The use of acoustical cues for prey detection by the Indian False Vampire Bat, *Megaderma lyra*

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Summary. 1. The response of the echolocating bat, *Megaderma lyra*, was tested to different kinds of prey in an outdoor cage. The bats caught larger flying insects (moths, beetles, grasshoppers, and cockroaches) on the wing and also picked up arthropods (solifugid spiders, beetles and cockroaches) and small vertebrates (mice, fishes, frogs and geckoes) from the ground. After touching the prey with the muzzle, the bats were able to differentiate between species. Scorpions and toads were not taken by *M. lyra*.

2. In lighted and in dark conditions, *M. lyra* detected and caught prey only when it moved. Dead frogs briskly pulled over the floor were also detected and caught, whereas stationary dead frogs were disregarded by the bats (Table 1).

3. When dead frogs were pulled over the watered surface of a glass plate to eliminate noises by motion, the motion no longer alarmed the bats. From the results of these experiments it was concluded that *M. lyra* detects prey on the ground by listening to the noise of the moving target only, and not by echolocation (Table 1C, Fig. 1). Furthermore, *M. lyra* were not attracted by frog calls.

4. *M. lyra* differentiated between palatable frogs and non-palatable toads only after touching the prey with the muzzle.

5. Experiments with freshly killed frogs coated with toad secretions or covered with toad skins indicate that *M. lyra* differentiates between frogs and toads by chemical means. There was no evidence that these prey were differentiated by means of echolocation.

Introduction

The Indian False Vampire belongs to a heterogeneous group of echolocating bats which are called gleaners (Fenton 1984). Gleaning bats prefer to capture prey from ground and water surfaces. *Megaderma lyra* eats the larger arthropods and vertebrates of suitable size e.g. frogs, geckoes, lizards, fish, mice, birds and other bat species (Advani 1981; Habersetzer 1983). *M. lyra* is a large bat (bodyweight 30–38 g) with large, medially fused pinnae which form a unified auditory receiver directed towards the ground. This species is also an excellent flyer capable of hovering and even of flying backwards. The False Vampire emits very brief (0.4–1.0 ms) broadband echolocation signals of low intensity (less than 80 dB SPL) consisting of 3–6 harmonics, which cover a frequency range of 20–120 kHz. During obstacle avoidance and when snatching mealworms in flight from forceps, *M. lyra* consistently emits echolocation signals, even in bright daylight (Möhres and Neuweiler 1966). However, in a more natural situation when *M. lyra* is required to detect and catch prey in complete darkness, it is capable of flying towards the target, locating and successfully capturing it, often without emitting a single echolocation sound (Fiedler 1979). *M. lyra* are also attracted by tape-recorded rustling noises produced by moving mice on the floor, and will even attack the broadcasting loudspeaker.

In the natural habitat *Macroderma gigas*, the Australian relative of *M. lyra*, is attracted by a Audubon bird caller, and individuals may fly as close as a few centimetres around the head of the experimenter (Coles and Neuweiler, unpublished observations). *Antrozous pallidus*, another gleaning bat species, is also attracted by the noises of prey moving on the ground and does not emit echolocation signals during the approach and attack of prey (Bell 1982).

All the above observations suggest that gleaning bats may detect and locate prey on the ground facultatively or exclusively by listening to rustling noises produced by the targets, without the aid

of echolocation. The present study therefore reports observations and experiments on the prey-catching behaviour of *M. lyra*, in an attempt to answer the question of the sensory mechanisms by which this gleaning bat detects prey.

Materials and methods

All observations and experiments were performed in an outdoor cage in the Botanical Garden of Madurai University, India, and the bats were maintained in the natural climate and diurnal cycle. The flight cage measured 7.5 × 3.4 × 3.5 m and contained a dark enclosure at one corner of the ceiling so that the bats could seek refuge during the day. On the floor of the flight cage, an artificial pond was dug (4.15 × 2.30 × 0.64 m) in which frogs were maintained. A total of 24 *M. lyra* (11 males and 13 females) were caught at the caves at Keela Kuilkudi and Pannianmalai, about 10 km from the University campus and housed in the outdoor cage. The bats were fed daily between 18 and 22 h, which corresponds to their natural activity period. The food for the bats consisted of frogs, mice and cockroaches, depending on availability.

All experiments and observations were conducted during the evening up to midnight using room light. The use of visual cues for prey detection was excluded by repeating all experiments in darkness and monitoring the bats with an infrared night vision scope.

