

# Foraging behaviour and echolocation in the rufous horseshoe bat (*Rhinolophus rouxi*) of Sri Lanka

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**Summary.** In October 1984 foraging areas and foraging behaviour of the rufous horseshoe bat, *Rhinolophus rouxi*, were studied around a nursery colony on the hill slopes of Sri Lanka. The bats only foraged in dense forest and were not found in open woodlands (Fig. 1). This strongly supports the hypothesis that detection of fluttering prey is by pure tone echolocation within or close to echo-cluttering foliage. During a first activity period after sunset for about 30–60 min, the bats mainly caught insects on the wing. This was followed by a period of inactivity for another 60–120 min. Thereafter the bats resumed foraging throughout the night. They mainly alighted on specific twigs and foraged in flycatcher style. Individual bats maintained individual foraging areas of about 20 × 20 m. They stayed in this area throughout the night and returned to the same area on subsequent nights. Within this area the bats generally alighted on twigs at the same spots. Foraging areas were not defended against intruders. The bats echolocated throughout the night at an average repetition rate of  $9.6 \pm 1.4$  sounds/s. While hanging on twigs they scanned the surrounding area for flying prey by turning their bodies continuously around their legs. On average they performed one brief catching flight every 2 min and immediately returned to one of their favourite vantage points. Echolocation sounds may consist of up to three parts, a brief initial frequency-modulated (FM) component, a long constant frequency (CF) part lasting for about 40–50 ms, and a final FM part again (Fig. 4b, c). Adult males and females emitted pure tone frequencies in separate bands, the males from 73.5–77 kHz and the females from 76.5–79 kHz (Fig. 5). During scanning for prey from vantage

points, the bats mostly emitted pure tones without any FM component (Fig. 4a). The last few pure tones emitted before take-off were prolonged to about 60 ms duration. The final FM part was therefore not an obligatory component of the echolocation signals in horseshoe bats. During flight and especially during emergence from the cave, most sounds consisted of a pure tone and loud initial and final FM sweeps. We therefore suggest that the initial FM part might also be relevant for echolocation. From our observations we conclude that the FM components are especially important during obstacle avoidance. In most sounds emitted in the field a fainter first harmonic was present. It was usually up to 30 dB fainter than the second harmonic, but in some instances it was as loud or even distinctly louder than the second one (Fig. 6a). Even within one sound the intensity relationship between the two harmonics may be reversed. We therefore suggest that the first harmonic is an integral part of the signal and relevant for information analysis in echolocation.

## Introduction

Horseshoe bats have become a center of interest in auditory research. For echolocation they emit rather stereotyped CF/FM signals consisting of a pure tone component (CF), lasting for 10 to more than 100 ms, terminated by a brief frequency-modulated (FM) component (Schnitzler 1968). Detailed cochlear and neuronal studies have shown that audition in horseshoe bats is uniquely adapted to the pure tone component of the echolocation call. In an “acoustical fovea” in the cochlea a narrow frequency band of about 5 kHz around the CF echo frequency is represented in an expanded

fashion over more than a half turn of the basilar membrane (Bruns 1976; Neuweiler et al 1980; Vater et al. 1985). In the same way as the foveal space of the retina is vastly overrepresented in the visual nuclei of the brain, this foveal frequency band (74–79 kHz in *Rhinolophus rouxi* from Sri Lanka) is strongly over represented in the ascending auditory pathway. Neurons narrowly tuned to the individual echolocation frequency are extremely sensitive to frequency modulations (Schuller and Pollak 1979; Schuller 1979; Vater 1982; Feng and Vater 1985). Recently Schuller (1984) has demonstrated that wing beats of flying insects show up in the pure tone echo as fast rhythmical frequency and amplitude modulations and are distinctly encoded by these “foveal” auditory neurons.

Apparently these specific mechanisms of the auditory system render echolocation of horseshoe bats highly sensitive to moving targets. This could be interpreted as an adaptation to echolocation in dense vegetation where potential prey, e.g. flying insects, have to be differentiated against random echo noise returning from foliage (Glaser 1974; Neuweiler 1976; Schnitzler 1978).

In contrast to the rather detailed assumptions about the echolocation behaviour inferred from auditory research in rhinolophids, information on their actual foraging and echolocation behaviour in natural habitats is scanty. Phillips (1935, 1980) briefly mentions that rufous horseshoe bats fly low over the ground and sweep along the verges of jungles, amongst tree trunks or up and down the banks of streams. They frequently alight and hang from low-growing twigs. They will also enter bungalows and verandas. It is suggested that *Rhinolophus rouxi* returns every night to the same foraging area, which it defends against intruders. Griffin and Simmons (1974) observed *Rhinolophus ferrumequinum* circling around trees in a cemetery in Pisa, Italy. Recently Schnitzler et al. (1985) have analyzed the echolocation calls of a single specimen of *Rhinolophus rouxi* which they observed foraging in flycatcher style on a tree for 30 min.

The purpose of this study was to analyze systematically the foraging and echolocation behaviour of *Rhinolophus rouxi* in its natural habitat and to test whether the behaviour observed in the field conforms to the detailed predictions from auditory research.

## Methods

This study was performed by a team of nine persons from 1 to 30 October 1984 at a nursery cave of *Rhinolophus rouxi* in Haputale District, Sri Lanka (6° N, 81° E). In October this

cave harbours a nursery colony of approximately 150,000 rufous horseshoe bats. On 24 nights two to five teams of two observers each monitored the area around the cave in a diameter of about 5 km. Specific details of the habitats are given later.

Observations were recorded either in notebooks or on tape on a minute to minute basis. We used QMC-Mini-bat detectors to monitor the echolocation calls of horseshoe bats over distances of up to 20 m. The directionality of the QMC Mini allowed us to find echolocating bats, in turn permitting us to photograph foraging sites and foraging bats.

Echolocation sounds of foraging and flying bats were recorded in two ways: firstly, the sounds were picked up by QMC-microphones, amplified by a custom-made amplifier (Schröder, Erlangen) and then recorded on videotape by a modified portable videorecorder (Panasonic VHS NV-100). This modified video-recording system allowed us to record signals from 15–200 kHz with a signal/noise ratio of 35 dB. These recordings were analyzed in Munich with a homemade, high-speed sound analyzer system based on transient recorders, a spectrum analyzer and a PDP 11/23 computer. The analysis yielded spectrograms and sonagrams of sounds with a frequency resolution better than 1.6 kHz and a time resolution of about 0.9 ms. Secondly, sequences of heterodyned echolocation sounds were recorded from the QMC-Mini-bat detectors by putting the microphone of a cassette tape recorder close to the loudspeaker of the bat detector. These tape recordings were plotted on a strip chart by a Watanabe inkwriter via a transient recorder (time resolution: 9 ms/mm). Since the QMC-heterodyning device faithfully preserves sound durations of long echolocation signals such as those from horseshoe bats (Miller and Andersen 1984), we analyzed recorded heterodyned sequences of echolocation sounds for interval and sound durations.

