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Authors: Marimuthu, Ganapathy, Rajan, Koilmani Emmanuvel, Kandula, Sripathi, Parsons, Stuart, and Jones, Gareth

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Effects of different surfaces on the perception of prey-generated noise by the Indian false vampire bat *Megaderma lyra*

GANAPATHY MARIMUTHU[1], KOILMANI EMMANUVEL RAJAN[1, 3], SRIPATHI KANDULA[1],
STUART PARSONS[2], and GARETH JONES[2]

[1]*Department of Animal Behaviour and Physiology, School of Biological Sciences,*
Madurai Kamaraj University, Madurai 625 021, India; E-mail: gmari@eth.net
[2]*School of Biological Sciences, University of Bristol, Woodland Road, Bristol BS8 1UG, Great Britain*
[3]*Department of Molecular Recognition and Biostructure, Institute of Biotechnology, National University*
Autonomous of Mexico, APDO 510-3, Cuernavaca, Morelos 62250, Mexico

The low- and high-frequency components of a rustling sound, created when prey (freshly killed frog) was jerkily pulled on dry and wet sandy floors and asbestos, were recorded and played back to individual Indian false vampire bats (*Megaderma lyra*). *Megaderma lyra* responded with flight toward the speakers and captured dead frogs, that were kept as reward. The spectral peaks were at 8.6, 7.1 and 6.8 kHz for the low-frequency components of the sounds created at the dry, asbestos and wet floors, respectively. The spectral peaks for the high-frequency sounds created on the respective floors were at 36.8, 27.2 and 23.3 kHz. The sound from the dry floor was more intense than that of from the other two substrata. Prey movements that generated sonic or ultrasonic sounds were both sufficient and necessary for the bats to detect and capture prey. The number of successful prey captures was significantly greater for the dry floor sound, especially to its high-frequency components. Bat-responses were low to the wet floor and moderate to the asbestos floor sounds. The bats did not respond to the sound of unrecorded parts of the tape. Even though the bats flew toward the speakers when the prey generated sounds were played back and captured the dead frogs we cannot rule out the possibility of *M. lyra* using echolocation to localize prey. However, the study indicates that prey that move on dry sandy floor are more vulnerable to predation by *M. lyra.*

Key words: *Megaderma lyra*, gleaning, passive sound localization, prey detection

INTRODUCTION

Several species of microchiropteran bats glean prey from surfaces (Marimuthu, 1997). They use passive sound localization to capture prey that move on different surfaces such as the ground (Bell, 1982, 1985; Fenton *et al*., 1983; Anderson and Racey, 1991; Arlettaz *et al*., 1995), foliage (Belwood and Morris, 1987; Arlettaz, 1996; Arlettaz *et al*., 2001), bark (Faure and Barclay, 1992, 1994) and water (Tuttle and Ryan, 1981). Under natural conditions, terrestrial prey often moves on more than one type of surface. The frequency, intensity and spectral quality of prey-generated sound will vary depending on the type of surface on which it moves. This may in turn affect the ability of gleaning bats to detect the same or even similar-sized prey. Fuzessery *et al*. (1993) showed that the response shown by pallid bats *Antrozous pallidus* varied, based on the kind of substratum on which the prey was tossed. The Indian false vampire bat *Megaderma lyra* feeds on large insects and small vertebrates such as frogs, mice, geckos and even smaller bats (Brosset, 1962; Advani, 1981; Habersetzer, 1983). It listens for the sound produced by prey moving over the ground (Marimuthu and Neuweiler, 1987) and is even thought to capture them occasionally without using echolocation (Fiedler, 1979). However, recent reports suggest that *M. lyra* employs echolocation to capture prey on the ground (Schmidt *et al*., 2000) as well as from the surface of water (Marimuthu *et al*., 1995).

Our preliminary observations showed that *M. lyra* captured more freshly killed frogs when they were pulled over dry sandy floor compared to wet sandy floor and asbestos. In the present study, the sound of a freshly killed frog being dragged over three substrata was presented to *M. lyra*, and its responses analyzed.