During each experiment, echolocation sounds of *M. lyra* were detected by a QMC-ultrasound microphone and recorded on a high-speed tape recorder (Lennartz, 76 cm/s).

Results

Prey-catching behaviour

The initial observations concerned conditions under which *M. lyra* became alerted to and caught prey that moved spontaneously in the cage or was introduced by the experimenter. It was found that the bats were able to catch flying insects as well as arthropods and vertebrates moving on surfaces. Flying insects were intercepted aerially, and after capture the bats returned to their roost with the prey in the mouth and consumed it at the roost. A total of five moths, three beetles and one cockroach with bodylength ranging between 2 and 4 cm were caught in this way. The bats emitted echolocation sounds continuously during these insect capture flights in the dimly lit outdoor cage.

In addition, beetles, cockroaches and grasshoppers were caught whilst walking or jumping on the floor of the cage. Furthermore, four solifugid spiders and eleven freshwater crabs (bodylength approx. 2.5 cm) were caught quickly when they started to run over the floor. There was no indication that the bats paid any attention to stationary arthropods, even if they were only a few centimetres from their heads. However, as soon as these potential prey started to move the bats directed their heads towards the target. A few seconds later the bats flew off, briefly hovered over the target and then descended on the prey, grasping it in the mouth. Then the bats immediately flew from the ground and returned to the roost to consume the prey. The freshwater crabs which ran over the floor were caught without hesitation in eight trials. Interestingly, three other crabs were approached repeatedly but not caught by *M. lyra*. After removal of their claws, when these crabs started to run again they were quickly caught. It is not clear why the bats refused to catch clawed crabs in these three cases whereas the other eight crabs were caught with intact claws. In this context, it is well known that the megadermatid bat *Cardioderma cor* can prey successfully on poisonous scorpions (Vaughan 1976). However, *M. lyra* was observed to land close to scorpions but never touched them, returning to the roost.

Most of the vertebrates that the bats preyed upon were introduced into the cage by the experimenter. However, two geckoes, one running over the floor and another along a wall, were detected quickly and captured by a single *M. lyra*. In further tests, seven field mice (*Mus booduga*, bodylength up to 7 cm) and 15 laboratory mice placed on the floor of the cage were detected and caught by the bats within 1 min. Usually the bats grasped a mouse at the front and carried it off to the roost. There the bat manipulated the mouse with the help of the wrists in order to bite the ventral neck. The bats then closed the jaws firmly around the throat of the mouse until it suffocated. Also, three live fish (*Ophiocephalus* spp., bodylength 8 cm), which had been thrown on the floor and were flipping their tails, were caught swiftly and consumed by *M. lyra*. Even when freshly killed bats (*Hipposideros speoris* and *H. bicolor*) had been thrown on to the floor of the cage, the bodies were immediately picked up and consumed completely by *M. lyra*.

Frogs were found to be a preferred food item for *M. lyra*, and as in all other observations, frogs were detected and caught only when moving or after jumping, usually with no chance of escape. Experiments with the South American frog-eating bat *Trachops cirrhosus* have shown that frog calls might attract bat predators (Tuttle and Ryan 1981). On three occasions in the present study frogs in the artificial pond of the cage called loudly for several minutes. However, *M. lyra* showed no reaction to long duration and loud calling even though the frogs were only a few meters away. As soon as these frogs moved or jumped they were detected and caught immediately by the bats.

Table 1. Experiments in prey detection on the ground by *Megaderma lyra*

	No. of expt	Number of flights towards and captures of							No reaction
		Dead frog	Stationary frog	Moving frog after					
				1st	2nd	3rd	4th	up to 11th jump	
A. Living frogs versus dead frogs									
In light	31	0	0	0	6	4	8	13	0
In darkness	8	0	0	3	4	0	1	0	0
B. Pulling dead frogs over floor									
In light	54		0	37	9	6	2	0	0
In darkness	11		0	11	0	0	0	0	0

	Frog pulled over glass					Frog pulled over floor			
	1st	2nd	3rd	4th	5th pull	1st	2nd	3rd	4th–6th pull
C. Dead frogs pulled over glass									
In light	62	0	0	0	0	0	42	9	5	2	4

Under lighted conditions the bats did not inspect the pond, where frogs frequently protruded their heads above the water surface. However, in darkness, 3 out of 15 bats were observed to skim over the pond surface continuously for a total of almost 2 h with few interruptions. Finally the bats dived quickly to the water surface and flew off with a frog in the mouth. As far as can be determined by observation with an infrared night vision scope and acoustical monitoring, the frog targets with heads protruding out of the water did not move or produce any sounds. Echolocation sounds were emitted continuously by the bats during these flights.

