bats (10–15 g).

In the field experiments, three mantises were captured and then dropped unharmed. Mantises are not distasteful to bats since *M. californicus* and *E. fuscus* find *P. agrionina* completely suitable as food, and other laboratory experiments (D. D. Yager and M. B. Fenton, unpublished observations) have shown that these two species of bats readily eat *M. religiosa* and *Stagmomantis centralis* as well. We suspect that the mantis may have responded to capture by striking out with its spined forelegs and startled the bat into releasing it.

At this time, the question of whether bats in the field include mantises in their diet remains open. Some gleaning bats do eat mantises (Fenton *et al.* 1981), but there is currently no information regarding mantis predation by obligate aerial insectivores.

Can mantises evade bats?

Auditory capability

The auditory system of the mantis is capable of, and may be specialized for, mediating bat-evasion responses. In *M. religiosa* (Yager and Hoy, 1989), information from the single, midline ear in the ventral metathorax is transmitted towards the brain by an interneuron with properties ideal for an escape system: very short (<10 ms) latencies, a large-diameter axon with correspondingly high conduction velocities (>4 ms⁻¹), moderately strong habituation, and no spon-

taneous activity. Audiograms from over 30 species of mantises (Yager, 1990, and unpublished data) show that, in virtually all cases, the regions of best sensitivity lie between 20 and 60 kHz, exactly the frequency range used by most aerially insectivorous bats (Fenton and Fullard, 1979). In mantises there is a strong correlation between wing length and ultrasound sensitivity, even within species: in general, flightless mantises do not hear ultrasound while winged forms do (Yager, 1990).

Behavioral efficacy

The behavior triggered by the auditory system is clearly effective in avoiding capture by bats: all the five mantises that performed evasive maneuvers escaped the wild bats, while five of the six that did not were captured (Table 3). Roeder and Treat (1960) computed a 44 % selective advantage in evading capture of responding over non-responding moths, and Miller (1980) determined a value of 47 % for green lacewings. Our data give a value of 83 % for *P. agrionina* males, though this may be an overestimate due to small sample size.

This effective evasion is mediated by ultrasound detection alone. Our control experiments indicate that general visual disturbances do not trigger the full behavior, though bright light appears to influence the direction of the turn. In the field at night, vision could not provide the mantis with warning of an approaching bat.

Our fixed gun data allow an even more detailed assessment of the mantis escape system. The output of our batgun is 104 dB SPL at 10 cm which is approximately the same as the output of many common bats which are aerial insectivores (Griffin, 1958). Our fixed gun results are, therefore, comparable to the natural situation. The mantis first responds to bat-like ultrasound at 10 m from the source, i.e. to ultrasound at 64 dB SPL. Since we know the normal flight speed of the mantis, we can compute the escape times available to the mantis for different bat closing velocities (Fig. 5). We also know the latency of the mantises' response (Fig. 5, dashed lines) and can assess the range of bat call intensities permitting adequate time to respond for each closing velocity. The figure shows that *P. agrionina* will not have enough warning from any bat whose cries are less than 75–80 dB at 10 cm regardless of closing velocity. Conversely, this mantis will

Table 3. *Results of field experiments presenting mantises to bats*

	Number of responders	Responders captured	Number of non-responders	Non-responders captured
<i>Lariurus borealis</i> (<i>P.a.</i>)	5	0	2	2
<i>Lariurus cinereus</i> (<i>P.a.</i>)	0	—	1	0
<i>Lariurus borealis</i> (<i>M.p.</i>)	0	—	3	3

The results are reported as number of trials.