MATERIALS AND METHODS

Experimental Design

Bats were captured using a nylon mosquito net on their return flight to a cave before sunrise. The cave is situated at the Pannian hill complex, about 10 km northwest from the Madurai Kamaraj University campus (09°58’N; 78°10’E).

A total of 14 (7 ♂♂ and 7 ♀♀) *M. lyra* were used. Bats were held individually in an experimental room (4.5 m length × 4.5 m breadth × 3.6 m height) and exposed to 12:12 h light-dark cycle. A stage (2.7 m × 2.7 m × 0.5 m) with a dry sandy floor, abutting the walls at the southern and western sides, was available in the room. At a height of 1.5 m from the floor of the stage, a sheet of wire-mesh (30 cm × 30 cm) was fixed vertically to the south-west corner of the wall. The bats could comfortably roost at the wire-mesh. The maximum and minimum temperature inside the room was 33.4 ± 2.9°C and 30.7 ± 0.7°C, respectively. The maximum and minimum humidity was 88.9 ± 8.6% and 54.6 ± 10.6%, respectively (OAKTON Hygrothermograph, Cole-Parmer Instrument Company, USA). Two or three days were allowed for the bats to acclimatize to the new environment during which they were fed with live frogs that were released on the stage.

In our previous study (Marimuthu and Neuweiler, 1987), *M. lyra* responded very well not only to the sounds of a dead frog but also to a small stone being pulled on a dry sandy floor. Hence in the present study, the rustling sound created when a freshly killed frog was pulled with a long thread, on three different substrata (dry sandy floor, wet sandy floor and asbestos sheet), was recorded and played back to each bat individually. Such recordings, using a dead frog, were technically easier than using a live frog. Asbestos was chosen, in addition to the natural sandy floor, as asbestos-roofed huts can be found in the foraging areas of *M. lyra*. Prey organisms such as mouse and gecko usually move over the roof of these huts. We presumed that it is possible for *M. lyra* to hunt over them. Since the sound of the frogs being dragged contained both sonic and ultrasonic frequencies (Marimuthu and Neuweiler, 1987), different sets of equipment were used to record and playback the dragging sound. Only one set of recording was done for each substrate. Each recording contained the sounds of a dead frog pulled at least 30 times. We were interested in whether the bats were responding to the low- or high-frequency components. The simplest way of doing this was to playback either low- or high-frequency sounds and compare the behaviours elicited from the animals. The low-frequency components of the sound were presented to the bats in separate experiments from high-frequency sound. Presentation of sound from the three substrata and that of control sounds were done randomly. Experiments were conducted under dim incandescent light of 0.2 lux (UDT Optometer, USA), which facilitated observation of the bats’ responses. This illumination is less than that of a clear full moon light (0.3 lux).

Recording and Playback Techniques using Low-Frequency Sound (< 15 kHz)

The first set of seven bats (3 ♂♂, 4 ♀♀) were used in this series of experiments. The sound created when a single freshly killed frog (*Rana cyanophylictis*; body length 5.4 cm) was pulled over the three substrata was recorded in a separate, relatively noise-free room, using a UHER M650 microphone connected to a SONY Professional Walkman WM-D6C (frequency response 40 Hz–15 kHz ± 3 dB). The recorded sounds were played back in the experimental room using a NAD 304 amplifier (NAD Electronics, London, UK) connected to a CELESTION KR1 speaker (frequency response 90 Hz–20 kHz; Celestion Industries Inc., Holliston, USA). The speaker was fixed to the base of the stage, facing the ceiling. The distance between the roosting site of the bat being tested and the speaker was approximately 2 m.

