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ORIGINAL ARTICLE

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Hunting in unfamiliar space: echolocation in the Indian false vampire bat, *Megaderma lyra*, when gleaning prey

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Abstract The literature suggests that in familiar laboratory settings, Indian false vampire bats (*Megaderma lyra*, family Megadermatidae) locate terrestrial prey with and without emitting echolocation calls in the dark and cease echolocating when simulated moonlit conditions presumably allow the use of vision. More recent laboratory-based research suggests that *M. lyra* uses echolocation throughout attacks but at emission rates much lower than those of other gleaning bats. We present data from wild-caught bats hunting for and capturing prey in unfamiliar conditions mimicking natural situations. By varying light level and substrate complexity we demonstrated that hunting *M. lyra* always emit echolocation calls and that emission patterns are the same regardless of light/substrate condition and similar to those of other wild-caught gleaning bats. Therefore, echoic information appears necessary for this species when hunting in unfamiliar situations, while, in the context of past research, echolocation may be supplanted by vision, spatial memory or both in familiar spaces.

Keywords Chiroptera · Echolocation · Prey detection · Orientation · Spatial memory

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Introduction

For most animals, prey detection and localization is a multisensory process, but in some situations sensory information is only available to predators through a single modality. For example, in complete darkness the barn owl, *Tyto alba*, can hunt using only prey-generated sounds (Dusenbery 1992). Still, this nocturnal predator has large eyes well suited for the detection and localization of prey under low-light conditions (van der Willigen et al. 2003). In the wild and under laboratory conditions, barn owls often hunt over small hunting grounds from familiar perches (Fast and Ambrose 1976; Konishi 1983). Similarly, in familiar settings some bats that take prey from substrate (i.e., gleaning bats) locate prey in darkness using prey-generated sounds without the use of echolocation (Fiedler 1979; Arlettaz et al. 2001). Fiedler (1979) reported that the Indian false vampire bat, *Megaderma lyra*, hunted live mice in complete darkness successfully with or without the use of echolocation.

However, Schmidt et al. (2000), using more sensitive recording equipment, demonstrated that Fiedler's results might reflect the use of microphones insensitive to the low-intensity echolocation calls of this species. Stoneman and Fenton (1988), using recording equipment comparable in sensitivity to that used by Schmidt et al. (2000), found that *M. lyra* emitted calls under familiar conditions in darkness during only 80% of gleaning attacks. This value dropped to 20% when lighting conditions approximated a moonlit night, corroborating evidence (Bell 1985; Bell and Fenton 1986; Grant 1991) that some species of gleaning bat (e.g., *Macrotus californicus, Nyctophilus* spp., *Plecotus auritus*) augment or supplant echoic information with visual information under familiar and adequately lit conditions (Bell 1985; Bell and Fenton 1986; Grant 1991; Eklof and Jones 2003). Therefore, the hypothesis that vision can supplant echolocation has remained viable.

During nightly forages in the wild, *M. lyra* hunts small vertebrates (e.g., frogs, small lizards and mammals) and large invertebrates apparently from both familiar perches and over unfamiliar ground (Marimuthu and Neuweiler

1987; Audet et al. 1991). To our knowledge, all studies to date on the echolocation behavior of *M. lyra* gleaning prey have used familiar flight rooms and predictable flight paths possibly mimicking conditions experienced when hunting from a familiar perch over a known hunting ground. Here, in unfamiliar settings and using unpredictable prey trajectories, we investigated whether, and at what rates, *M. lyra* emits echolocation calls when gleaning prey under conditions approximating bright, moonlit nights and dark, moonless nights. We compared these emission rates to those of previous studies of this species and other gleaning species. We also compared the echolocation calls used when bats hunted in darkness over simple, intermediate and complex terrestrial surfaces to test the prediction that as substrate complexity increased calls would become shorter and contain more energy at higher frequencies. In closing, we discuss the relative importance of echolocation, visual information, spatial memory and attention for gleaning under different lighting conditions, in familiar versus unfamiliar spaces and over different substrate types. We believe that further use of this bat will provide valuable insights into the interaction of sensory processes and spatial memory that enables target realization in animals.