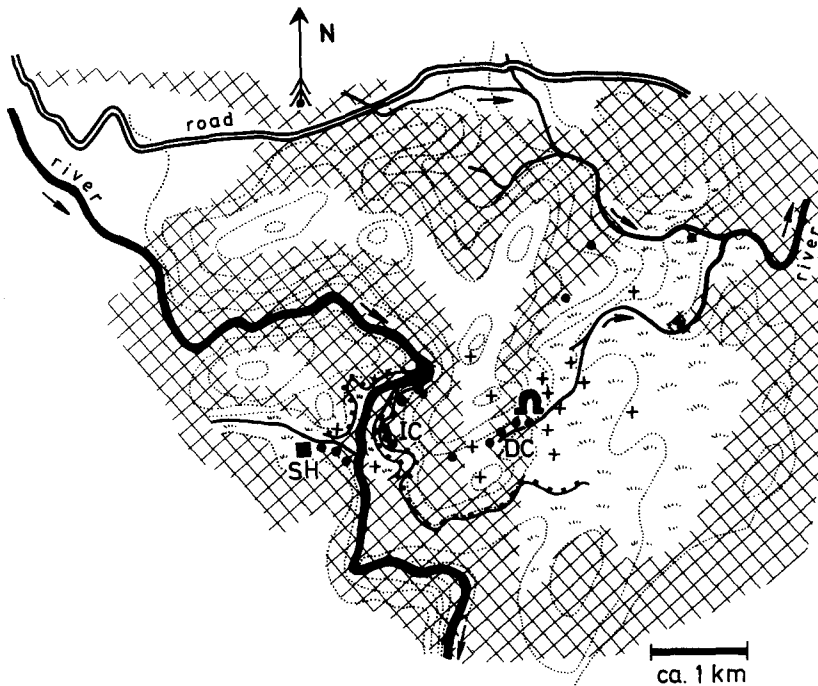
We also documented bats and their activities photographically with high-speed flash photography. Individual bats were light-tagged (Buchler 1976) so that we could observe them in the open. In the forest, however, light-tagged bats could not be observed. Bats were caught with a handnet as they emerged from the cave in large numbers.

## Results

### *Cave site and departure for foraging*

The cave is situated on the eastern slope of a rather steep range of hills the lower parts of which along with accessible slopes had been cleared and were under cheena cultivation (Fig. 1). The lowlands were either irrigated paddy fields or burnt-down patches of land yielded crops in peanuts, sugarcane and vegetables. The creeks and rivers running through the agricultural land were mostly fringed by dense galleries of tall trees and thick bushes. Conspicuously, the slopes and the areas close to the rivers were covered by tall, thick and often impenetrable jungle forests whereas the rocky hill tops (500–600 m above sea level) consisted of clear savannah-like forests with large single trees and wide patches of high grass.

Owing to the slowly expanding cheena cultivation, the cave itself was now situated at the fringe



**Fig. 1.** Foraging areas of horseshoe bats around the cave ( $\Omega$ ). *Hatched areas*, dense forests and jungles; *areas with grass signature*, cultivated land; *white areas*, open forests; *line with dots*, irrigation channel; *crosses*, observation sites where horseshoe bats did not forage consistently; *black dots*, observation sites where horseshoe bats foraged throughout the night. Note that consistent foraging only occurred in dense forests and jungles. *DC*, dry creek; *IC*, irrigation channel; *SH*, schoolhouse area

of original forest but a narrow rocky ridge a few meters north of the cave was still covered by bushes and trees and connected the cave with forest about 50 m uphill from the cave.

The cave has four major entrances, one running vertically through huge rocks, the others opening towards the southeast. The lowest and largest one leads down about 6 m underground before opening into a hall about 15 m high. From there smaller passages lead deeper into the hill. In October 90% of the departing bats were females while in September 1984 and in March 1983 fewer bats occupied the cave, suggesting that during the second half of September and the beginning of October female horseshoe bats congregate there. Young were born during the first half of October, and the last pregnant female was caught on 13 October.

The bats left the cave to forage shortly after sunset, e.g. on 2 October the first bat emerged at 18.01 hours. Over our observation period the time of the first emergence slowly advanced to 17.45 hours by 26 October. We could not find any obvious correlation between the timing of the first emergence and the weather conditions. The first rains began on 19 October. The bats left the cave as usual in large numbers despite continuous rain, and by the time the rain had stopped between 18.00 and 19.00 hours most of the bats were already out. On 25 October a heavy thunderstorm started at about 17.30 hours but despite torrential rain, horseshoe bats flew out towards their foraging sites, albeit in smaller numbers. At 19.00 hours we

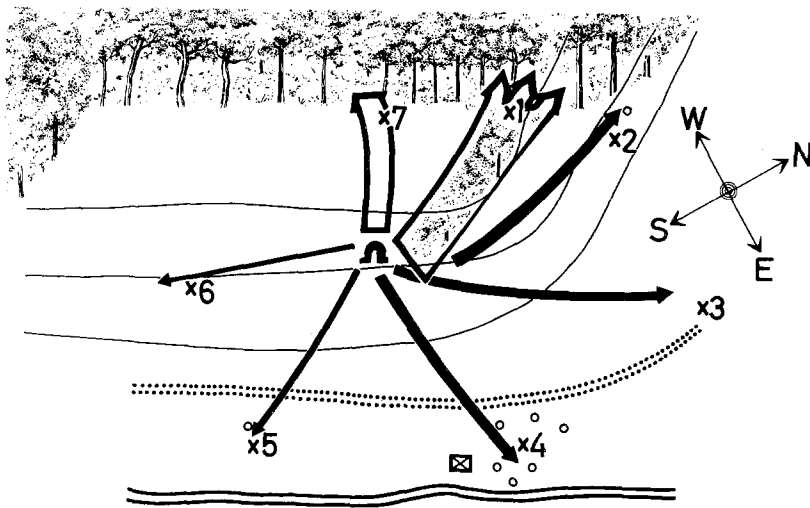
found a huge crowd of horseshoe bats in a vestibule close to the cave mouth suggesting that in heavy rain the bats delayed their departure.