Recording and Playback Techniques using High-Frequency Sound (15–120 kHz)

The second set of seven bats (4 ♂♂, 3 ♀♀) were used in this series of experiments. All of them were tested with sounds from dry floor and only four of them were tested with sounds from asbestos and wet floor. The dragging sound was recorded using an S-25 bat detector (frequency response 20–120 kHz ± 3 dB; Ultra Sound Advice, UK) linked to a Portable Ultrasound Signal Processor (PUSP, sampling rate 448 kHz with 8-bit precision; Ultra Sound Advice, UK), set to time expand the input signal 10-times. The output from the PUSP was recorded using the Sony Professional Walkman WM-D6C. In order to playback the time-expanded sounds, they were recompressed (using the PUSP) and broadcast using an S-55 ultrasound amplifier (18–300 kHz ± 3dB) and a S-56 ultrasound loud speaker (10–200 kHz; output level > +85 dB SPL at 0.25 m, 10 to 150 kHz; both Ultra Sound Advice, UK).

General Playback Methods and Data Analyses

A portable oscilloscope (PHILIPS: PM 3010) was connected to the amplifier output to confirm the transmission of signals. The sound pressure level of the dragging sounds was measured at a distance of 15 cm (from the microphone to the head of the frog) using a Brüel Kjaer sound level meter (2234 with 1/4 inch microphone 4135) while they were being recorded, and this level was maintained during playback. The unused parts of the cassette used to record the dragging sounds was played back as a control. During each observation one to seven sounds were played back and responses shown by the bats quantified. However, a maximum of 20 sounds were played back and under such situations if the bats did not respond, it was counted as ‘no response’ (see below).

A freshly killed frog (body length approximately 3.0 cm) was placed, as a reward for the bats, above the speaker when playing back the low-frequency sound, and very close to the speaker when playing back the high-frequency sound. Both speakers were covered with a piece of nylon mosquito net, to avoid damage when the bats landed on them.

The signals were analyzed using a Digital Signal Processing Sonograph (Kay 5500, transform size 512 pts, sampling rate 32 kHz (effective rate 320 kHz) with 8-bit precision). The frequency containing most energy in each dragging sound was measured from a power spectrum of the entire signal.

The responses shown by the bats to playback of low- and high-frequency sounds were classified into the following five mutually exclusive behavioural categories:

1. No response: The bats did not leave the roost.
2. Weak response: The bats flew down across the room and returned to the roost after reaching a height of more than 50 cm from the floor of the stage.
3. Moderate response: The bats flew down towards the speaker and returned to the roost after reaching a height of less than 50 cm from the floor of the stage.
4. Capture attempt: The bats flew down, landed near the speaker but returned to the roost without capturing the frog.
5. Successful capture: The bats flew down, hovered over the speaker, landed on or near the frog, captured it, then flew back to the roosting site and consumed the frog.

At the end of the experiments, the bats were released near the capture site during the hours of darkness. The unused frogs were released into a nearby pond. The data were analyzed by using SIGMA STAT (ver. 1.01, Jandel Corporation, Jandel GmbH, Germany). Data are given as $\bar{x}$ ± SE.

RESULTS

Characteristics of the Dragging Sounds

It is clear that the sounds created when a dead frog was dragged on the dry, asbestos and wet floors contained both low- and high-frequency components (Table 1). The intensity of the low-frequency sounds created on dry floor and asbestos was similar while that from the wet floor was less intense (Fig. 1A). However, the intensity of the high-frequency sounds from dry floor was higher compared to sounds from the asbestos and wet floor, which were similar in intensity (Fig. 1B). The intensities of the entire sound signals measured while recording when the dead frog was pulled on dry, asbestos and wet floors were 65.2 ± 0.5 dB

TABLE 1. Frequencies ($\bar{x}$ ± SE) with most energy for the low- and high-frequency components of dragging sounds on three substrata and number of days ($\bar{x}$ ± SE) taken by the bats to show a response. Samples sizes (the number of sound pulses used to measure frequency and the number of animals responded, respectively) are shown in parentheses