Methods

Animals and outdoor enclosure

Our experiments were conducted at Madurai Kamaraj University (MKU) near Madurai, Tamil Nadu, India (9°58′N, 78°10′E) from January to March 2003. We used 12 adult male *M. lyra* caught as they returned to a cave about 10 km west of MKU. To ensure the unfamiliarity of the two experimental foraging areas, bats were housed together until used as subjects in an outdoor enclosure (L 7.5 × W 3.4 × H 3.5 m), provided with a variety of large insects each night and hand fed pieces of market-bought fish twice a week. During the first night of experimentation, individual bats were transferred to one of two unfamiliar flight rooms (described below) and presented with a total of two to four prey items each. During the second night, bats were moved to the flight room they had not yet experienced and again presented with a total of two to four prey items. Therefore, during experiments, each bat hunted alone and was presented with a total of six prey items over two consecutive nights. Bats spent as few as 3 and as many as 15 days in captivity. All bats were released at point of capture when data collection for this study was completed.

Unfamiliar flight rooms and prey trajectories

We took several steps to maximize the novelty of the experimental conditions under which the bats hunted. We used two similar indoor flight rooms (each approx. H 2.5 × W 2.5 × L 4.0 m) that differed with respect to the position of potential roosting locations and other minor characteristics (e.g., position of disabled exhaust fan). For each individual no more than four trials were conducted in either room (typically three for each bat in each room). We varied prey trajectory between trials; no bat encountered the same prey-path twice in succession (see Fig. 1). Furthermore, each bat experienced each light/substrate combination only once (for a total of six trials per bat). We counterbalanced exposure sequence to light/substrate conditions between subjects to control for possible ordering effects.

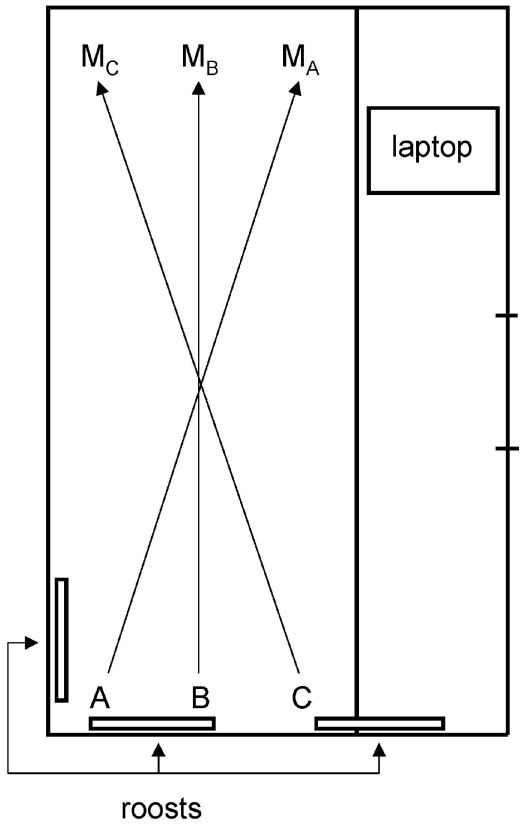

Fig. 1 Schematic of flight room from above depicting the three prey paths (*A, B* or *C arrow* indicates direction of movement) used to elicit hunting behaviors from *Megaderma lyra*. Three positions of microphone (M_X) reflect prey path used during trial as indicated by subscript. The *unmarked line* represents a 50-cm-high partition between the foraging area and the rest of the room

On a 1.5×3.8-m area within each flight room (Fig. 1), we tested the bats' abilities to detect, locate and capture frogs from three substrate conditions: (1) lexan polycarbonate (equal to the unriffled surface of the small, ephemeral, lily pad-laden ponds where we caught the frogs); (2) open sand (common substrate around ponds); and (3) a mosaic of low-lying grasses, naturally curved over and less than 10 cm in height, and small rocks (approximately 6 cm in diameter) spread over sand (removed from and arranged as found between ponds).

A trial began with the prey item's first landing and ended when the bat caught it and flew off to roost and feed.

Prey items

Seventy-two frogs (*Rana cyanophlyctis*, *R. tigerina*) were caught in these ephemeral ponds around MKU as required.