Surveys of emerging bats around the cave and observations of arriving and passing horseshoe bats in foraging areas suggested that most bats left the cave within 20 min. For example, of 14,500 bats emerging from the cave on 16 October more than 80% left the cave before 18.10 hours, or within 26 min of the first departure (Table 1). By 31 min the frequency of passing bats at the observation sites sharply dropped to a few per minute and then the continuous stream of bats dissociated into small groups or single bats with rapidly increasing pauses between their appearance. At the cave mouth, however, the exodus of horseshoe bats never really stopped. Interestingly, in the early morning the frequency of emerging bats increased again between 3.00 and 5.30 hours with a peak at 5.00 hours. We do not know why a larger number of bats left the cave shortly before dawn. Apparently they stayed outside only for a short period, since at 5.40 a.m. the last bats reentered the cave.

The counts of emerging bats at seven different observation spots around the cave also confirmed that most departing bats flew directly into the dense forests (85% of the bats counted: sites 1, 7 and 2 in Fig. 2 and Table 1). The remaining 15% flew northeast to southwest over agricultural land. Those bats observed on site 6 in Fig. 2 flew rapidly over the burnt-down slope into a narrow spit of

**Table 1.** Number of horseshoe bats visually identified departing from the cave in seven different directions (observation sites 1–7, compare Fig. 2) from 17.40 to 18.30 hours on 16 October 1984

Time	Number of bats departing from cave as observed at sites 1–7 around the cave (see Fig. 2)							Total 1–7	Percentage of total
	1	2	3	4	5	6	7		
17.40–17.50 hours	540	–	–	–	–	–	60	600	4
17.50–18.00 hours	~3,440	212	100	155	21	42	880	4,850	33
18.00–18.10 hours	~4,100	592	440	462	225	109	910	6,838	48
18.10–18.20 hours	1,090	88	128	137	101	23	150	1,717	12
18.20–18.30 hours	220	37	46	59	48	3	50	463	3
17.40–18.30	9,390	929	714	813	395	177	2,050	14,468	100
Percentage of total	65	6	5	6	3	1	14	100	



**Fig. 2.** Flight directions of horseshoe bats departing from the cave as observed at sites 1–7 on 16 October, 1984. The width of the arrows indicates the percentage of horseshoe bats flying in that direction (for figures see Table 1). Structured areas, dense forest and a row of bushes and trees connecting the cave to the forest; dotted line, irrigation channel; circles, single trees;  $\square$ , 'carpenter's' hut; double line, trail, length of trail about 200 m

forest which covered a dry creek running down from a small pass between two hills.

The flight paths of the emerging horseshoe bats were unmistakably specific. When emerging from the cave mouth they flew rather low over the ground (c. 1 m) and sped towards the next cover. Nearly two-thirds of the observed bats immediately flew into the ridge of thick bushwork and trees a few metres north of the cave, and used this narrow bridge of original vegetation to the forest as their main flight path. They did not use the open flight corridor above the foliage of the bushes and below the tree top canopy, but flew right through the dense meshwork of twigs, thorns and foliage. It was fascinating to observe how hundreds and hundreds of bats successfully slipped through apparently impenetrable bush.

These flight paths within vegetation were in sharp contrast to those of the large (60 g) *Hipposideros lankadiva* which left the cave at the same time but flew at or just below tree top level several

metres above the horseshoe bats. These "two-storied runaways" for the two species were also observed within the adjacent forests; they also foreshadow the different foraging strategies of the two species. Within the forests horseshoe bats continued to fly low and, wherever possible, under cover. The reasons for this behaviour are not clear. Three times we saw two Crested hawk eagles (*Spizaetus cirrhatus*) arrive at the cave just before the emergence of the bats. The birds caught one or two horseshoe bats, but we did not see them hunting bats elsewhere.

#### Foraging sites and foraging behaviour

A detailed simultaneous monitoring of different habitats around the cave disclosed a clear picture of the preferred foraging areas. Horseshoe bats were only found in jungles and densely overgrown forests (filled circles in Fig. 1). The most frequented areas was a dry creek south of the cave

running through dense forests where we could observe horseshoe bats for hours. We never observed horseshoe bats over paddyfields and open grassland, nor did they forage in the open woodland on the hilltops. The bats only passed through the fields and orchards, occasionally starting to forage on their way, or hung on trees for a few minutes.

Most parts of the jungles and forests were impenetrable by us so we focused our observations on three sites where we found horseshoe bats every night (Fig. 1):

- (a) A 800-m long footpath from the “schoolhouse” ran through patches of forests along a creek eastwards to a patch of paddyfields surrounded by a U-shaped range of hills
- (b) The irrigation channel running about 50 m above the paddyfields along the forest-covered hill slope. The uphill side of the channel was a very steep bank densely covered with trees and bushes, whereas along the downhill side we could monitor about 400 m along the irrigation channel from a narrow trail (overgrown by tall grass).
- (c) A 1-km long trail along a dried-up creek southwest of the cave allowed us access through dense jungle uphill towards a pass where the vegetation opened into a clear forest area.

The patterns of bat activities were similar at the three sites. Horseshoe bats arrived a few minutes after emergence from the cave and for the first 30–60 min they flew around and through the canopy of trees, along and over bushes continuously catching insects. Foraging flights were low, beneath tree top level. In the schoolhouse area we twice saw horseshoe bats foraging about 10 cm over the ground. As the pursuit progressed the bats spent increasingly longer periods hanging on twigs of trees and bushes, and after another 30–80 min, continuous flight activity ceased.

After this initial activity period in all observed areas there was a period of varying length when we encountered few horseshoe bats. On 15 of the 24 nights this “silent period” usually occurred between 19.00 and 21.00 hours. For example, on 12 October at the irrigation channel we observed full foraging activity up to about 19.50 hours, and from then until 20.30 hours we detected but two passes by horseshoe bats; from 20.30 to 21.00 hours we found none in the area. In the schoolhouse area the silent period occurred from 19.25 to 20.30 hours on 24 October, and on 18 October from 18.30 to 20.15 hours. At the irrigation channel the few bats detected during the silent period rapidly moved across the channel either uphill into the forest or downhill into the gallery between paddyfields and the channel suggesting that during

this period the bats remained more inside the forest. During the silent periods no increase of returning flights at the cave entrance was observed, and therefore it is unlikely that the bats returned for lactating their young.

Bats resumed foraging after this silent period and continued throughout the night. In the second foraging period the bats almost always hunted from perches such as twigs, making brief flights and returning to the very same perch. The short flights were usually less than 5 m, typical of flycatcher hunting (Shortridge 1934; Schnitzler et al. 1985).