With the exception of the three cases where frogs were caught after a long searching period, *M. lyra* approached and caught arthropods or vertebrates only when they moved. Clearly, movement of prey is an important prerequisite for detection by *M. lyra*, and moving prey may be detected by vision, by echolocation or by listening to noise. In order to decide which of these sensory cues apply to the catching behaviour of *M. lyra*, a series of simple experiments have been performed with frogs as targets.

Detection of frogs by Megaderma lyra

Initially, the observation that *M. lyra* was alerted and attacked moving targets only was quantified as shown in Table 1 A and Fig. 1. Both a freshly killed frog and a live frog (*Rana tigerina*, body-length 3–7 cm) were placed on the floor of the cage.
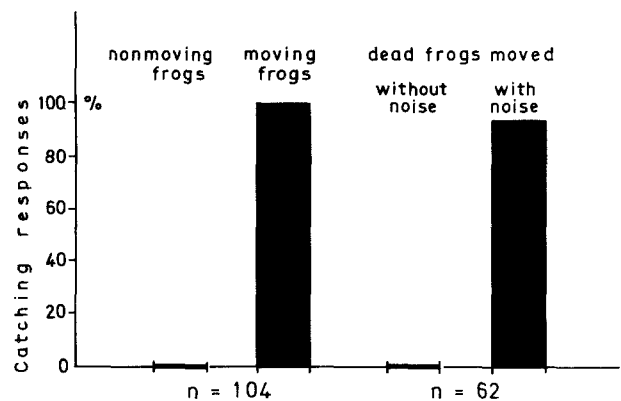

Fig. 1. Percentage of catches for stationary versus moving frogs and for dead frogs moved by pulling, with and without generating noise

In none of the 31 two-choice trials did the bats pay any attention to the dead frog. The live frog usually remained immobile and jumped away after 5–20 min (frogs which had not moved within 20 min were removed from the experiment). The bats did not react to the live stationary frogs, but as soon as the frogs started to jump, bats detected and usually caught them after the second or third jump. The experiments were repeated in darkness to exclude visual cues, and the catching behaviour was observed with an infrared night vision scope. As Table 1 A indicates, the results in darkness were the same as in lighted conditions, and in fact the bats' reaction was faster. In darkness, three frogs were caught after the first jump, compared to no

captures when the cage was lighted. It is concluded that moving prey was not detected visually.

In the next experiment, two freshly killed frogs were offered as prey, with one placed on the floor as in the previous experiment and the other tied to a long piece of string. The frog attached to the string could be pulled in jerks for a brief period of time over the floor for a distance of 10–15 cm. Both dead frogs were placed about 1.0–1.5 m apart on the floor of the cage, and were not moved for 20 min. During this time no bats showed any reaction whatsoever to the stationary dead frogs. When one of the frogs was pulled briefly the bats were alerted immediately. In most cases (68%) the frog was caught after the first pull (Table 1B and Fig. 1) by the bats landing close to the frog (within 5–15 cm) and moving towards it. The complete sequence, from take-off to capture, lasted no longer than 5 s. In 54 trials the bats never reacted to the dead frog which was not moved. When 11 trials were repeated in darkness, the performance of the bats was faster than in the light, and in each case the frog pulled by the string was caught within several seconds after the first pull (Table 1B). The results of these experiments demonstrate that bats distinguished between moving and stationary targets and not between live and dead frogs.

It is possible that dead frogs pulled by string could be detected by echolocation or the scratching noises (Fig. 2) which occur when the body is moved over the earth floor of the cage. In order to avoid any noise from the pulled frog, the trials were repeated, but with the frog pulled across the surface of a glass wetted with water (100 × 20 cm). Initially, the dead frog was placed on the glass plate for 15 min without pulling, and during that time none of the bats reacted to the target. Then the frog was pulled up to the end of the glass plate for 5 trials and also pulled over the floor for up to 6 trials. In 62 trials, the bats never reacted to any of a sequence of 5 pulls of a dead frog over the wet glass plate (Table 1C and Fig. 1). No sounds or noises could be detected by the microphone or the unaided ear when the frogs were moved over the glass plate. However, as soon as scratching noises (Fig. 2) occurred as the frogs were finally pulled over the floor, *M. lyra* became alarmed immediately and the frog was caught after the first pull in 42 of the 62 experiments (Table 1C). In 4 experiments the bats did not react even after the frog was pulled 6 times over the floor.