Frogs were killed using cranial and spinal pithing. To control for the possible effects of prey size on echolocation behavior (Schmidt et al. 2000; Leippert et al. 2002) we used frogs 3–4 cm in body length. We tied 4-m lengths of thread (0.2 mm diameter) to an ankle of each freshly killed frog. Rather than drag the frog across the substrate, we used the thread to hop would-be prey slowly across the floor, thus simulating the movement of a frog. Unlike the gleaning phyllostomid *Trachops cirrhosus* (Tuttle and Ryan 1981), *M. lyra* does not respond to the mating calls of male frogs (Marimuthu et al. 1995) nor is it often successful at locating and capturing silent, stationary prey (Fiedler 1979; Marimuthu and Neuweiler 1987; personal observations). Therefore, using hopping frogs, *M. lyra's* preferred food during the time of our study, better mimicked natural hunting scenarios than would have stationary prey items. We moved frogs approximately 20–35 cm each 'hop'. The average arc height was approximately 5–10 cm above each substrate, including above the low-lying grass. We landed the frogs approximately 0.6 times/s.

Darkness trials

Each bat experienced each of the three substrate types once in the absence of light. We ensured complete darkness by disabling all possible light sources in the windowless experimental rooms, closing the door (which was sealed with thick, black plastic around the four edges), turning off the lights in the connecting hallway and closing the door at the end of this hallway. Bats were observed during foraging trials using an infrared sensitive night vision scope with a built-in infrared LED light source (Night Owl Explorer NOCX3).

Moonlight trials

Each bat experienced each of the three substrate types once in the presence of light. Using a light meter (Gossen Ultra-Pro) we found that light levels reflected from the sand on clear, moonlit nights nearby the cave where the bats were caught ranged from 0.210 to 0.380 l× 1 m above the ground. We wrapped the 20 W fluorescent light tube in each room with a light filter to reduce light intensity to approximate that of a full moonlit night. Light levels (measured using the same light meter 1 m above the ground) reflected from 12 equidistant positions on the floor of each foraging area (Fig. 1) were 0.274±0.32 l× (mean±SD, room 1) and 0.290±0.47 l× (room 2). These light levels approximate those reported by Bell (1985) and Stoneman and Fenton (1988) using *Macrotus californicus* and both *M. californicus* and *Megaderma lyra*, respectively, as subjects. Bats were observed during foraging trials with the naked eye.

High frequency sound recording

Call sequences emitted during foraging trials were recorded using a D 980 Ultrasound Detector (Pettersson Elektronik AB) using the high frequency output with the high frequency gain set at most sensitive. This microphone was placed just above the floor of the flight room and directed 10° up from horizontal (see Fig. 1 for placement of microphone relative to prey trajectories). This arrangement forced the bats the fly towards the microphone increasing signal-to-noise ratio at the microphone as the attack progressed (i.e., the first call recorded was, at times, emitted more than 3 m from the microphone; the last call before landing was, at times, emitted less than 50 cm from the microphone). Microphone output was passed through a F2000 Control/Filter Unit (Pettersson Elektronik AB) with gain set to 'low' before input to a computer (Dell Notebook C800, Pentium III 800 MHz processor, 512 MB RAM) using a DAQCard-6062E (National Instruments) as interface. Data were stored as .wav files using BatSound Pro v. 3.30 (Pettersson Elektronik AB) software in high speed sampling mode (357.1 kHz sampling frequency, circular buffer, 10-s storage time, 150 kHz external anti-aliasing filter).

Sound analysis

Using BatSound Pro v. 3.30, we high pass filtered .wav files at 12 kHz (filter type: Butterworth, filter order: 8). We began sound analysis at the first call in each sequence for which we could extract all relevant information (i.e., good signal-to-noise ratio). For all sequences, time between calls (inter-pulse interval) and call duration were measured from oscillograms. For sequences recorded in darkness, the peak frequency of the dominant harmonic and highest frequencies of each of the other harmonics were estimated for each call using power spectra. To this end, 512-point fast Fourier transformations (power spectra) were generated for each call also using a Hanning window to reduce the accidental inclusion of background noise.

We also noted the dB difference between peak frequency of the fundamental harmonic (i.e., the first harmonic) and the peak frequencies of the other harmonics (Fig. 3). We then corrected dB intensities of each harmonic using the sensitivity curve for our D980 microphone when calibrated against a Brüel and Kjaer 1/4 inch microphone (grid off) and a Brüel and Kjaer 2610 amplifier. Relative to the fundamental harmonic (i.e., first harmonic), this resulted in an average increase of 3.4 dB to the peak frequency (PF) of the second harmonic, an average increase of 2.1 dB to the PF of third harmonic, an average increase of 7.9 dB to the PF of the fourth harmonic and an average increase of 12.7 dB to the PF of fifth harmonic. After adjustment, the dominant harmonic (i.e., the harmonic of greatest intensity) was identified and noted for each call. A sixth harmonic, which was sometimes recorded, was excluded because it was unlikely that the faint echoes returning from this part of a call were audible to this bat (Neuweiler et al. 1984; Schmidt et al. 1984).