Foraging perches were leafless, dead twigs protruding below the canopy, branches overhanging trails and clearings or dry twigs protruding from the foliage of bushes. The bats often chose twigs which protruded into open airspaces under cover and from there scanned the space by continuously turning their bodies around their feet through an angle of about 200°. When hunting in this way the bats readily tolerated our presence, and in some cases we even stood right under a bat hanging only 2.5 m above the ground. Sometimes the bats would tolerate the Mini-Bat detector within 30 cm and they were not disturbed by our talking into a dictaphone or by QMC-Mini representations of their own echolocation calls. Shining a light was sometimes tolerated but a brisk and noiseless movement of the hand towards a bat hanging on a twig 5 m away immediately caused it to fly away.

Horseshoe bats foraging in the flycatcher style remained for long periods in one area but used different perches. For example, in the dry creek we observed one bat hanging for 1 h under the canopy of a tree but on different twigs. The longest continuous time on one perch for the bat was 34 min. From the total number of foraging sequences observed, 86 were recorded in detail and noted on tape. The mean time on the same twig was 7 min and during that time a bat made on the average 3.5 catching flights. The fastest sequence of catching flights were 4 within 2 min. Catching flights usually lasted less than 1 s. Within one foraging area only a few distinct perches were consistently used. This became clear when we continuously monitored known individuals over longer periods. In the schoolhouse area and dry creek valley we repeatedly observed individual bats for up to 70 min and 63 min respectively. At the irrigation channel we continuously observed a single bat visually and acoustically for 3 h from 23.25 to 02.27 hours and on another night for 4 h and 48 min (20.22 to 01.10 hours).

As an example, the activity pattern of the bat

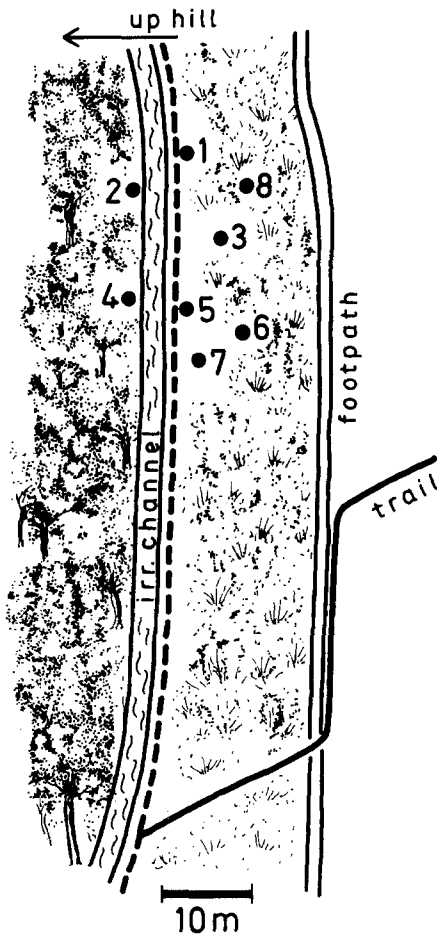


Fig. 3. Foraging area of an individual horseshoe bat observed for 4 h and 48 min continuously. During that time the bat alighted on specific twigs of trees and bushes indicated by the numbers 1–8. *Left* of irrigational channel dense jungle; *right* of it dense bushes and trees; *dashed line* trail along irrigation channel

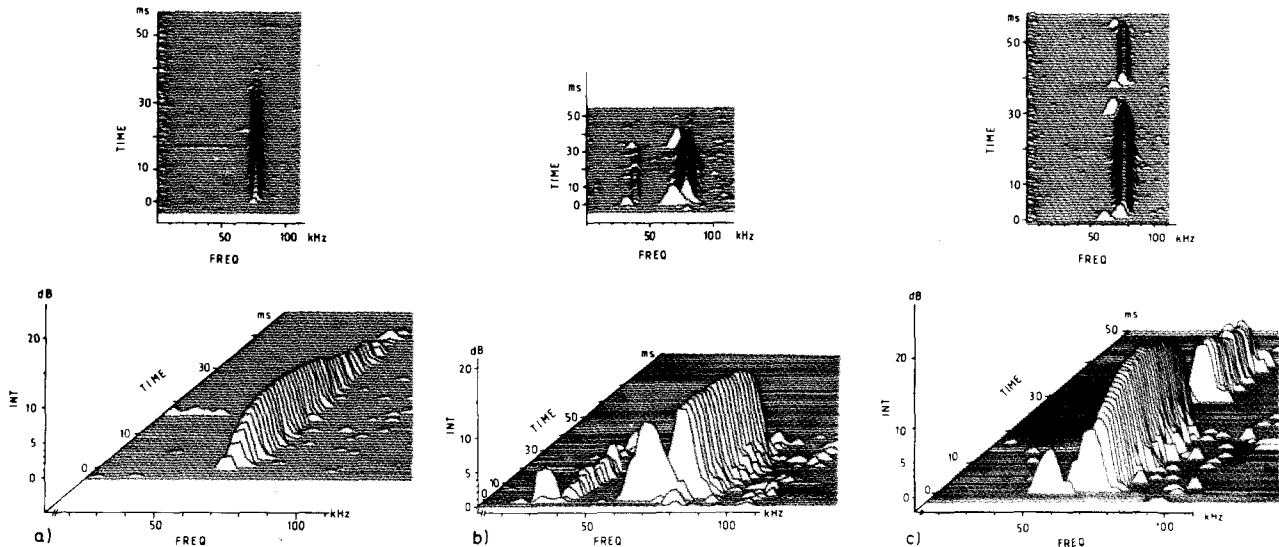
during the last observation period mentioned above will be described in detail (Fig. 3). This bat was active over 25 m on both sides of the channel and within this range also flew into bushes and trees on the downhill side of the channel. It never moved into the forest on the uphill side. The total area covered by the bat was about 25 by 12 m, i.e. ca. 300 m<sup>2</sup>. However, the bat spent most of its time on bushes and trees on the borders of the channel where it preferred certain twigs of two trees on the uphill side and four on the downhill side. The perches were a dry and leafless twig protruding below the canopy about 2.5 m over the trail (1 in Fig. 3), a single leafless twig on a tall tree about 6–8 m above the channel (2 in Fig. 3), a leafless twig of a large tree pointing into open space about 4 m above the bush within the downhill slope (3 in Fig. 3), a dry twig overhanging the

trail on a tree about 6 m above the trail (6 in Fig. 3), the upper of three thin arms of a leafless twig about 3 m above the trail (5 in Fig. 3), a twig of a large bush slightly inclined over the channel (4 in Fig. 3), and a twig not clearly defined in the top level of a tree adjacent to the trail on the downhill side (7 in Fig. 3). The last twig was about 8 m above the ground (8 in Fig. 3). In an irregular and unpredictable pattern the bat moved between the different roosting sites and always alighted not only at the same twig but also on the same spot of the twig, usually near the outer end. From 20.22 to 01.10 hours the bat made 49 shifts between the twigs, and never stayed longer than a few minutes (up to 16 min) in one place. It most frequently (14 ×) alighted on tree no. 2 where it spent a total of 75 min but only 13 min maximally in one sequence. The bat spent two-thirds of its time on seven trees, mostly on no. 2, 5 and 7 (Fig. 3). Six times the bat also flew into various bushes more downhill towards the fields, and altogether spent 30 min there.

