Stationary prey insures life and moving prey ensures death during the hunting flight of gleaning bats

G. Marimuthu

Department of Animal Behaviour and Physiology, School of Biological Sciences, Madurai Kamaraj University, Madurai 625 021, India

While flying, the microchiropteran bats emit brief sounds of high frequencies (15–200 kHz) through the mouth or the nostrils and listen to the echoes reflected from obstacles and prey. The information from the echoes provides the bats an auditory representation of their surroundings with much precision. It is known that sympatrically living echolocating bat species search for prey at different foraging zones. Their audition and structure of the emitted sound signals are adapted to the specific foraging areas and hunting behaviour. A few species of bats use the foraging strategy of gleaning, i.e. capturing prey from the ground and other surfaces including water. Most of the gleaning bats are carnivorous. They use the noise associated with the movement of the prey as the principal cue to detect them on the ground without using echolocation. They use echolocation while capturing prey in the air or on water surface. However, the pattern of echolocation is not similar to the typical pattern shown by other microchiropterans. Normally the hearing sensitivity of the bats is neurologically tuned to the high frequencies of their echolocation calls which vary from species to species. In addition, the ears of gleaning bats are more sensitive to the low frequency noise (5–20 kHz) created by the movement of the prey. Passive listening to the prey-generated noise might be more economical, by collecting available information through the ears, without using echolocation. Such passive method of prey detection is also used by other echolocators like killer whales.

Bats and echolocation

Bats are unique in that they are the only flying mammals, they hang upside down and use echolocation. The microchiropteran bats, smaller and insectivorous, are equipped with an effective system of echolocation for orientation, and to detect and capture prey. The megachiropterans, larger and frugivorous, do not echolocate but have a well-developed visual system for orientation. While flying, the microchiropterans emit a variety of trains of high frequency, brief echolocation sounds consisting of frequency modulated (FM) or constant frequency (CF) signals or a combination of both, with or without harmonics. Such rapid sequences of inaudible (to humans) vocalization are emitted either through the mouth or through the nostrils and bats listen to their echoes reflected from prey and other objects around them. Echolocation enables bats to obtain detailed information about the size, shape, position, range and velocity of flying insects[1]. A typical sequence of echolocation exhibited by pipistrelle bats while detecting and capturing insects has been reported recently[2]. Several field studies showed that different species of microchiropterans forage in distinct habitats that impose very different acoustical constraints on the auditory detection of prey. The type of echolocation signals emitted by each species is associated with its foraging habitat. Neuweiler[3] has distinguished four classes of foraging habitats of bats found in and around Madurai. They are: i) foraging in open spaces, ii) foraging close to or within vegetation, iii) gleaning from leaves and from ground and iv) gleaning from water surfaces. He made an extensive correlation between the preferred foraging habitat and best hearing frequency in echolocating bats. This article is restricted to the foraging behaviour of gleaning bats, emphasizing the methods they use to detect prey.

Gleaning bats

Nearly 30% of about 540 species of Microchiroptera are carnivorous. They hunt for prey by gleaning, i.e. capturing prey on the ground, from tree bark, cliff faces, foliage or from water surface. Table 1 lists a few species belonging to different microchiropteran families that have converged upon the strategy of gleaning[4–20]. Bats like *Antrozous pallidus*[21] and *Megaderma lyra* (personal observations) are captured in small mammal traps, and in the lowest panel of the mist nets at less than a metre above the ground, respectively at their foraging areas. This shows that they spend time on or near the ground possibly searching for prey. Highly manoeuvrable flights and the ability to hover are the essential features for gleaning[22]. Broad, short wings contribute to manoeuvrability, and bats with such wings have often been

Table 1. List of gleaning bats and the surfaces on which they detect and capture prey