We noted the peak frequency of the second harmonic from the power spectrum (FFTs); the second harmonic, unlike the fundamental, was present in all calls.

Table 1 Call repetition rate (calls/s) during each of the two calling phases of gleaning attack and pre-capture silent period compared between three substrate types using three repeated measures one-way ANOVAs [n=12 in all cases, we set α_1=0.05/3=0.167, α_2=0.05/2=0.25 and α_3=0.05 for (sequential Bonferroni correction, Rice 1989)]

Class	Substrate type	Moonlight (mean±SD)	Darkness (mean±SD)	P (α)
Opening (calls/s)	Plexiglas	16.73±3.41	14.97±3.60	
	Sand	13.58±3.22	12.23±3.00	
	Scrub	12.42±4.64	13.99±2.57	0.806[a](0.050)
Closing (calls/s)	Plexiglas	42.67±4.20	41.45±10.50	
	Sand	45.65±11.52	43.32±9.89	
	Scrub	44.00±10.76	37.05±7.04	0.623 (0.025)
Last call to contact (ms)	Plexiglas	25.76±15.86	14.67±13.61	
	Sand	12.39±7.52	12.64±7.49	
	Scrub	28.31±45.14	19.03±22.67	0.595[a](0.167)

[a] Data violated Mauchly's test of sphericity, thus P was adjusted (Huynh-Feldt's epsilon)

Table 2 Three call parameters in two phases of gleaning compared between three substrate types using three repeated measures one-way ANOVAs [n=12 in all cases, we set α_1=0.05/2=0.025 and α_2=0.05 for each call parameter for within phase comparisons (sequential Bonferroni correction, Rice 1989)]

Parameter	Phase	Plexiglass (mean±SD)	Sand (mean±SD)	Scrub (mean±SD)	P (α)
Call duration (ms)	Opening	0.69±0.22	0.73±0.26	0.79±0.18	0.197 (0.025)
	Closing	0.40±0.06	0.43±0.13	0.46±0.17	0.240 (0.050)
Peak frequency (2nd harmonic) (kHz)	Opening	45.10±1.90	46.70±2.10	46.60±2.60	0.122 (0.025)
	Closing	44.40±1.80	45.10±2.30	45.40±3.00	0.423 (0.050)
Dominant harmonic number (after calibration)	Opening	2.70±0.60	3.20±0.80	2.90±0.70	0.101 (0.025)
	Closing	3.40±0.50	3.30±0.80	3.40±0.90	0.916 (0.050)

We measured time elapsed from last call emitted (or recorded) to the bat's initial contact with substrate from spectrograms and oscillograms (the bat hitting the ground produced sound more intense than either a frog's landing or an echolocation call). In this same fashion, we measured rate of sound production resulting from prey landings in each sequence (see Fig. 3).

We divided individual call sequences into phases using the terminology and methodology of Griffin et al. (1960), Kalko and Schnitzler (1989), Ratcliffe and Dawson (2003), and Surlykke and Moss (2000). To this end we used interpulse interval (IPI) to designate phases and phase changes. Briefly, we designated calls in sequence with randomly varying IPIs of greater than 50 ms as 'opening' calls and those increasing in minimum frequency and decreasing in IPI (10 ms<IPI<50 ms) as 'closing calls' (Ratcliffe and Dawson 2003). Opening calls preceded closing calls. We use the terms opening and closing in lieu of 'search' and 'approach' because in our study the bats initiated their flights and emitted their first detected echolocation call only after the prey's first or second landing. Search would therefore be an inaccurate term because the bat had presumably detected the prey before emitting echolocation calls. Prior to the bats' landing, we did not observe the buzz phase calls (IPI<10 ms) typically found in aerial hawking attacks (Griffin et al. 1960; Kalko and Schnitzler 1989; Surlykke and Moss 2000; Ratcliffe and Dawson 2003). For both light and dark trials, we calculated the call repetition rate for each bat for each of the six conditions for both opening and closing phases. We used a repeated-measures general linear model to compare call emission rates for both opening and closing phases and time from last call to contact between the six light/substrate combinations (Zar 1996).