Three times, in time spans of 7, 2 and another 2 min, the bat foraged on the wing, flying up and down the channel in swings of 10–15 m. During the complete observation period the bat unremittingly echolocated and we observed 75 catching flights, i.e. 1 flight/3.8 min on the average. Neither the echolocation sequences nor the behaviour of the bat gave us any clear-cut indications which of the flights were successful. At 1.10 hours the bat flew off from tree no. 5 at a faster speed than during foraging and disappeared along the channel.

From this and comparable observations we received the impression that individual bats have distinct foraging sites, corroborated by finding that certain twigs were used by a bat every night at about the same time. On a twig of a bush in the schoolhouse area and on the twig of tree no. 1, we found a foraging bat every evening over six consecutive nights. From sound recordings, visual inspection and photographs (for the bat from the irrigation channel) we suggest that these were the same individual bats foraging there every night.

On 16 October along the dry creek over a distance of about 1 km we detected 14 bats foraging in flycatcher style; typically we encountered a bat every 70–100 m. Along 200 m at the irrigation channel after the silent period we never found more than 3 bats foraging at the same time in different parts of the area, and in the schoolhouse area 7 bats occurred over 800 m. However, twice in the dry creek area and once at the irrigation channel we observed another bat fly to a tree where a bat



**Fig. 4a–c.** Sonograms of typical echolocation sounds of *Rhinolophus rouxi*. Upper chart, time/frequency diagram; lower chart, time/frequency/relative intensity diagram of the sounds. **a** A pure tone sound (CF type) typically emitted while hanging on a twig and scanning for prey flying by. **b** A FM/CF/FM sound with first harmonic, typically emitted during flight, e.g. when flying through the cave mouth. **c** Two FM/CF/FM sounds emitted during cruising flight

was perched already. The “visiting” individuals stayed for 4–36 min and also made frequent catching flights. The two adjacent bats could easily be distinguished by the different frequencies of their echolocation calls as heard by detector. In none of the three cases did we notice any change in the behaviour of the resident bat, and both continued to forage in flycatcher style. These observations indicate that individual foraging areas are not territories because they were not defended against intruders. In the schoolhouse area we found two different bats sequentially on the same twig, indicating that the same foraging area could be used by different bats sequentially.

Although this pattern of continuous flight, silent period and then flycatcher hunting dominated, there was some variation in it. After strong thunderstorms (19 October – irrigation channel; 27 October – dry creek) we found horseshoe bats more frequently flying than hanging on trees. At the irrigation channel from 18.16 to 22.05 hours, we counted 29 bats flying up and down or across the channel, and in one case observed a bat circling within a range of about 10 m under the canopy of the tree for 4 min. Over 4 h we found only one bat perched for more than 2 min. In the dry creek from 21.00 to 22.30 hours we observed only three perched horseshoe bats but detected 27 passes by bats flying up and down under the canopy over the river bed. This is in sharp contrast to our observations in the same area only 3 days previously when we found 13 bats hanging on trees and heard just two passes in the same area over 2.5 h. A chan-

ge in quantity and/or quality of insects triggered by the rain could have caused this distinct change of behaviour. In any case our observations prove that horseshoe bats adjust their foraging behaviour between catching insects continuously on the wing and catching in flycatcher style.

#### *Return flights to the cave*

By midnight at the irrigation channel and in the schoolhouse area we observed horseshoe bats flying straight and fast towards the cave. Observations at the cave and a steady increase in bats homeward bound towards dawn (up to 10–35 bats/h by 05.00 hours) support this view. The highest rate of home fliers occurred after 5.20 hours when it was bright enough to read a newspaper. At the schoolhouse area and at the irrigation channel from 05.00 to 05.43 hours 70–80 bats flew rapidly towards the cave, with more than 50% of them flying home between 05.25 and 05.35 hours.

As long as it was dark many of these bats flew at head level and above, occasionally interrupting their straight flight paths for brief foraging bouts. However, after dawn (05.15 hours) all of the horseshoe bats stopped foraging and flew low above the ground, staying within the foliage. The flight through the bushes was again accompanied by *Hipposideros lankadiva* flying in the same direction but at a faster speed and at treetop level far above. The last horseshoe bat was seen at 05.41 hours.

The observations at the foraging areas agree with those at the cave. From 18.30 hours single

**Table 2.** Echolocation sound patterns emitted by rufous horseshoe bats in different behavioural situations. CF alone: sound only consisted of a long pure tone, FM up/CF sound started with an upward frequency modulated part and continued as pure tone. FM up/CF/FM down: the pure tone component was preceded and terminated by a brief modulated part, the final one was frequency downward modulated. CF/FM down: the pure tone component was terminated by a frequency modulated part. Numbers in brackets give the number of sounds

Behaviour	No. of sounds analyzed	Percentage of sounds belonging to the sound types			
		CF alone	FM up/CF	FM up/CF/FM down	CF/FM down
Perched and scanning	1,385	90 (1,249)	9 (122)	1 (12)	0.1 (2)
Perched and take-offs	733	52 (384)	0	30 (219)	18 (130)
During flights	232	19 (44)	9 (20)	52 (122)	20 (46)
Emergence from cave (obstacle avoidance)	587	0	0	70 (411)	30 (176)