L. borealis bats attacked both *Parasphendale agrionina* (*P.a.*) and *Miomantis paykullii* (*M.p.*) in the field tests.

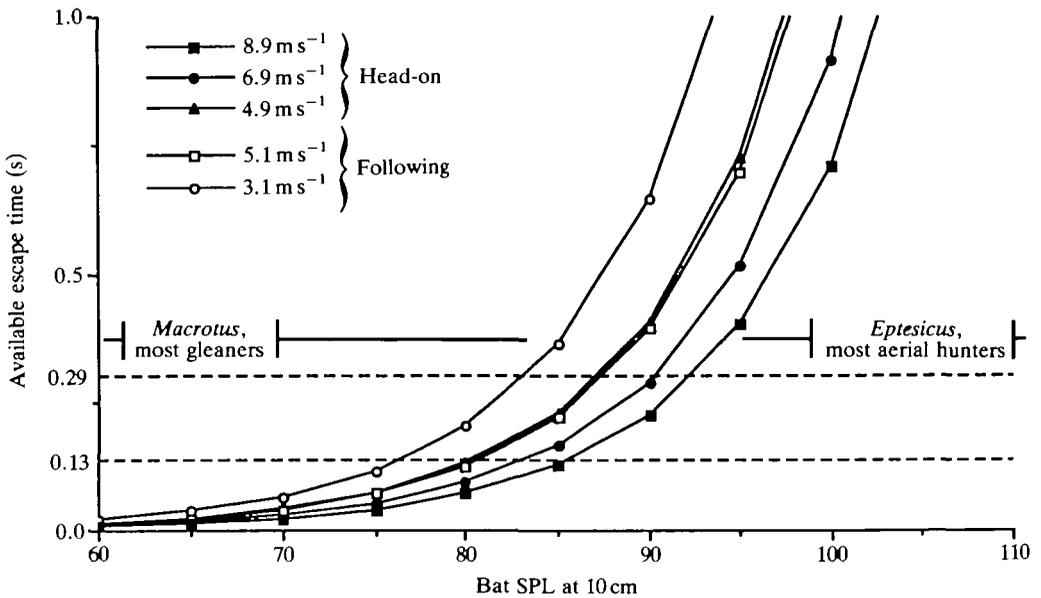


Fig. 5. Predictions, based on results from this study, of the time a mantis has between detecting a bat and interception by the bat. Assumed are a mantis flight speed of 1.9 m s^{-1} and bat speeds of 3, 5 and 7 m s^{-1} (which are constant), mantis behavioral threshold of 64 dB SPL and bat call frequencies of 40 kHz . The curves are for closing velocities in the two extreme cases: approaching each other head-on and the bat approaching the slower flying mantis from behind. The dotted lines show the range of behavioral latencies seen in our experiments. *Parasphendale agrionina* males will not have time to evade bats with low-intensity calls, but should escape from the typical aerial hunter using high-intensity cries. *Parasphendale agrionina* males will not have time to evade bats with low-intensity calls, such as *Macrotus* and other gleaners, but should escape from the typical aerial hunter such as *Eptesicus* using high-intensity cries.

always have time to escape bats using ultrasound at $\geq 90\text{--}95 \text{ dB}$, even with the most disadvantageous closing velocity. For all but the two highest approach speeds, bats with cries of $85\text{--}90 \text{ dB}$ will also be evaded.

These computations suggest that many echolocating bats will be at a considerable disadvantage when hunting *P. agrionina*. A bat with high-intensity calls will first detect a 60 mm sphere at 9.5 m (Kick, 1982) and an insect with a 60 mm wingspan at a shorter distance, making the situation even worse for the bat. The bat does, however, have a major advantage that may account for the attacks on *P. agrionina* that did not result in evasive maneuvers and led to capture of the mantis. The beam of ultrasound emanating from the mouth or nose of insectivorous bats may be narrow (Novick, 1977), and mantises outside the beam would not detect the calls of the bat. If the bat suddenly turns towards the mantis at close range, it may be able to detect and attack the insect before it can respond. Some bats may have responded to their early detection by prey by adopting inconspicuous

echolocation calls (Fenton and Fullard, 1979; Fullard and Thomas, 1981), and many hipposiderid and rhinolophid bats use frequencies greater than 70 kHz, beyond the most sensitive hearing range of the mantis (see above and Yager and May, 1990). Because the mantis's threshold to sounds above 70 kHz is much higher than 64 dB SPL, the family of curves in Fig. 5 is shifted to the right and, thus, as the bats become less conspicuous, they have an increased chance of capturing the mantis before it can respond.

Aerial insectivores vs gleaners

Although flying *P. agrionina* males are well protected against attack by bats when in flight, they appear to be vulnerable when stationary on a substratum. Gleaning bats typically use short (<1 ms), low-intensity (<80 dB) echolocation calls with most energy above 60–70 kHz (Fenton, 1990), characteristics making the calls inconspicuous to the mantis. For example, the echolocation calls of *M. californicus* (50 dB at 10 cm; energy between 60 and 100 kHz), would not be audible to *P. agrionina* (Yager and May, 1990; D. D. Yager, unpublished data). *P. discolor* would be detectable, but only at very close range, not allowing adequate reaction time. Even when stationary mantises are being approached by a bat they can hear perfectly well (*E. fuscus* in our stationary tests) *P. agrionina* males show no response to the ultrasound. In mantises, active evasion is linked to flight.