Substrata	Low-frequency		High-frequency	
	kHz	days	kHz	days
Dry floor	8.6 ± 0.18 (12)	6.0 ± 0.49 (7)	36.8 ± 0.83 (14)	6.2 ± 0.55 (7)
Asbestos	7.1 ± 0.16 (13)	6.2 ± 0.37 (5)	27.2 ± 1.64 (14)	6.3 ± 0.33 (3)
Wet floor	6.8 ± 0.07 (15)	7.0 (1)	23.3 ± 0.65 (14)	6.7 ± 0.33 (3)

SPL, 64.2 ± 0.4 dB SPL and 61.5 ± 0.5 dB SPL, respectively (for each $n = 10$).

Bat-Responses to Low-Frequency Sound

Out of seven *M. lyra* tested, all responded to the sound of a frog being dragged across the dry floor, five to the asbestos floor, but only one to the wet floor. The number of playback sessions conducted with the sounds from the dry, asbestos, and wet floors were 149, 84 and 68 respectively (Fig. 2A). In fact, the bats began to show response only 6–7 days after the initiation of playing back the sounds from all the three substrata (Table 1). Such periods of latency to the sounds from the three substrata were not significantly different (One Way ANOVA, $F_{4,\,20} = 0.19$, $P >> 0.05$). The numbers of weak and moderate responses and capture attempts to the sounds from the three substrata were not significantly different when they were compared to each other ($F_{2,\,9} = 0.49$, $P >> 0.05$). The number of successful captures in response to the sounds from dry and asbestos floors was also not significantly different ($\chi^2 = 1.88$, *d.f.* = 1, $P > 0.05$). However, the numbers of successful captures in response to sounds from the dry floor ($\chi^2 = 12.6$, *d.f.* = 1, $P < 0.001$) and asbestos ($\chi^2 = 5.09$, *d.f.* = 1, $P < 0.05$) were significantly greater when each was compared to responses to sounds from the wet floor. The single bat that responded to the sound from wet floor did not demonstrate all possible responses. For example, it did not respond moderately nor made capture attempts in any of the 68 playback sessions (Fig. 2A). Successful captures

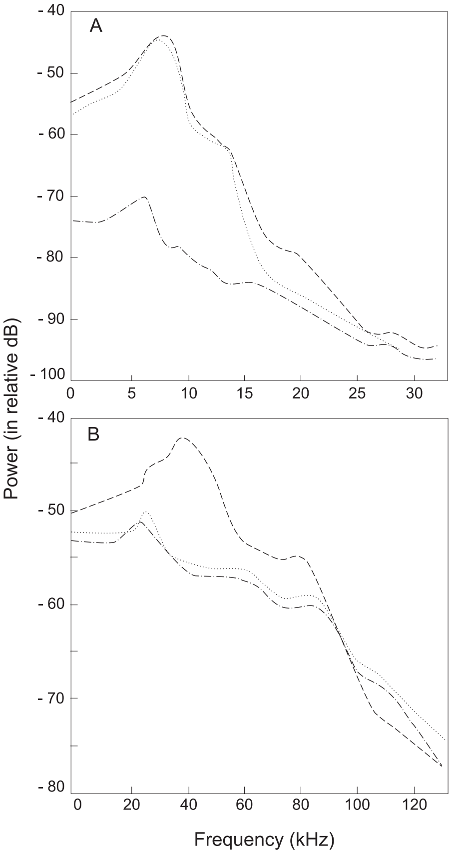

FIG. 1. Representative power spectra of (A) low-frequency component and (B) high-frequency component of noise created when a dead frog was jerkily pulled on dry sandy floor (broken line), asbestos (dotted line) and wet sandy floor (dotted broken line)

occurred six times more on dry floor than on wet floor and success on asbestos fell between these two extremes. Thus, it is evident that bat-responses were greater to the sound from the dry and asbestos floors compared to the sounds from wet floor. This indicates that the low-frequency sound produced when a frog is dragged across a wet floor might be more difficult to localize or less tempting to the bats. None of the bats responded to the control sounds (41 playback sessions in total).