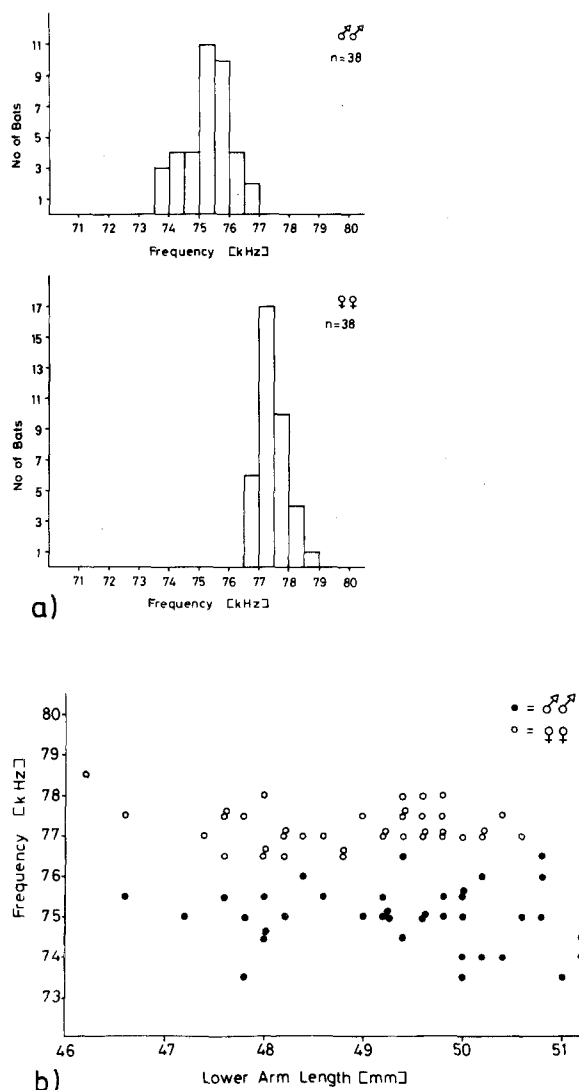
bats returned to the cave, and after 23.30 hours the numbers returning steadily increased, peaking as late as 05.30 hours. At 05.45 hours a thick stream of horseshoe bats flew into the cave mouth, and only 3 min later the last bat was seen disappearing into the cave. The horseshoe bats approached the cave again at head level or below, and directly entered the cave without circling around it.

#### *Echolocation sound patterns and frequencies*

In horseshoe bats the classical structure of an echolocation sound is considered to be a long CF component ending in a brief FM sweep (Schnitzler 1968). In our field recordings sound structures were much more variable. Most of the sounds we recorded in different situations consisted of a CF component 40–50 ms long. According to the behavioural situation horseshoe bats added brief initial upward FM sweeps or terminal downward FM sweeps (Fig. 4).

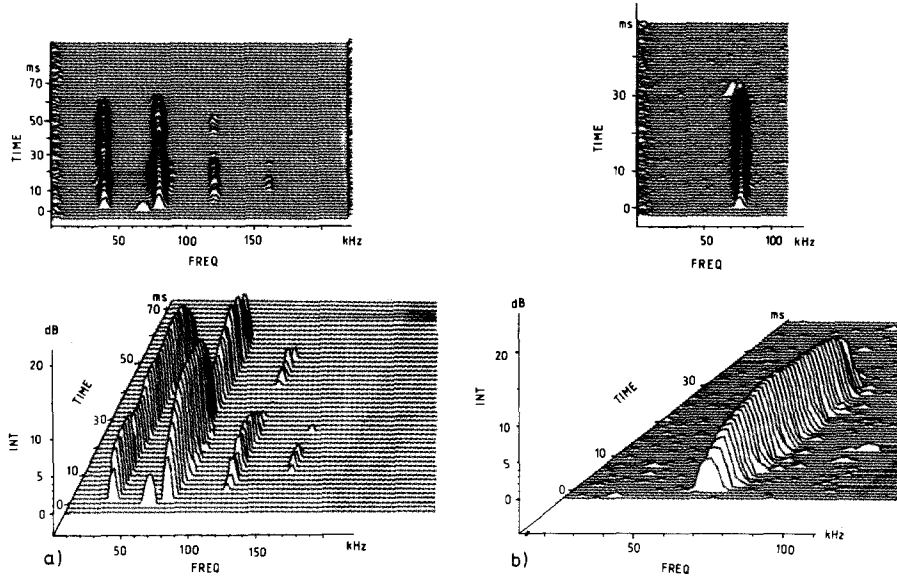
While hanging on twigs and scanning the surroundings for flying prey the bats usually emitted CF calls that lacked or ended in faint FM components. Most (90%, Table 2) sounds recorded in these situations consisted of a CF tone. FM components, when added, were usually initial upward sweeps. Only 2 of 1385 sounds from scanning bats showed the classical pattern of CF/FM. FM components were never more intense than the CF part.

The frequency of the emitted CF is maintained within the sequences of sounds recorded from individuals hanging on twigs. However, a frequency analysis of sounds from handheld horseshoe bats randomly caught while emerging from the cave showed a bimodal distribution of emitted CFs between males and females (Fig. 5a). Males' CF calls



**Fig. 5a, b.** Frequencies of the CF component of echolocation sounds emitted by 38 males (♂) and 38 females (♀). **b** the sex-specific difference in sound frequency is not correlated to the size of the specimens as measured by their lower arm length





**Fig. 6a, b.** Sonograms of echolocation sounds in *Rhinolophus rouxi*. Upper chart, time/frequency diagram; lower chart, time/frequency/relative intensity diagram. **a** A FM/CF sound with a strong first harmonic which is sometimes louder than the second one (see depression in the second harmonic at 78 kHz). The sound was emitted by a bat hanging on a twig, shortly before take-off. **b** A FM/CF/FM sound emitted by a flying bat returning to a twig

were between 75–76 kHz and females' between 77 and 78 kHz. There was little overlap between them, and the difference in sound frequency is not due to any sex-specific difference in body size (Fig. 5b).

Typically the echolocation sounds consisted of a very strong second harmonic between 75 and 78 kHz, and a 10–30 dB fainter first harmonic. In many sounds the first harmonic was not detectable (not analyzed in detail) and occasionally we detected a third harmonic (115 kHz), usually when bats emerged from the cave (Figs. 4 and 6a).

Sometimes in the schoolhouse area and irrigation channel we could only hear bats with the Mini-Bat detector set at 40 kHz. This was not due to poor calibration of the detectors. We documented 12 of these cases in detail. On 14 October one of us (U.H.) saw a perched horseshoe bat continuously emitting sounds at about 40 kHz with no or only faintly detectable components close to 80 kHz. One minute later the bat switched to sound emissions at 80 kHz with a faint 40 kHz component. The bat made a brief flight and returned to the same twig and again emitted sounds at about 40 kHz. The bat continued to do so until it disappeared a few minutes later. These observations and a similar one from 11 October suggest that rufous horseshoe bats shift the power of their sounds between the first and second harmonic. Inversions of amplitude relationships between second and first harmonic also occurred during the course of an echolocation sound (Fig. 6). Strong first harmonics were frequently recorded in sounds emitted shortly before take off.