Bat species	Surface	Author and reference
Antrozous pallidus; (V)	ground	Bell[4] Fuzessery *et al.*[5]
Cardioderma cor; (M)	ground	Ryan and Tuttle[6]
Macrotus californicus; (P)	ground	Bell[7]
Macroderma gigas; (M)	ground	Kulzer *et al.*[8]
Megaderma lyra; (M)	ground	Fiedler[9], Marimuthu and Neuweiler[10]
	water	Marimuthu *et al.*[11]
Micronycteris hirsuta; (P)	foliage	Belwood and Morris[12]
M. megalotis; (P)	foliage	Belwood and Morris[12]
Myotis blythii; (V)	ground and foliage	Arlettaz[13]
M. emarginatus; (V)	ground	Schumm *et al.*[14]
M. evotis; (V)	ground	Faure and Barclay[15]
M. myotis; (V)	ground	Arlettaz[13]
M. septentrionalis; (V)	bark trellis	Faure *et al.*[16]
Nycteris grandis; (N)	ground	Fenton *et al.*[17]
N. thebaica; (N)	ground	Fenton *et al.*[17]
Otonycteris hemprichi; (V)	ground	Arlettaz *et al.*[18]
Plecotus auritus; (V)	ground	Anderson and Racey[19]
Tonatia sylvicola; (P)	foliage	Belwood and Morris[12]
Trachops cirrhosus; (P)	water	Tuttle and Ryan[20]

M – Megadermatidae, N – Nycteridae, P – Phyllostomidae, V – Vespertilionidae.