From the above results it is concluded that *M. lyra* detected prey only by target noises (Fig. 2) and not by echolocation. Since all of these experiments were performed under lighted conditions,
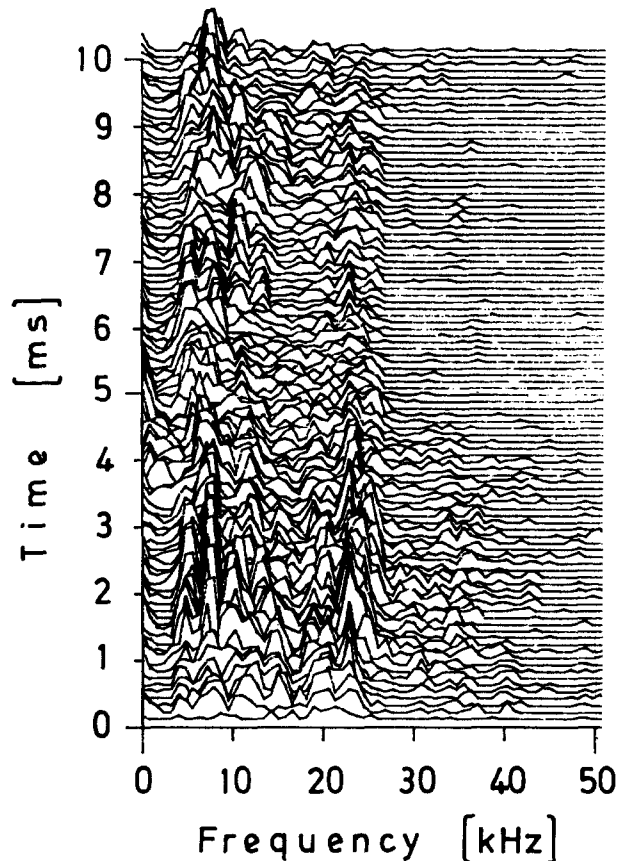

Fig. 2. Spectro-temporal energy distribution of the noise generated by a freshly killed frog pulled briskly over the earth floor of the cage

it reinforces the idea that vision is not involved in the detection of a moving target.

Prey discrimination

M. lyra does not accept all prey of a suitable size, e.g. a scorpion was approached but not seized, as mentioned above. The bats also differentiated between frogs and toads since three different species of frogs (*Rana tigerina, Rhacophorus maculatus* and one unidentified species) were consumed but three species of toads (*Bufo melanostictus, Uperodon systema* and one unidentified species) were rejected. In 20 trials with *B. melanostictus* and 86 trials with *U. systema* the bats approached the toads (bodylength 4–8 cm) in all but 4 presentations, in the same way as they did frogs, i.e. as soon as movement started. The bats landed close by the toads but as soon as they touched the prey with the muzzle the bats took off again, leaving the toad behind. In only 4 of over 100 presentations, the bats did not react, even to a moving toad.

When toads were touched by the bats or the experimenters, they inflated their air-sacs, thereby considerably enlarging the body size. The air-sacs were punctured in 59 *U. systema* and these non-inflated toads were touched by *M. lyra*, as in the case of intact toads, the bat took off again in 37 cases (63%) without the toad. A total of 19 non-inflated toads were grasped by the bat and carried to the roost. These toads were not consumed and were dropped by the bats within 10 s. However, three non-inflated toads were also consumed, leaving only the intestines, with no apparent ill effects on the bats. Whereas no inflated toads were taken, one third of the non-inflated toads were caught but later dropped by the bats and only a few were eaten. Apparently, in non-inflated toads there is less complete protection against bat predation.

As toads were avoided only after contact with the bats, it is assumed that *M. lyra* recognizes toads by chemical means from skin secretions. This assumption was tested by coating the frontal areas of freshly killed frogs (*Rana tigerina*) with a secretion from the parotid glands of *Bufo melanostictus*. The coated dead frogs were then pulled over the floor as in the previous experiments. In 20 out of 22 trials the coated frogs were caught and carried to the roost, but dropped after 3–62 s. If a frog which had been coated on the head with secretions was caught by the rear legs, the frog was eaten as far as the head, which was then dropped on the floor. Coated frogs which had been dropped on the floor were carefully washed with water and sand and then pulled over the floor again. A total of 20 discarded, coated frogs which had been washed were captured again, but now the bats consumed them all.