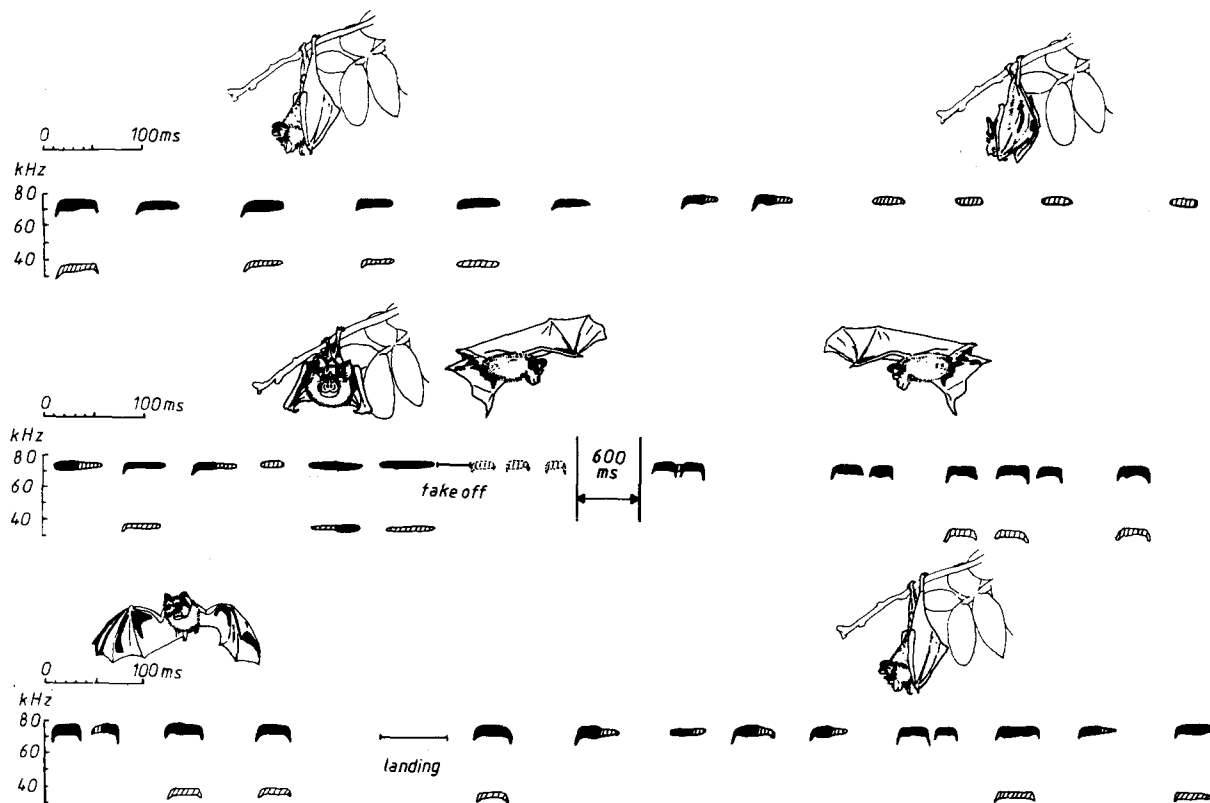
Of 117 *R. rouxi* caught at random from the cave entrance, 84 emitted loud second harmonics and faint first ones, while 23 females and 6 males

emitted second and first harmonics of about equal intensities; another 4 females emitted very loud 40 kHz sounds with faint or missing second harmonics. These results suggest that the first harmonic may be an important component for echo processing in horseshoe bats.

A further complication was provided by six *R. rouxi* that were best monitored between 60 and 65 and 35 kHz, and another three bats that emitted sounds around 50–55 kHz. Two of the latter group were visually identified as rhinolophids. One of them appeared a little bit more bulky than most rufous horseshoe bats. It could have been *R. luctus*, the only other horseshoe bat species of Sri Lanka, which emits 42 kHz (Roberts 1972). The other one was observed by two of us for several minutes at a range of less than 0.5 m in bright moonlight and was identified by both observers as *R. rouxi*.

The echolocation calls of bats perched on twigs and scanning their surroundings rarely contained FM components. When present FM sweeps never exceeded 10 kHz or about two-thirds the bandwidth of FM components emitted in the laboratory. However, our impression is that FM components were more frequently emitted when the bat became alert. Immediately before take-off on a capture flight, the last few sounds were always prolonged pure tones with no detectable FM components at all (Fig. 7).

As soon as the bat took flight the echolocation calls included the CF component and initial and/or final FM sweeps (Table 2) with frequency bands of up to 16 kHz. About 25% of the sounds of flying bats still lacked a final FM sweep, and only some included an initial one. All echolocation sounds ( $n=587$ ) from bats emerging from the cave



**Fig. 7.** Sequence of echolocation sounds (schematized sonagrams) of a horseshoe bat hanging on a twig, then flying off and returning to the same spot as indicated. Dashed parts in the sonagrams indicate low intensity components ( $<6$  dB rel. int.). Note the two long pure tones emitted just prior to take-off

**Table 3.** Number ( $n$ ) and percentage of sounds having initial and final FM sweeps with different band widths. FM up  $>$  FM down: initial FM part of echolocation sound is broader than final part; FM up  $\approx$  FM down: both parts of about the same band width; FM up  $<$  FM down: final FM sweep is broader than initial one

Behaviour	FM up $>$ FM down		FM up $\approx$ FM down		FM up $<$ FM down		Total	
	$n$	%	$n$	%	$n$	%	$n$	%
Cruising flights	39	17	104	45	87	38	230	100
Emerging from cave	65	11	345	59	177	30	587	100
Both situations	104	13	449	55	264	32	817	100

mouths invariably featured loud and wideband final FM sweeps in the “conventional” laboratory fashion and most of these sounds also included an initial upward FM sweep (Fig. 4).

In 68% of the ( $n=817$ ) echolocation sounds we analyzed that had both FM components, the initial FM was as broad as or even broader than the final one (Table 3). This suggests that the initial FM component is not just a byproduct of sound emission and may be an important carrier of echo information. From this we concluded, that both FM components may be important for obstacle avoidance in echolocation, while the long-lasting

CF component may be more important for prey detection. The widely used term “CF/FM echolocation” or “CF/FM-bat” for horseshoe bats is misleading and must be replaced by the term FM/CF/FM since in the natural habitat the initial FM sweep is as common as the terminal one.

