

ECHOLOCATION IN A SOUTH INDIAN BAT COMMUNITY*

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EVER since research in echolocation started¹ scholars were puzzled by the rich variety of echolocation sounds emitted by insectivorous bat species. The most common types are

- (a) brief (1–5 milli-seconds) frequency downward modulated pulses covering at least one octave, say from 80 to 40 kHz. These sounds are called *FM-sounds*.
- (b) Frequently bats also emit pure tones or constant frequency sounds, *i.e.* *CF-sounds*, lasting 6 to 200 ms.
- (c) Some species combine the two types to a so-called *CF/FM-sound* and many species even change the type of sound used under different circumstances.

The question arises whether these variations in sound structure are adaptations of the echolocation system to different ecological constraints. To verify this one has to know first whether the different bat species have different and distinct foraging areas or they opportunistically hunt at any place where insects are abundant.

We studied therefore a community of nine insectivorous bat species living sympatrically around Madurai University Campus in larger numbers. We found that indeed these nine species had distinctly different foraging areas² which could be divided into three types:

(1) *Surface gleaner*: In Madurai one species, *Megaderma lyra* (M.l.), belongs to this group. This bat preferably flies very low over ground and water or it might alight on a low hanging twig. It searches the surface for a suitable prey, from grasshoppers, spiders and crabs to frogs, birds and mice. They detect their prey by the noise made by the prey when it moves. For detecting even the faintest noise source *Megaderma* has large ear conches which are fused in the midline. They form a uniform concave receiver antenna for noise coming from the ground and render audition in *Megaderma* much more sensitive than in any other mammal including echolocating bats. Whereas in bats absolute sensitivity in hearing is not better than in

humans (0 dB Sound Pressure Level) in *Megaderma* thresholds go down to –25 dB SPL for frequencies commonly occurring in rustling noises (15–60 kHz).
 (2) *Foraging close to and within the foliages*: In Madurai two species, *Hipposideros speoris* (H.sp.) and *Hipposideros bicolor* (H.b.), always keep very close to vegetation. The smaller of the two species, *H. bicolor*, skillfully flies through the foliages, through hedges and even through thorny bushwork, where they catch flying insects by the wing. *H. speoris* prefers to fly more outside around the trees and bushes. Both species, however, emit the same type of echolocation signal. It is a combined CF/FM-pulse consisting of a 5–10 ms pure tone of ca. 132 kHz (*H. speoris*) and ca. 155 kHz (*H. bicolor*) terminated by a brief FM-sweep. This type of a signal is especially well suited to cope up with the problem of detecting a prey in densest vegetation, as we shall see later.

(3) *Open air forager*: Most species prefer to catch the insects in open and obstacle free air. However, this large foraging zone is stratified into three distinct heights.

(a) *Lower corridor*: At lower heights up to about tree top level, frequently *Pipistrellus mimus* (P.m.) and *Pipistrellus dormeri* (P.d.) are searching for food. In a style like butterflies they skillfully fly between trees and bushes, sway along verandas, through open halls etc., but usually keep away from objects by about 1 m.

(b) *Middle corridor*: At about tree top level and above we see *Rhinopoma hardwickei* (Rh.h.) flying around in fast sweeps and catching insects continuously on the wing.

(c) *Upper corridor*: Well above vegetation, so to say in the “deep sea” of the air, the fastest flying bats are hunting insects in fast and long sways. These are the swallows among the bats, the slender winged *Taphozous kachhensis* (T.k.) and *Taphozous melanopogon* (T.m.) as well as *Tadarida aegyptiaca* (T.a.).

Interestingly, all species foraging in open air, no matter at which height, emit two different echolocation signals. While still searching for insects they often emit long narrow band or even pure tone signals. However, as soon as an insect has been detected they transfer the pure tone into brief FM-signals while

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approaching the prey. The long pure tone signal is adapted to detection of a target, since all sound energy available is put into one frequency band, which is that of best hearing. The FM-signal is more suited for location of the prey since brief broadband signals are more apt for carrying precise range information. The range between target and bat is read from the time which elapses between emission of the echolocation signal and the arrival of the echo. From this study it became obvious, that sympatrically living insectivorous bat species divide the available insect resources by specifically adapting to different foraging zones as described above. They achieve this differentiation by shaping both signal emission and capacities of hearing to the needs of the different foraging zones. In each species the frequency range of highest sensitivity in audition always coincides with that of the echolocation signals containing most sound energy.