Finally, a few freshly killed toads with the skins removed were offered to the bats. These naked dead toads were caught after being pulled across the floor, but after some chewing the bats dropped the toads. Also, freshly killed frogs were covered with toad skins and offered to the bats. In this case the covered frogs were caught, but within seconds they were dropped to the floor again. When the same frog was offered with the toad skin removed, it was caught and completely eaten.

From these experiments it is concluded that *M. lyra* may be able to differentiate between toads and frogs chemically, by tasting or smelling the skin secretions.

Echolocation

The above experiments demonstrate that moving prey on the ground is not detected by echolocation.

In spite of these observations, bats emitted their typical short-duration, broadband signals continuously as soon as they were alerted. Sequences of echolocation sounds were recorded throughout the approach and capture of the prey and also during the return flight to the roost. An initial survey of several hundred sonar pulse sequences indicates that no specific relationship exists between sonar emission and prey type or approach to the target. The type of echolocation sound emitted was the stereotyped brief multi-harmonic pulse described by Möhres and Neuweiler (1966). Sonar pulse sequences of bats hunting in the light or in darkness are very similar and are indistinguishable in each condition. It is suggested that echolocation is used for general orientation and not for detection of prey on the ground.

Discussion

False Vampire bats are difficult to observe in nature (Habersetzer 1983). Compared with the other bat species found in Madurai, they are the last to leave the caves, at a time when it is fully dark and they fly low over ground. According to observations of *M. lyra* by radio telemetry, these bats spend at least 75% of the night perched on rock faces, branches of bushes or trees close to the ground (0.5–1.5 m). Skimming over the ground and the surfaces of water was not frequently observed in *M. lyra*. Habersetzer (1983) has assumed that *M. lyra* spend most of the night hanging at some favourite roosting sites and listened for moving prey. Beneath the roosting sites of *M. lyra* piles of droppings were found which contained the remains of frogs, birds, rodents and other bats. Since the question of how *M. lyra* detects prey on the ground could not be answered in the field, it was necessary to observe bats in an outdoor cage to try to solve this problem.

M. lyra is a so-called whispering bat, which emits faint (60–80 dB SPL) and very short duration (0.4–1.0 ms) echolocation pulses consisting of 3–6 harmonics (Möhres and Neuweiler 1966; Habersetzer 1983). The presence of multiple harmonics results in a broadband signal, which ranges in energy from 20 to 120 kHz. It has been suggested that such a broadband signal might be optimal for distinguishing various surface structures, e.g. mouse fur compared to patches of grass, due to spectral differences in the echoes (Habersetzer and Vogler 1983). However, Fiedler (1979) has shown that *M. lyra* can detect and catch a mouse without echolocation.

The results reported in the present study demonstrate unequivocally that prey on the ground was detected only when it moved. The experiments with dead frogs pulled across the floor of the cage, in comparison to frogs pulled over a wet glass plate, suggest that the prey was detected by the noise of movement. Typically, stationary and totally silent prey were never detected by *M. lyra*. These observations make sense, since in a natural habitat such as grassland, scrub jungles etc. potential prey such as mice, frogs and birds move or sit under cover and therefore detection by echolocation may be impossible. In addition, the echolocation sounds emitted by *M. lyra* are low in intensity and the echolocation range is probably short. As for owls (Payne 1971), a good foraging strategy for *M. lyra* is based on waiting for rustling noises coming from ground, passively locating the sound source and then flying towards it. Thus, echolocation might be used for obstacle avoidance during flight, and also may help to inspect the prey at close range. Recent studies of audition indicate that *M. lyra* is adapted for such an acoustic method of prey location. The large, centrally fused pinnae of *M. lyra* produce pressure gains which result in hearing thresholds of -25 dB SPL between 15–22 kHz and -15 dB SPL between 55–60 kHz (Neuweiler and Rübsamen, submitted for publication). In addition, inferior collicular neurons frequently have upper thresholds at 40–50 dB SPL and are specifically responsive to noise signals (Rübsamen and Neuweiler, in preparation). Such features of the auditory system make *M. lyra* highly sensitive to very faint rustling noises. For example their is little doubt that the bats used in the present study, which caught spiders in the outdoor cage, detected them by their running noises. Such rustling noises generated by movement in general contain considerable energy in the lower ultrasonic frequency range from 18–25 kHz (Fig. 2), which is the band to which auditory neurons are most sensitive to noise in *M. lyra* (Rübsamen and Neuweiler, in preparation).