Bat-Responses to High-Frequency Sound

Out of seven bats tested, all responded to the sound from the dry floor. Out of four bats tested in the experiment with sound from asbestos and wet floors, three responded to both while the fourth bat did not respond to both. Number of playback sessions conducted with the sounds from dry, asbestos and wet floors were 69, 68 and 63, respectively (Fig. 2B). The weak and moderate responses to the sounds from the three substrata were not significantly different $\chi^2 = 0.47$, *d.f.* = 2, $P >> 0.05$). Interestingly, in all playback sessions not all bats exhibited capture attempts in response to the sounds from all the three substrata. Whenever the bats landed near the speaker, this was always followed by successful captures. The number of successful captures was significantly higher for sound from the dry floor compared to the asbestos ($\chi^2 = 4.97$, *d.f.* = 1, $P < 0.05$), and wet floors ($\chi^2 = 4.88$, *d.f.* = 1, $P < 0.05$). However, responses to the asbestos and wet floors were not significantly different ($\chi^2 = 0.02$, *d.f.* = 1, $P >> 0.05$). This indicates that the high-frequency sound produced when a frog is dragged across asbestos and wet floors is less intense and apparent to the bats (Fig. 1B). None of the bats showed any response to the control sounds (36 playback sessions in total). Thus, it is evident that in this set of experiments, bat responses were greater to sound from dry floor than to sounds from asbestos and wet floors.

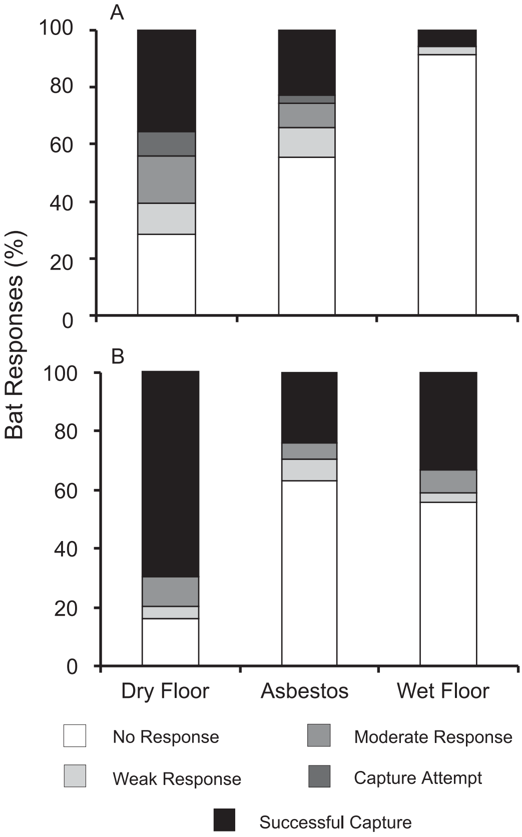

FIG. 2. Categories of responses shown by *M. lyra* to low-frequency (A) and high-frequency (B) components of frog pulling noise from dry sandy floor, asbestos and wet sandy floor

Interestingly, the number of successful captures was significantly higher in response to the high-frequency sounds recorded from the dry ($\chi^2 = 5.93$, *d.f.* = 1, $P < 0.05$) and wet floors ($\chi^2 = 9.50$, *d.f.* = 1, $P < 0.01$), compared to low-frequency components. There was no significant difference in the number of successful captures between low- and high-frequency playback sounds from the asbestos floor ($\chi^2 = 0.95$, *d.f.* = 1, $P > 0.05$).