For dark trials, we averaged the individual call values for each bat for call duration, peak frequency of the second harmonic, and dominant harmonic number within opening and closing phases to avoid pseudoreplication (Ratcliffe and Dawson 2003). We used three repeated-measures general linear models (Zar 1996) to compare call duration, peak frequency of second harmonic, and dominant harmonic number between substrate conditions. Because we divided our call sequences into opening and closing phases, we protected all statistical analyses herein using sequential Bonferroni corrections (Rice 1989; see Tables 1 and 2 for alpha levels). We did not compare call characters of different phases because assignment to phase does not ensure statistical independence between phases (Siemers et al. 2001). All analyses herein were conducted using SPSS v. 10 (licensed to M.B. Fenton).

Comparative data collection and analyses

To contrast call emission in *M. lyra* from our study and from those of Fiedler (1979) and Schmidt et al. (2000) with those of wild caught bats hunting in unfamiliar space from two distantly related gleaning species, we used BatSound Pro v. 3.30 to measure IPI, call duration, and time between last call to contact for three *Nycteris grandis* echolocation call sequences recorded as bats gleaned frogs from the ground and for six *Myotis septentrionalis* echolocation call sequences as bats gleaned moths from a vertical, bark covered trellis (call parameters for these sequences described in Fenton et al. 1983 and Ratcliffe and Dawson 2003, respectively). For both species, original recordings were made using a QMC 200S Microphone and a RACAL

4D high-speed tape recorder operated at 76 cm/s. Both *N. grandis* and *M. septentrionalis* have relatively small eyes compared to *M. lyra* and neither has been reported to use vision in lieu of echolocation under any circumstances.

Results

General observations

Each bat began each attack sequence after the frog's first landing by flying to a point 30–50 cm directly above where the frog had made initial contact with the substrate. Then each bat flew approximately 90–240 cm in pursuit of prey before attacking and capturing it. We only observed hovering before capture once, specifically when bat 6 hunted in the dark over sand. *M. lyra* landed directly over the frog in 58 trials and within 5 cm of the frog in the remaining 14 trials. These 14 trials were distributed without discernible pattern between frog species, light levels, and substrate types.

Light versus dark trials

Echolocation calls were detected and recorded from all bats under every light/substrate condition (total 72 trials: 12 bats, 6 trials per bat). Analyzed sequences averaged 1,536 ms/1,617 ms (Plexiglas: light/dark), 1,729 ms/1,633 ms (sand: light/dark), and 1,729 ms/1,478 ms (scrub: light/dark) in length from the first detectable opening call to the bats' contact with the substrate. From the 12 bats, we analyzed 2,863 echolocation calls (opening: 956; closing: 1,907). However, we used individual bats, not calls, as the basic statistical unit. With or without Bonferroni correction, repetition rate did not differ significantly within phase between light/substrate combinations (Table 1). *M. lyra* emit, on average, 13.99 calls/s during opening phase and 42.36 calls/s during closing phase. Similarly, time between last call and contact did not differ with respect to light/substrate condition (Table 1). The last airborne attack call was emitted, on average, 18.79 ms before contact with the substrate.

Call design with respect to substrate type

All calls analyzed were frequency modulated with multiple harmonics (Table 2 and Figs. 2 and 3). With or without Bonferroni correction, within opening and closing phases of gleaning attacks, call duration, peak frequency of second harmonic, and dominant harmonic did not differ significantly between substrate types (Table 2).