M. lyra has good hearing sensitivity down to 1 kHz (Neuweiler et al. 1984; Schmidt et al. 1984). Therefore it is very surprising that the bats in the present study did not react to calling from frogs in the artificial pond. Interestingly, the African megadermatid bat, *Cardioderma cor,* catches frogs and fails to be attracted by frog calls as well (Ryan and Tuttle 1987). Such behaviour is in sharp contrast to that of the unrelated phyllostomatid bat species *Trachops cirrhosus*, which is clearly attracted to frog sites by the calls and even differentiates between palatable and non-palatable species

by call type (Ryan and Tuttle 1983). At present the only explanation for this difference of behaviour with respect to frog calls is not a deficiency in audition but a species-specific difference in prey-catching behaviour, with the *T. cirrhosus* being highly specialized. In contrast, the Old World megadermatid bats are less selective, in the sense that they will listen to and locate all kinds of noise. Megadermatids thereby accept a wide range of food, from flying insects to freshwater crabs, frogs and other bat species. The Australian megadermatid species, *Macroderma gigas*, has the same prey-catching behaviour as the Indian False Vampire (Kulzer et al. 1984) and is readily attracted to artificial sound sources such as bird call imitations (Coles and Neuweiler, unpublished observations). In fact any noise source which would indicate a moving target probably elicits an approach response in megadermatid bats. In the present experiments, even stones pulled over the floor were attractive to *M. lyra* and were abandoned only after the bat had touched the target.

M. lyra does not catch every item which can be located. For example, toads were rejected in the present experiments, and this strongly suggests that they are recognized as unpalatable food, but only after a chemical sensation, perhaps by taste, or even after touch. The involvement of touch in prey differentiation can be inferred from the observations that toads with non-inflated air-sacs were not completely rejected. In addition, dead frogs covered with a toad skin secretion were always grasped by the bats and dropped afterwards. This type of behaviour may be explained also by a greater effect of the skin secretion when the skin was stretched by air-sac inflation and faster evaporation or dilution of the secretion when the toad skin was placed on a non-secretory surface such as a frog skin. Therefore, with the evidence to hand, the question of whether touch assists the bats in differentiating prey remains to be answered. It appears that prey differentiation is achieved at close range only, and it is suggested that echolocation plays a minor role, if any, in target differentiation.

The above conclusion is not supported by observations in darkness, where several bats scanned the pond surface and finally caught a frog. Passive acoustic location did not appear to be involved and in these cases, as in all other prey capture flights monitored, *M. lyra* emitted echolocation sounds continuously while skimming over the surface of the pond. These frogs may have been detected by echolocation, as a target protruding from the smooth water surface. Fishing bats detect prey

by echolocating along the water surface (Suthers 1965). In the natural habitat *M. lyra* has not been observed flying over rivers, but several *M. lyra* have been trapped in nets placed over the water of a river. Advani (1981) found the scales and bones of fish in the faeces of *M. lyra* and suggests that they may detect and catch prey which disturb the water surface. Echolocation might be a good method of detecting such protruding targets from the smooth water surface.

The following strategy for prey detection by *M. lyra* might be possible. These bats mainly subsist on ground-dwelling arthropods and vertebrates, and *M. lyra* frequently spends long periods hanging from twigs and rock faces which are close to the ground. During this period bats wait and listen for noises in the environment which may indicate moving prey. Such a strategy has been described for the African megadermatid bat, *Lavia frons* (Vaughan and Vaughan 1986). However, in contrast to *M. lyra*, *L. frons* pursues flying prey only and will not search for food on the ground. Vaughan and Vaughan suggest that insects might be detected by echolocation as well as by the flight noise. As shown in the present study, *M. lyra* does not detect prey on the ground by echolocation but only by listening to the sounds produced by moving prey. Nevertheless, when *M. lyra* scans the water surface it may, in addition, detect prey by echolocation. The returning echoes from protruding targets in the water should be easily distinguished from echoes returning from the smooth water surface. Finally, flying insects might be detected by *M. lyra* by listening to flight sounds, by echolocation, or even by vision, as suggested for *Lavia frons* (Vaughan and Vaughan 1986).

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