The foreleg extension observed after the bat landed was clearly triggered by vibrational or visual and not auditory disturbance. This display is fundamentally different in its extent and time course from the arm extension triggered by ultrasound (Yager and May, 1990).

Virtually nothing is known about the activities of mantises on substrata at night. Some African gleaning bats (*Nycteris* spp.) eat mantises (Fenton *et al.* 1981), but in an extensive study of insectivorous gleaning bats in Panama, a region rich in mantis fauna, Belwood (1988 and personal communication) did not find evidence of significant predation on mantises. Mantises may avoid the predation pressure exerted by gleaning bats because they do not move around on the ground or branches or because they stay largely hidden.

The exclusive association of ultrasound-induced evasive maneuvers with flight may be a widespread phenomenon. It has been noted in behavioral tests with another, unrelated mantis species, *Creobroter gemmatus* (Stoll) (Yager and Hoy, 1986b). Tethered flight and behavioral tests have also shown similar flight gating to occur in green lacewings (Miller and Olesen, 1979) and in crickets (Nolen and Hoy, 1984). M. B. Fenton and D. D. Yager (unpublished data) found that *M. californicus* and *Megaderma lyra* Geoffroy invariably caught crickets (*Gryllus bimaculatus* De Geer and *Teleogryllus oceanicus* Le Guillou) when the bats hunted in darkness, a situation where they use their echolocation (Bell, 1985; Fiedler, 1979). In room light the same bats failed to catch the same crickets because the crickets visually detected and then avoided the approaching bat. Like the mantis, stationary, walking or calling crickets showed no response to approaching echolocating bats or to artificial bat calls. In contrast, Werner (1981) has shown

that some stationary moths respond to ultrasonic pulses with a well-defined crouching behavior, and Treat (1955) saw non-flying moths respond in a variety of ways to an uncalibrated ultrasound source.

The function(s) of hearing in praying mantises

We have shown that ultrasonic hearing provides the sensory input that allows male *P. agrionina* to evade bat attacks, but this may not mean that predator avoidance is the only function for hearing among the praying mantises. Within the Lepidoptera and Orthoptera, some species with tympanate hearing probably or certainly use it for bat detection, while other species use their auditory capability additionally or alternatively for other functions, primarily mate attraction or courtship (Michelsen and Larsen, 1985; Spangler, 1988*b*). Two pieces of evidence suggest that this may also be the case among the 1900–2000 species in the suborder Mantodea.

First, whereas eight of the ten mantis species we have tested (D. D. Yager and M. L. May, unpublished data) show in-flight responses to ultrasound, two have not responded at all. In some responsive species, e.g. *M. paykullii*, the frequencies of maximum auditory sensitivity are 90–130 kHz, beyond the bandwidths used by many bats, but within the range commonly used by some rhinolophid and hipposiderid bats (Fenton and Bell, 1981). In these cases, 40 kHz stimuli do not match the normal cues and elicit no response. Both non-responsive species, *M. religiosa* and *Tenodera aridifolia sinensis*, however, have audiograms similar to that of *P. agrionina*. In these species, we still may not be providing important cues (specific temporal patterns, FM sweeps, etc.) that bats in their normal habitat would be giving. Nevertheless, the alternative possibility is that these species may not use their hearing for bat detection.

Second, the mantis *C. gemmatus* has a strongly W-shaped audiogram with equal sensitivities at 2–4 and 25–50 kHz (Yager and Hoy, 1986*b*). These mantises show a very strong in-flight evasive response to ultrasound, but the function of the low-frequency tympanate hearing is completely unknown.

Regardless of the solutions to these puzzles, it is clear from the very high occurrence of ultrasonic hearing among mantises (Yager, 1990), the pronounced physiological and behavioral specializations for evasion (Yager and Hoy, 1989), and the pressure bats can exert on nocturnally flying insects, that ultrasound-mediated bat avoidance is of major importance to praying mantises.

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