Unexpectedly, the bats produced echolocation calls while on the ground in 64 of 72 trials. Most of these calls were too intense for the microphone's chosen sensitivity (i.e., clipped) and could not be accurately analyzed for frequency parameters. Including only those sequences where calls were recorded while bats were on the ground, we calculated the average number of bursts, average burst duration (in ms) and call emission rate (calls/s) within bursts for each bat and used these values to calculate overall average values for each light/substrate condition. All 12 bats produced calls during at least four of their six trials. Eight of the 12 bats emitted calls on the ground during dark, Plexiglas trials producing an average of 3.3 bursts, each of 83.9 ms average duration with an average emission rate of 66.2 calls/s. During light, Plexiglas trials, 10 of 12 bats produced an average of 2.7 bursts, each of 91.7 ms average duration and average emission rate of 51.7 calls/s. During dark, sand trials, 7 of 12 bats produced an average of 2.5 bursts, each of 63.4 ms average duration and average emis-

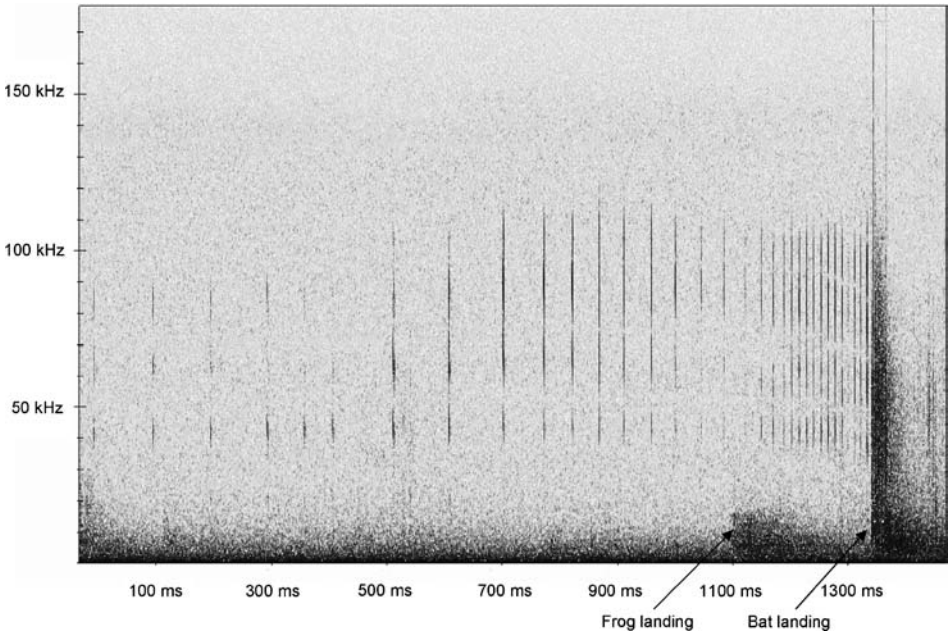

Fig. 2 Typical spectrogram for *M. lyra* during gleaning attack

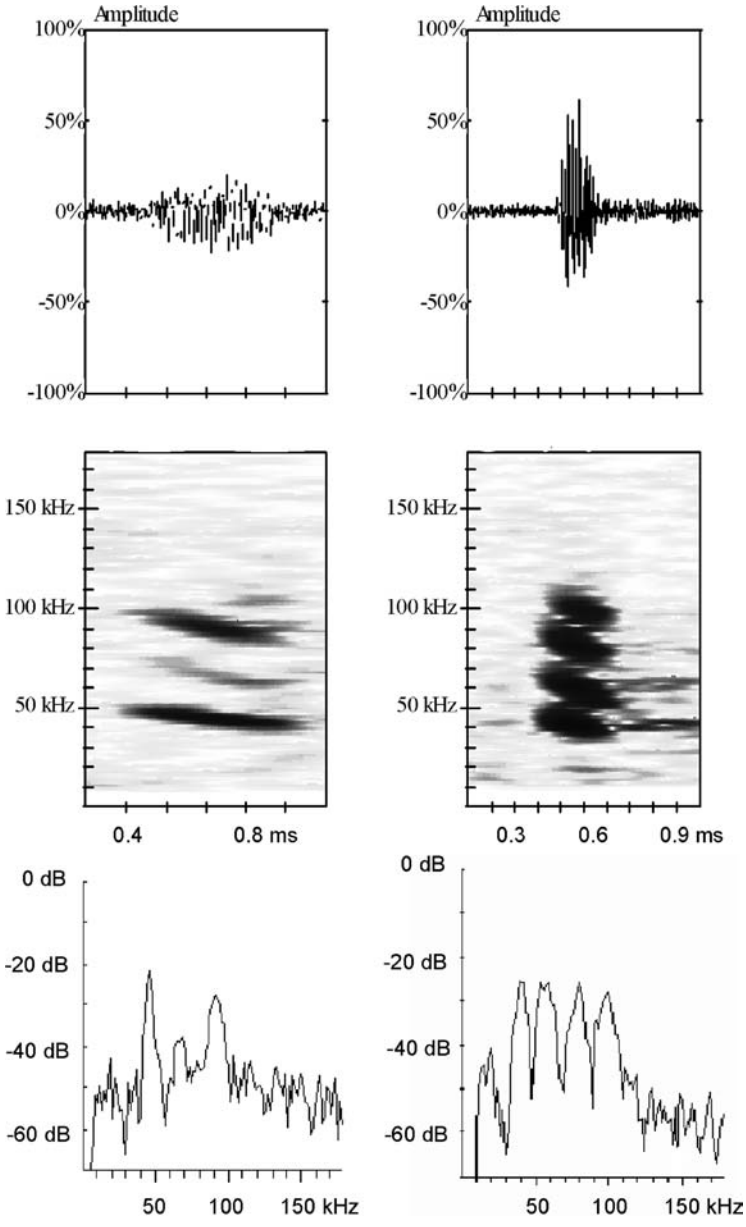

Fig. 3 Oscillograms (*top*), spectrograms (*middle*) and power spectra (*bottom*) illustrating an opening phase call (*left panel*) and a closing phase call (*right panel*) during gleaning attacks for *M. lyra*

sion rate of 66.7 calls/s. During light, sand trials, 9 of 12 bats produced an average of 2.8 bursts, each of 69.3 ms average duration and average emission rate of 77 calls/s. During dark, scrub trials, 9 of 12 bats produced an average of 2.4 bursts, each of 90 ms average duration and average emission rate of 64.5 calls/s. During light, scrub trials, 9 of 12 bats produced an average of 2.4 bursts, each of 70.3 ms average duration and average emission rate of 69 calls/s.

Comparative data: emission rate versus time to capture

N. grandis emitted, on average, 14.34 calls/s during opening phase; 52.73 calls/s during closing phase, while the last call was emitted 37.7 ms before contact. *M. septentrionalis* emitted 12.25 calls/s during opening phase; 28.64 calls/s during closing phase. The last call was emitted, on average, 90.6 ms before contact with the trellis (Ratcliffe and Dawson 2003).