Interestingly, the frequency range of the best hearing is lowest in the bat species foraging highest up in the air, (e.g. 17 kHz in *Tadarida aegyptiaca*). This best frequency in hearing becomes progressively higher as the level of flight is lower: 35 kHz in *Rhinopoma* foraging in the medium corridor, 54 kHz in *Pipistrellus*

flying at low levels and 134 and 155 in the two *Hipposiderid* species which always keep very close to vegetation³, figure 1.

Since reflectivity of sound waves is better at higher frequencies, high frequencies are principally better suited for echolocation. However, sound energy is absorbed rapidly as it travels through air at higher frequency. Therefore high frequencies such as 134 and 155 kHz in *Hipposideros* can only be used in echolocation over short distances. In contrast, *Tadarida aegyptiaca*, foraging high up in the air has to detect an insect prey over long distances in order to make its fast flights metabolically economical. Only low frequencies will not be absorbed within a few meters and therefore all fast bats flying high in the air will emit low frequencies. This is why these species emit and are most sensitive to low frequencies which a young person may easily hear. Thus emission of long pure tones of low frequencies and being most sensitive to low frequencies is an adaptation to echolocation over long distances in open air foragers (figure 1).

But how about bats which also emit pure tones, however, of high frequencies and combined with a terminal FM-sweep? As we have seen the