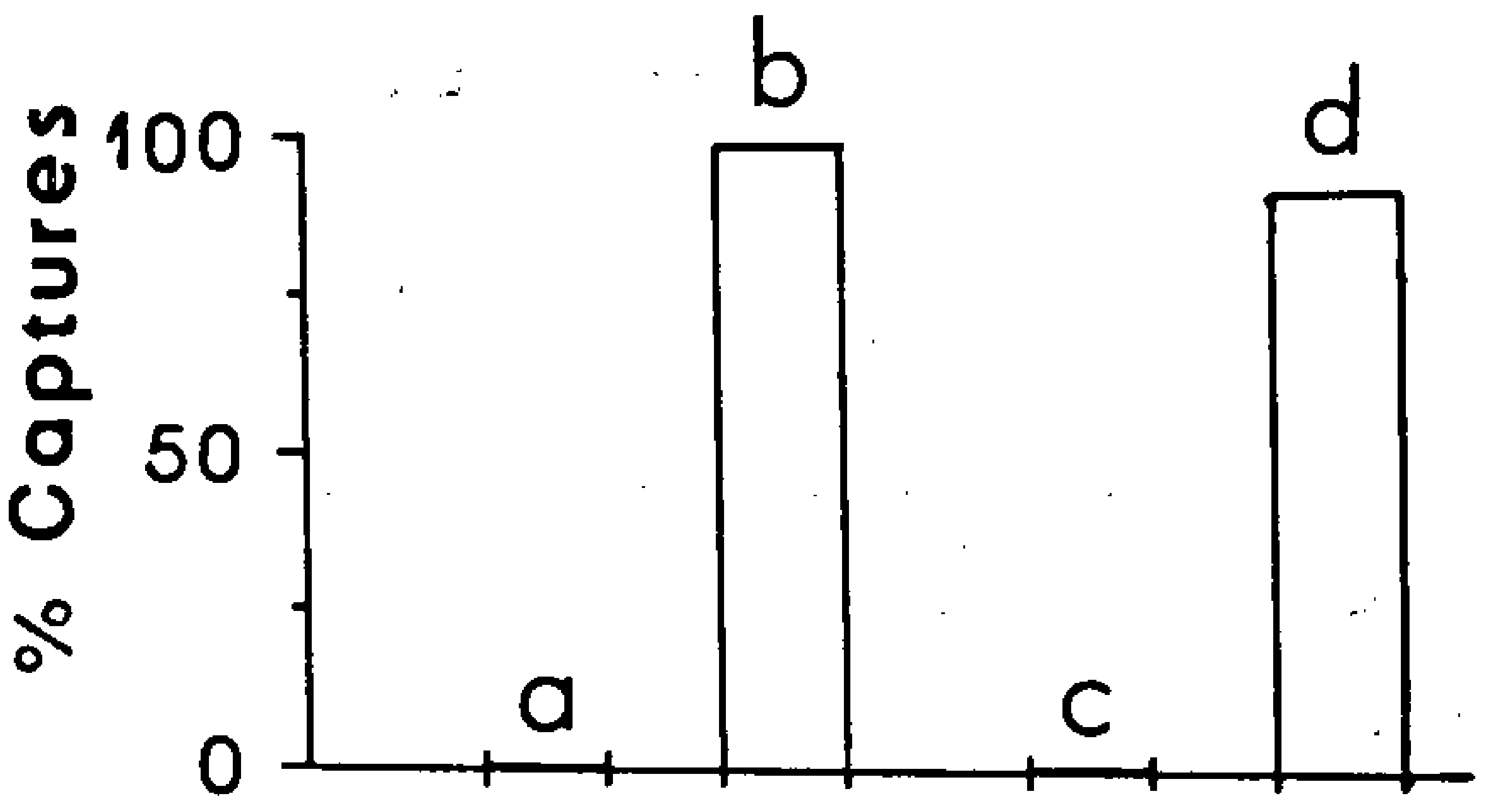

Figure 1. Percentage of captures made by *M. lyra* on live frogs ($n = 104$) when they were stationary (*a*) and moving (*b*) on the sandy floor; and when the freshly killed frogs ($n = 62$) were pulled on the wet glass plate (*c*, without noise) and sandy floor (*d*, with noise); modified from ref. 10.

considered as gleaners. Large pinnae are also characteristic of gleaning bats. An exception is *Euderma maculatum* (Vespertilionidae), a bat with proportionally largest ears among the chiropterans, which does not glean[23]. Most of the gleaners do not use echolocation to detect prey, instead they mainly rely on passive hearing by listening to the rustling noise produced by the movement of the prey.

The Indian false vampire bat *Megaderma lyra*

Megaderma lyra is one of the five species of bats belonging to the family Megadermatidae, distributed in the tropics of Australasia and Africa. It commonly occurs throughout India and lives in caves and unused buildings. Several minutes after sunset, *M. lyra* departs from the day roost and search for ground-dwelling prey such as frogs, mice, geckos and larger insects. while flying low over the ground. By conducting experiments under laboratory conditions, Fiedler[9] demonstrated that *M. lyra* could locate the noise of live mice in complete darkness without using echolocation.

Experiments conducted later at Madurai under semi natural conditions in an outdoor enclosure ($7.5 \times 3.4 \times 3.5$ m), showed that *M. lyra* detects and captures live frogs on a sandy floor only when the frogs jump, both under light and darkness[10]. The bats capture freshly killed frogs also when the frog is briskly pulled with a long thread over the floor. However, the bats could not detect stationary frogs, live or dead. In the next set of experiments, it was shown that the bats did not respond when the freshly killed frogs were pulled over a wet glass plate to prevent the noise associated with the movement of the frog. When pulling of the same frogs was continued on the floor, the bats approached and captured them (Figure 1). This clearly shows that *M. lyra* uses the noise of the moving prey as the principal cue for detection. The rustling noise, caused when the prey is moved, has a frequency range of 10–25 kHz. Electrophysiological experiments have shown[24] that the maximum hearing sensitivity of *M. lyra* also falls at a similar frequency range, which is consistent with the idea that bat uses passive hearing to detect prey. It is also seen that *M. lyra* has to touch the prey to decide whether it is palatable or not. For example, when the toad *Bufo melanostictus* jumped, the bat approached and attacked, but returned to roost immediately, leaving the toad on the floor.

In another set of experiments, we found out that *M. lyra* actively echolocated in darkness to detect and capture frogs from the surface of the water[11]. Frogs were available in an artificial pond ($4.2 \times 2.3 \times 0.6$ m) and were free moving and distributed themselves throughout the pond. Typically the frogs which stayed at the water surface showed a posture with the dorsal part of the head protruding out of the water. About 30 min after sunset, *M. lyra* began to fly over the surface of the pond. By landing at the edges of the pond intermittently, the bats undertook 'searching flights' in order to detect a frog with head protruding out of the water surface. Then they approached towards the frog with a rapid hovering flight and captured the frog with the mouth which created a sudden splash at the surface of the water. The frog did not show any movement. However, ripples were continuously produced by the movement of frogs staying at other parts of the pond. Figure 2 shows the daily pattern of searching flight activity of *M. lyra*. In most of the observations, the bats succeeded in capturing a frog. However on a few occasions the frogs apparently sensed