Discussion

To find a target an animal must incorporate novel sensory input and spatial memory, if available, of the surroundings. Predation offers a model for how animals integrate sensation and memory. Here we have shown that *M. lyra* emits echolocation calls throughout gleaning attacks on noisy, moving prey regardless of light condition or substrate similarly to gleaning species with relatively small eyes from two distantly related families (Vespertilionidae and Nycteridae; Teeling et al. 2002). This convergence or conservation of call emission rates during both opening and closing phases of gleaning attacks suggests these patterns

may represent optimal solutions to a common problem: obtaining information from echoes useful for capturing prey from surfaces.

Conversely, within opening and closing phases, calls did not differ in duration or frequency of maximum energy (neither dominant harmonic nor peak frequency of second harmonic) in relation to substrate type. This conservation of call design itself over different substrate types may represent a constraint with respect to design flexibility, relative to the broader bandwidth harmonics found in the calls of other bats (Ratcliffe and Dawson 2003; Siemers and Schnitzler 2004), in the ancient family Megadermatidae (Teeling et al. 2002; Springer et al. 2004).

In the laboratory, at least two gleaning vespertilionids, *Myotis myotis* and *M. blythii*, stop echolocating when approaching prey on complex backgrounds more than 1 s before capture (Arlettaz et al. 2001). However, in unfamiliar settings the gleaning vespertilionids, *M. septentrionalis* and *M. lucifugus*, emit calls up until less than 100 ms before capture (Ratcliffe and Dawson 2003). For *M. lyra*, we found no significant differences between the six light/substrate conditions with respect to time between last call and contact with prey/substrate. Regardless of light/substrate condition, *M. lyra* continued to emit calls almost until contact much like *M. septentrionalis* and *N. grandis*. This species therefore received echoic information reflected from the prey and substrate throughout all sequences in all light and substrate combinations and changes in the echo spectrum should have indicated changes in the position of the prey (Neuweiler 1989).