DISCUSSION

The results of the playback experiments confirm that *M. lyra* employs passive listening to locate prey (Marimuthu and Neuweiler, 1987). In addition, this study emphasizes that the quality of prey detection varies depending on the kind of substrate on which the prey moves. The absence of significant differences between percentage values for weak and moderate responses and capture attempts, to both low- and high-frequency sound components, indicate that the ability of bats to detect prey was apparently similar on all substrata. It is intriguing that the bats started reacting to the playbacks only after a week. Such observations raised a question — is it possible that they learned to react to just any audible broad band noise bursts by approaching the speakers and inspecting them for food? However, occurrence of more successful captures in response to the sound from dry floor rejects such hypothesis and demonstrates that *M. lyra* could readily detect prey that move on this substratum. Presumably, the higher intensity of the spectral peaks produced on dry floor (at 8.6 and 36.8 kHz) aided localization. Although the sound produced at the dry floor was relatively more intense than those produced at the other two substrata, all should have been easily heard by the bats, because *M. lyra* is known to be sensitive to low-frequency sounds (Neuweiler *et al.*, 1984). Hence it indicates that bats responded to a combination of frequency and intensity, i.e., sound must be in the correct frequency range and be loud enough for the bat to hear and be able to localize the position of the prey. Similarly, the pallid bat *Antrozous pallidus*, which is also a gleaner (Bell, 1982), exhibited more successful captures of prey (anesthetized crickets) when they were tossed on plastic compared to other substrata such as paper, wood and foam (Fuzessery *et al.*, 1993). Fuzessery *et al.* (1993) also suggested that the higher frequency of the spectral peak from sound produced on plastic (at 5–6 kHz) aided localization. The spectral peaks produced on paper and wood was at 3–4 kHz and that produced on foam was less than 1 kHz. More successful captures by *M. lyra* in response to the high-frequency sound from dry floor (ca. 40 kHz) may possibly be due to its greater sensitivity to these frequencies (Neuweiler *et al.*, 1984; Schmidt *et al.*, 1984). Moreover, the second harmonic of echolocation sounds of *M. lyra* also falls within this frequency range (Möhres and Neuweiler, 1966; Habersetzer, 1983). Even though we claim that *M. lyra* listens to the prey-generated sound its use of echolocation to localize prey on ground cannot be ruled out (see Schmidt *et al.*, 2000). However, if the bats had been solely reliant on echolocation, we would expect there to be little or no difference in the apparency of the frog-captures on the three substrata. Another megadermatid bat, *Cardioderma cor*, also responded to only the sonic frequencies of the sounds generated by prey (frog) movement on floor (Ryan and Tuttle, 1987). However, in an apparently similar experimental set-up to ours, the bats did not contact the speakers in their experiments. Since our experiments were conducted under the background of a dim light, the bats might have used their vision as a secondary aid to detect the frogs, especially after landing close to the speakers.

The possible mechanism for sound localization by *M. lyra* is based on binaural cues, mainly interaural intensity differences (IIDs). However, the authors have no evidence for the presence of such IIDs in the acoustic system of *M. lyra.* IIDs are less pronounced for lower versus higher frequencies, even within the ultrasonic range (Fuzessery and Pollak, 1984; Koay *et al.*, 1998). Localization of prey-generated sounds, especially very low frequency sounds, might require alternative mechanisms, such as reliance upon interaural time and phase difference cues (Stevens and Newman, 1936; Masterton, 1974). Since the frog-dragging sounds contain both low- and high-frequency components, we suggest that *M. lyra* may use binaural time- or phase-difference cues to detect low-frequency sounds (< 9 kHz), and binaural intensity differences to detect high-frequency sounds (> 15 kHz) during the process of localization of prey. It is still to be investigated whether sufficient interaural time and phase-difference cues are available to *M. lyra* in spite of its medially fused pinnae. Since *M. lyra* responded relatively well to the sounds of the dry sandy floor, playback experiments with similar kind of sounds having different intensities may be carried out in future.

Since asbestos and wet floors produced relatively less intense sounds, especially at higher frequencies it is probable that under natural conditions when prey organisms move on these substrata (e.g., wet sand due to rains and asbestos-roofed huts) they are less obvious to *M. lyra*. On the other hand, prey that move on dry sandy floors are more vulnerable to predation.

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