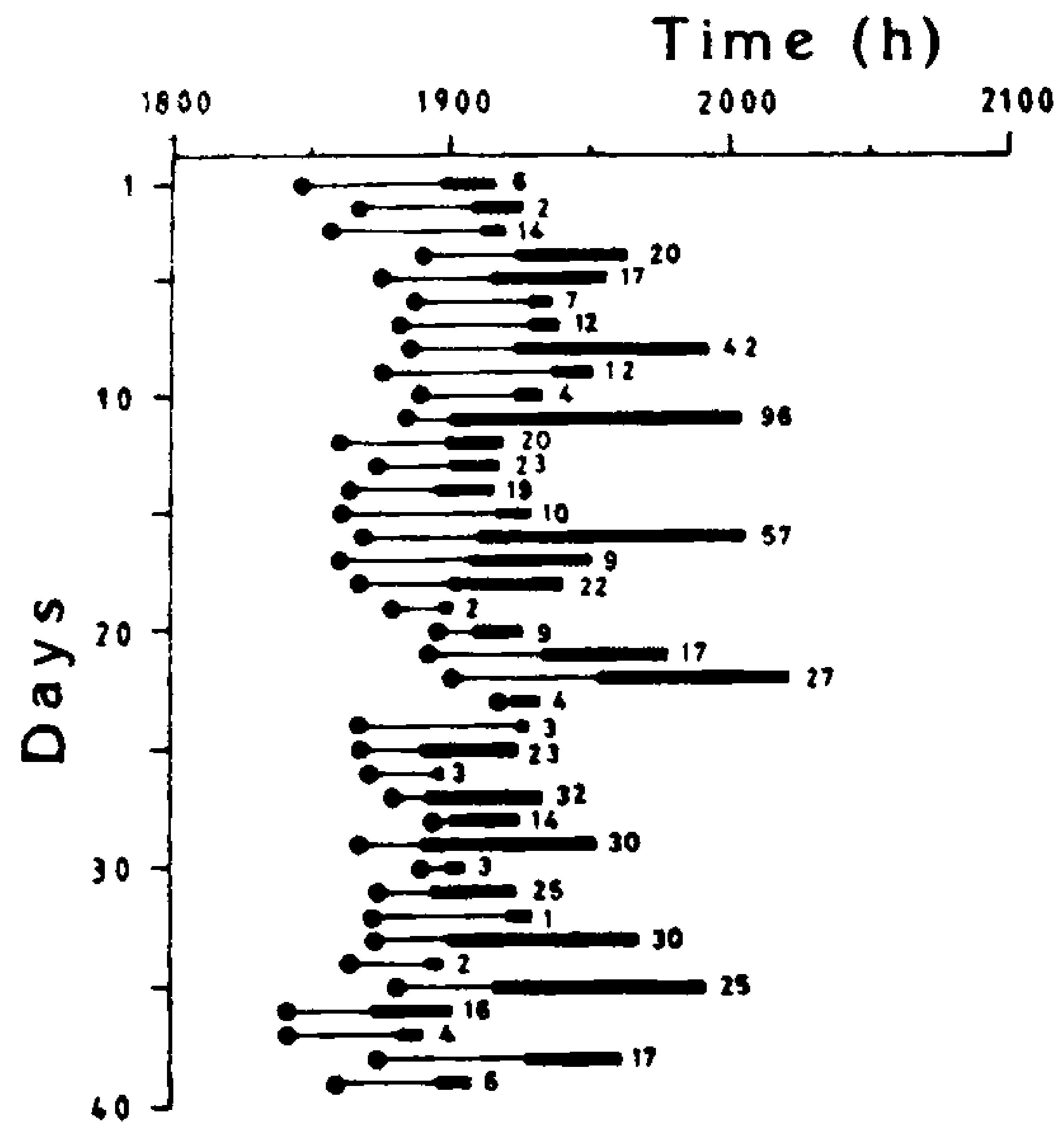

Figure 2. Representative pattern from the noctovision observations on day-to-day changes in the searching flight activity of *M. lyra* to detect and capture a live frog from the surface of the pond in darkness. Black circles indicate the time at which the bat flew out of the roost chamber (180 × 160 × 120 cm) situated at the ceiling of the outdoor enclosure. The horizontal lines following the black circles indicate the duration spent in grooming, stretching one or both wings, etc. before flying towards the pond. The black bands indicate the duration of searching flight (19.9 ± 20.2 min, mean ± SD, range 0.3 to 85.8 min, $n = 89$) to capture a frog at the surface of the pond. The inter-search flight interval was 40.3 ± 27.4 s (range 2 to 123 s, $n = 1041$). The number of search flights is given at the end of black bands and it was 17.1 ± 17.7 (range 1 to 96, $n = 89$).