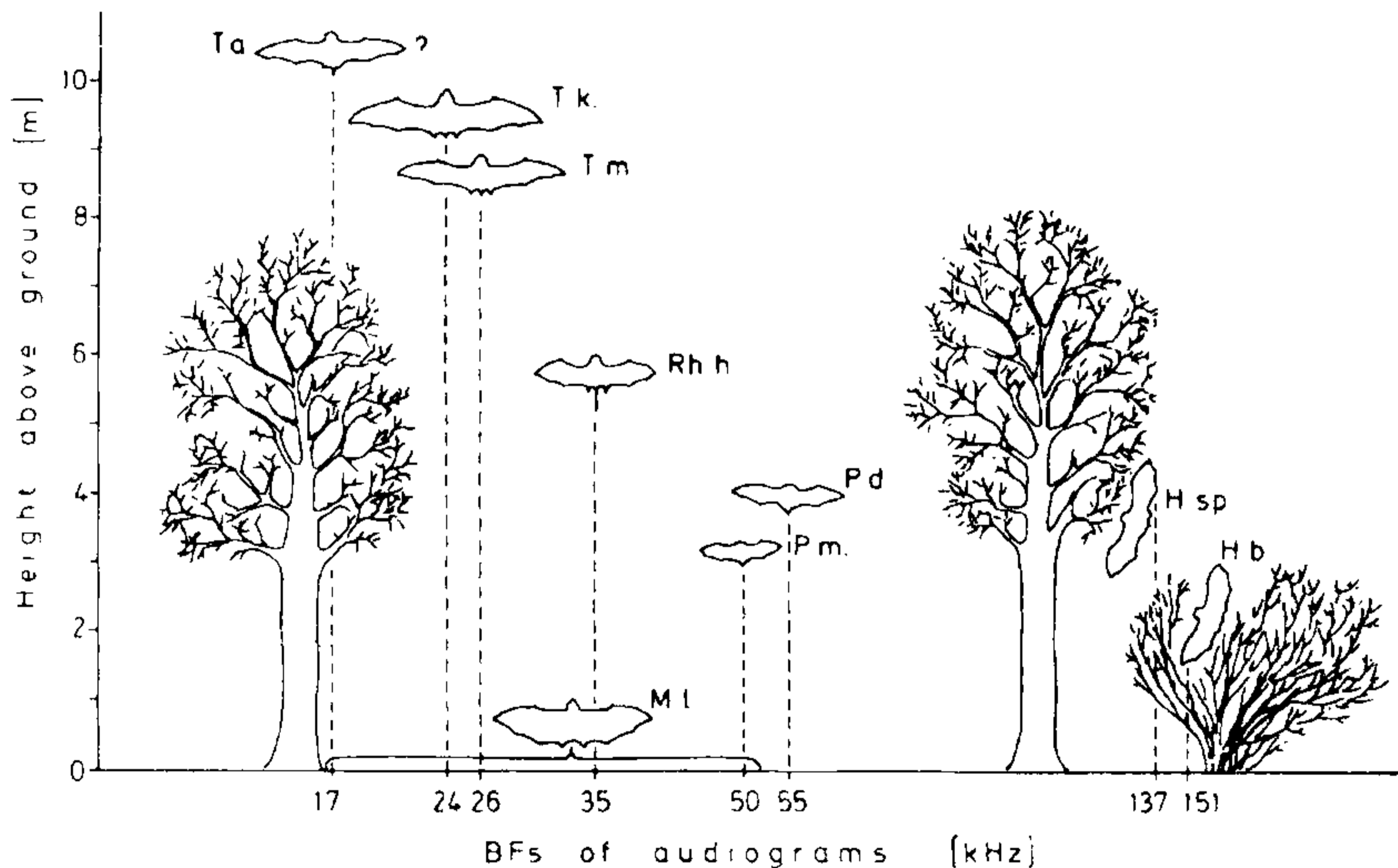


Figure 1. The best frequency of audition in echolocating bats is as lower as larger the distance over which a bat has to echolocate. BF (frequency of highest sensitivity) may be low in bat species foraging high up in the air and high in species foraging close to obstacles. Question mark indicates that the foraging are of T.a. is not precisely known (from 2). T.a. – *Tadarida aegyptiaca*; T.k. – *Taphozous kachhensis*; T.m. – *Taphozous melanopogon*; Rh.h – *Rhinopoma hardwickei*; P.d. – *Pipistrellus dormeri*; P.m. – *Pipistrellus mimus*; M.L. – *Megaderma lyra*; H.sp. – *H. speoris*; H.b. – *H. bicolor*.

Hipposiderid bats emit such signals and forage close to or within the foliage. Therefore they certainly do not echolocate over long distances. In these bats the pure tone serves an entirely different purpose: it makes a wing fluttering insect hearable to the echolocating bats in the midst of echo-noise consistently returning from all the leaves and twigs. This difficult detection problem is solved by specializing the echolocation system to detection of fluttering targets.

The emitted pure tone part of the echolocation signal will again be a pure tone when it returns from non-moving or randomly moving leaves and twigs. However, as soon as the pure tone hits onto a wing beating insect the rebounding echo will be no more a pure tone. Instead it will be frequency modulated in the rhythm of the wing beat since the moving insect wings induce a Dopplershift in the frequency of the reflected pure tone echo. Thus an echo returning from a flying insect will immediately pop out of the mass of pure tone echoes returning from the leaves by the frequency modulations recurring in the rhythm of the insect's wing beat. This wing beat detecting echolocation system is made absolutely noise resistant since each individual bat uses its own private frequency within a species-specific frequency range, e.g. 128–136 kHz in *H. speoris* and 150–157 in *H. bicolor*. This individual emitted frequency is matched by an extremely narrow filter in the inner ear which is precisely tuned to the individual echo frequency. This

individual "carrier" frequency is modulated by a few kHz due to the Dopplershifts created when the echo returns from the moving insect wings. This narrow frequency band of about 5 kHz around the individual carrier frequency, e.g. 133–138 kHz is represented in the cochlea in a vastly expanded fashion. We call this an acoustical fovea. It is unique to these bats and has not been described so far from any other animal.

The examples given from our Madurai study clearly show, that echolocation systems of different bat species may indeed be intricately specialized and adapted to the very specific needs of distinct foraging areas such as the spaces within the foliage and canopies of trees and bushes. They nicely comply to the ecological constraints the bat species is living in. Such driving forces in evolution reveal themselves when behavioural field studies are combined with neurophysiological studies in the laboratories as we have tried to do in our investigations on the bats of Madurai.

1. Griffin, D. R., *Listening in the Dark*. New Haven: Yale University Press, 1958.
2. Neuweiler, G., *Naturwissenschaften*, 1984, 71, 446.
3. Neuweiler, G., Singh, S. and Sripathi, K., *J. Comp. Physiol.*, 1984, A, 154, 133.

ANNOUNCEMENT

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The Smithsonian Institution in conjunction with the American Institute of Biological Sciences and the National Science Foundation will sponsor an international symposium on grass systematics and evolution at the Smithsonian in Washington, DC, from 27–31 July 1986.

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Housing for participants will be available at George Washington University, Washington, DC, and registration will cost \$75.00. For further information contact Louise Salmon, Meetings Manager, AIBS, 730 11th Street, Washington, DC 20001-4584. Tel. 202/628-1500.