There is ongoing debate about the use of echoes versus prey-generated noises by gleaning bats (Schmidt et al. 2000; Arlettaz et al. 2001; Ratcliffe and Dawson 2003). Given the rates of call emission relative to the rate of sounds produced by frogs' landings, information about prey position, which changed in both horizontal and vertical planes, was updated more thoroughly by echolocation than by prey-generated noises (i.e., landings). In novel hunting situations, the auditory scene (Bregman 1990; Barber et al. 2003) provided by echolocation may be more important than either prey-generated sounds or visual information. A recent study (Barber et al. 2003) suggests that when the gleaning bat *Antrozous pallidus* (Vespertilionidae) is processing echoic and prey-generated sounds in tandem, overall performance suffers, perhaps as a result of limited attention.

In many studies on microchiropteran echolocation behavior, bats can exploit familiar laboratory situations by flying along stereotyped and obstacle-free flight paths. In our study, bats could not use a stereotyped flight path because each flight room was novel and prey was never pulled along any one path twice in succession (see Fig. 1). The need to orient effectively in strange surroundings may partially explain the difference in call emission between our study and those of Fiedler (1979), Schmidt et al. (2000) and Stoneman and Fenton (1988). Using effectively the same recording equipment, we found *M. lyra* emitted calls more than two times to over three times more frequently during the closing phase than did *M. lyra* at the end of attack sequences in Schmidt et al.'s 2000 study (see Fig. 6 and text on page 981 of Schmidt et al. 2000). Further, the bats in our study emit echolocation calls comparable in duration and interpulse interval to the buzz phase calls of aerial hawking bats. However, they emit these calls while handling prey on the ground: to our knowledge this has only been previously reported for *Mysticina tuberculata*, a bat that is specialized for hunting terrestrially (Jones et al. 2003). Given the costs of echolocating while not in flight and at these emission rates (Speakman and Racey 1991), the possible function(s) of this behavior in both species is worthy of further investigation.

In the context of past research (Fiedler 1979; Stoneman and Fenton 1988; Schmidt et al. 2000), our findings indicate that *M. lyra* may use spatial memory, recalled with echoic and/or visual cues, to assess familiar hunting grounds (Neuweiler and Möhres 1967, reviewed by Gallistel 1990). However, Stamps (1995) suggested *M. lyra* may fly along fixed routes as a result of motor learning rather than spatial memory. Whatever the interpretation, *M. lyra* may rely on information other than that provided by echoes in familiar space.

Audet et al. (1991), using radiotelemetry, found that *M. lyra* uses both familiar and unfamiliar hunting grounds in the wild. Given the demands of hunting in a world that varies through space and time, spatial memory, rather than motor learning of specific flight paths, seems a more tenable explanation because prey will be found in different locations even if in the same familiar area. As a result, specific point A to point B flight paths would prove ineffectual for capture even at short distances.

We argue that as a consequence of using spatial memory, *M. lyra* stops emitting, or reduces the rates of emission of echolocation calls in familiar surroundings and suggest that the lack of use of echolocation in many laboratory studies of gleaning bats is probably due to training effects (i.e., laboratory artifact). However, such behavior in the wild would confer several benefits, including bats being able to pay more attention to prey-generated noises, and more successfully locate prey in highly cluttered environments (Arlettaz et al. 2001), rather than contend with processing both these sounds and echoes in parallel through the auditory system (Barber et al. 2003). Calling less frequently would reduce the cost of vocalizing at rates greater than wing beat frequency (Speakman and Racey 1991) and, interestingly, increase the susceptibility to predation of prey with bat-detecting ears on hunting grounds familiar to Indian false vampire bats.

Conclusion

M. lyra gleaned moving, noisy frogs from a variety of substrate types under both moonlit and lightless conditions. Echolocation calls were emitted throughout all attacks almost until capture and did not differ significantly, with respect to phase, in emission rate, duration, dominant harmonic number, or peak frequency of the second harmonic. Based on the results of previous studies, we suggest that

echolocating bats use spatial memory for navigation in familiar laboratory settings and, possibly, in their natural environments. Spatial memory may be of underestimated importance in the sensory ecology of foraging bats (see Schnitzler et al. 2003 for review) and in familiar laboratory settings (in which bats normally capture stationary prey) may result in reduced call emission rates or the cessation of calling entirely (e.g., *Nyctophilus* spp. Grant 1991; Bailey and Haythornthwaite 1998). However, for bats in the wild echolocation appears essential for successfully gleaning prey in unfamiliar and changing environments.

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