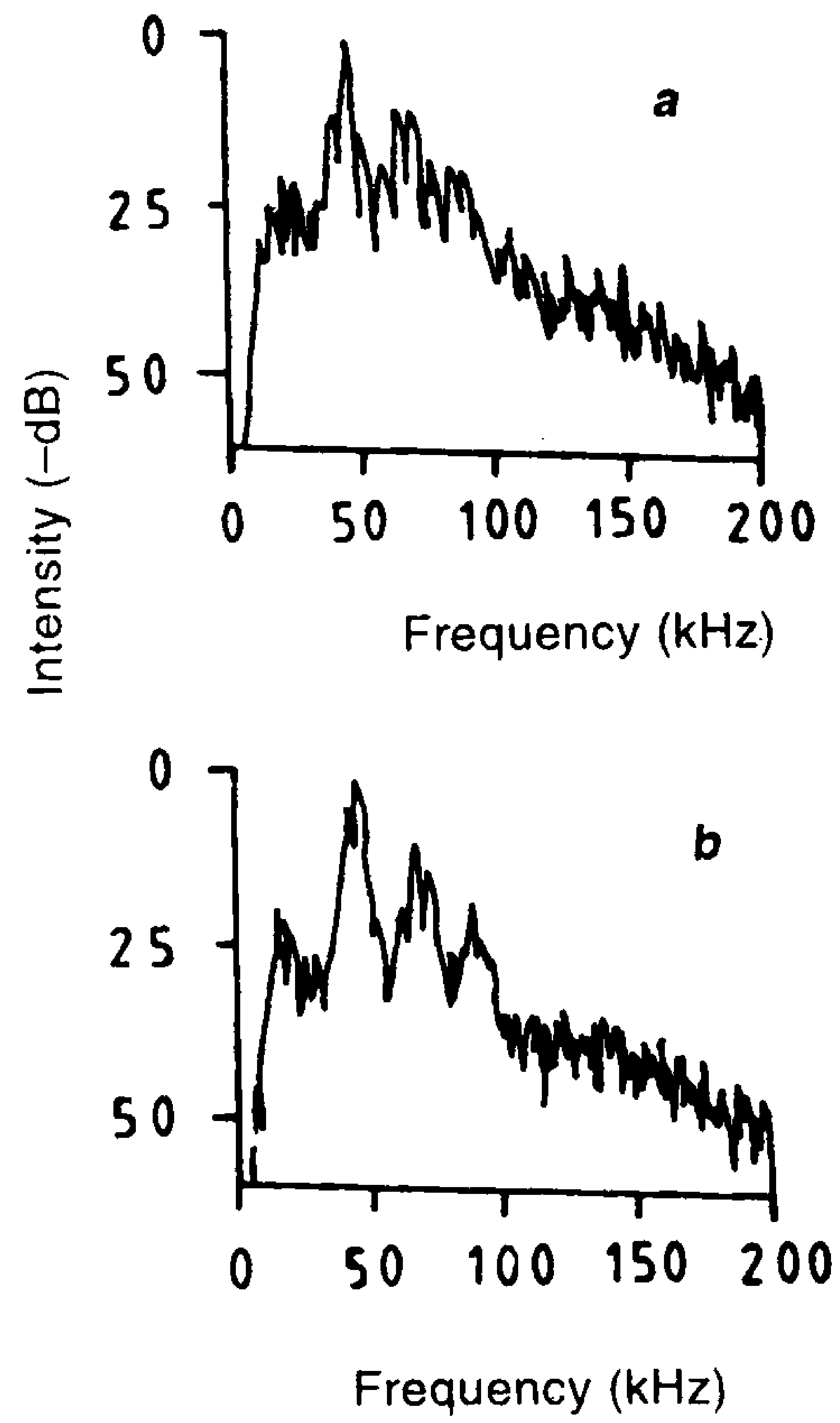

Figure 3. Spectrograms of typical echolocation sounds emitted by *M. lyra* before (*a*) and after (*b*) capturing a frog from the surface of the pond; modified from ref. 11.

Table 2. Searching flights of *M. lyra* to detect and capture a freshly killed frog at the pond in the given period of 20 min. The frog was fixed on a needle-topped and sand-filled ink bottle and the head of the frog adjusted in three positions

Position of the frog at the surface of pond	No. of searching flights (X ± SD)	Time taken to capture a frog (s, X ± SD)	Captures made (%)
Head exposed ($n = 52$)	1.7 ± 0.9 range 1–6	46.5 ± 52.1 range 2–288	100
Eyeballs alone exposed ($n = 39$)	11.6 ± 7.6 range 3–25	439.9 ± 339.9 range 30–1102	33.3
Entire head and body submerged just below water surface ($n = 26$)	23.2 ± 9.5 range 7–39	no capture, but touched water away from frog	Nil

the danger and dived into the pond as soon as the marauding bats hovered over them. In this situation, the bats either stopped hovering and resumed searching flights or touched the water with their mouths as it was too late to realize the escape of the prey. In this situation the bats stopped flying, spent a short period of time wiping their mouth with the wing membranes and then resumed the searching flights.

While flying at the surface of the water to detect a frog, *M. lyra* used echolocation. A bat detector (Flan 2) and QMC microphone connected separately to the channels of a Lennartz taperecorder were used to record the sounds at a speed of 76 cm/s. The sound analysis showed that *M. lyra* emitted multiharmonic echolocation sounds in all searching flights. Figure 3 shows that the second harmonic is the dominant part of the emitted spectrum (43.6 ± 3.5 kHz, mean, SD, $n = 182$). The sounds emitted about 500 ms before touching the water were too weak for spectral analysis. The final buzz is absent in the flights before capturing the prey. For further details, see Marimuthu *et al.*[11].

It is essential that the head of the frog has to be protruding out of the surface of the water for the bat to detect it. Freshly killed frogs were positioned in three different conditions in the pond: i) head exposed (as in live frogs), ii) the eye balls alone exposed and iii) the entire body submerged just below the water surface. It is clear from Table 2 that *M. lyra* detected and captured all the frogs when their heads were exposed, captured very few frogs (33%) when their eye balls alone were exposed, and that detection was *not* possible when the entire frog was submerged below the water surface. When the positions of the frogs were readjusted with their heads protruding out of the water surface, the bats captured the same frogs with alacrity. The smooth water surface might act as an acoustic mirror from which it is difficult for echolocating bats to receive an echo[1]. The water ripples and the objects protruding from the surface create a kind of texture on the water surface. The echolocation sounds and auditory system of *M. lyra* can detect such fine or coarse surface textures as coloured echoes[1].

Mixed blessing of echolocation

It is evident that echolocation is important in general navigation, for estimation of altitude and detection of obstacles. However, it is not the only method which bats employ to detect and capture prey. Several recent reports show that most of the gleaning bats do not require echolocation cues for prey detection. Plasticity in echolocation is observed in a few species. For example, when adequate illumination is available, *Macrotus californicus* uses vision to locate crickets[7]. Other species like *Antrozous pallidus*[25], *Plecotus auritus*[19] and *Myotis evotis*[15] display both aerial prey capture with echolocation and substrate-gleaning without echolocation. Similarly, *M. lyra* detects and captures prey both on land (using prey generated noise) and in water (using echolocation). Even though gleaning bats echolocate while capturing prey from air or water, their emission of sound sequences is not similar to the typical echolocatory pattern of other microchiropterans. For example, the rapid increase in pulse rate, i.e. feeding buzz emitted by the echolocating bats just before capturing insects, is not found in the echolocation behaviour of gleaners except *Antrozous pallidus*[25], *Myotis emarginatus*[14] and *Nycteris grandis*[17]. In fact the gleaners cease calling about 500 ms before capturing[5,11,15], presumably to avoid alerting the prey. Interestingly *M. lyra*[10], *Cardioderma cor*[6] and *Nycteris grandis*[17] do not respond to the calls of frogs. Similarly *Antrozous pallidus* fails to respond to cricket or katydid calls[5]. In contrast, the phyllostomid bats *Trachops cirrhosus*[20] and *Tonatia sylvicola*[12] respond positively to the advertisement calls of frogs and the mating calls of crickets respectively. *T. cirrhosus* uses both echolocation and passive audition while hunting frogs and is even able to differentiate edible frogs from poisonous toads by the type of their calls. A study[26] on its ear showed that *T. cirrhosus* is sensitive to very low frequencies of less than 5 kHz, which explains how it can hear the calls of frogs.

Thus for bats which use the gleaning strategy of foraging, either on ground or foliage, listening to prey-generated noises sounds might be a more economical way to detect prey than echolocation. Moreover, passive sound localization enables detection of prey even if they are located on 'noisy' substrates which would shield them from echolocation. Hence it is of great interest that the passive method of prey detection is used also by other echolocators like killer whales[27].

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