#### *Sound duration and repetition rate*

From 60 recorded echolocation sequences we analyzed the time course in 41 with the best signal/noise ratios. These recordings were made at the schoolhouse area, at the irrigation channel and

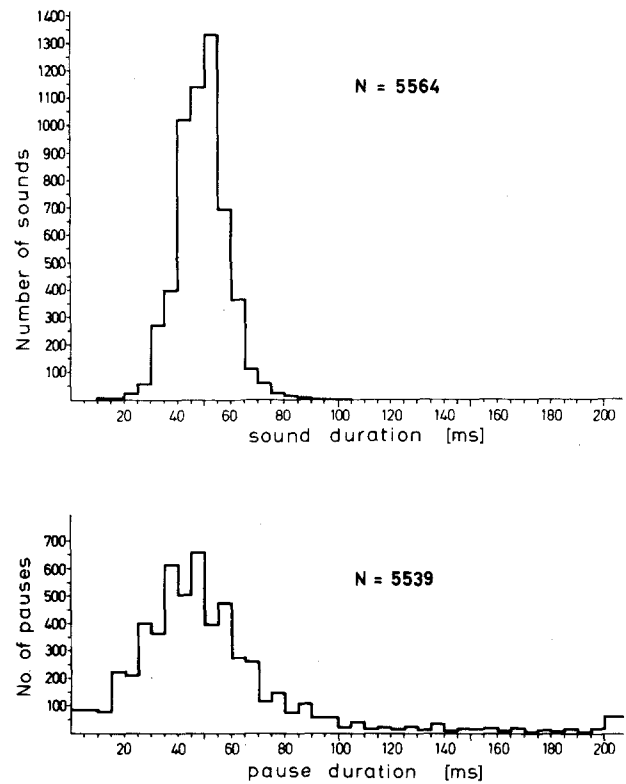
**Table 4.** Average time parameters of echolocation sound sequences of *Rhinolophus rouxi* recorded in the field. Interval: silent period between the end of the preceding and begin of the subsequent sound. Duty cycle: percentage of sequence duration filled with sound energy

Behaviour	No. of sequences	Sum of sequence duration (ms)	No. of sounds ( <i>n</i> )	Sound duration (ms) (SD)	Interval duration (ms) (SD)	Repetition rate sounds (per s)(SD)	Duty cycle (%) (SD)
Passing over	12	14,506	168	52.6 ± 4.6	34.9 ± 8.6	11.6 ± 1.3	61.0 ± 2.6
Perched and brief flight	6	80,417	843	45.5 ± 5.6	49.9 ± 4.6	10.5 ± 1.0	47.7 ± 3.2
Perched	23	473,633	4,554	45.5 ± 3.6	55.8 ± 13.4	9.6 ± 1.4	43.7 ± 6.2
Total average	41	568,556	5,565	46.0 ± 4.0	56.5 ± 12.4	9.8 ± 1.3	45.1 ± 5.8

along the dry creek from bats hanging on twigs, foraging in flycatcher style or just flying by. The longest sequence we analyzed lasted 58.5 s and the briefest, 0.6 s. A total of 568 s of sound recordings containing 5,565 echolocation calls was analyzed for sound durations and intervals (Table 4). The average sound duration was 46.0 ms ( $SD \pm 4.0$  ms, shortest sound 10 ms, longest sound 105 ms) and the average interval duration was 56.5 ms (Fig. 8). This means an average repetition rate of 9.8 sounds/s and a mean duty cycle of 45%. If a horseshoe bat spent the whole night outside it would emit about 405,000 sounds per night. Three longer sounds (225, 232 and 244 ms) showed deep amplitude modulations suggesting that each one consisted of three sounds separated by very brief intervals.

Interval durations were much more variable ( $SD \pm 12.4$  ms, Fig. 8). The shortest intervals (5 ms;  $n=81$ ) were not common. Longer ones (more than 100 ms) were occasionally heard from bats hanging on twigs. The invariable rattle of echolocation calls through a QMC-mini sometimes changed into a kind of stuttering for a second or so, and then the bat resumed its regular sound emission. The longest interval between calls was 2.6 s, and in all the sequences most of the 294 gaps were usually shorter than 350 ms. Only 6 gaps lasted more than 1 s. We heard long gaps only from bats hanging on twigs. The slowest sequence recorded within a faster series of echolocation calls came from the bat monitored for nearly 5 h at the irrigation channel. While hanging on a twig for 5.3 s the bat only emitted 26 sounds, i.e., a repetition rate of 4.9 sounds/s and a duty cycle of only 26.9%.

At the foraging sites bats immediately increased their pulse repetition rate when we stepped on dry twigs, approached the bats carelessly or made noiseless but fast movements. Repetition rates also increased before attack flights. We had the impres-



**Fig. 8.** Histograms of sound and pause durations from echolocation sound sequences in horseshoe bats (see also Table 4). *N*, number of sounds and pauses analyzed

sion that horseshoe bats responded to any alerting stimulus but especially to potential prey, with higher pulse repetition rates. Conspicuously, in most sound sequences emitted before a bat flew off for an attack, the last few sounds were longer (Fig. 7). This was distinct and allowed us to predict attacks. Typically in sound sequences just prior to a take-off for a catch, intervals are shortened by 49% and duty cycles increased by 43% compared to the total mean. From 17 of such sequences analyzed the average figures are: sound durations 50.7 ms (+10%), interval duration 29.3 ms

(–52%), repetition rate: 12.5 sounds/s (+27%), and duty cycle 64.2% (+42%). Thus a drastic reduction of interval length and an increase of sound duration of the last few sounds resulted in a distinct increase of the duty cycle whenever a bat started a catching flight. In such situations the duty cycle was never below 55% and reached its maximum at 74%.

The foraging *R. rouxi* we studied used long CF calls and high duty cycles. In flight or when alerted by prey or other stimuli the bats increased the duty cycle by drastically reducing interval time and slightly increasing sound duration; we rarely heard distinct final buzzes.

#### *Amplitude modulations*

Many of the sound sequences analyzed included echolocation sounds that were amplitude modulated so that the beginning and the end of the sound were accentuated and the middle part was relatively faint. In some cases the modulations were shallow, but in others, so deep that it was a matter of chance distinguishing between one deeply amplitude-modulated sound and two sounds separated by a very brief interval. Such amplitude-modulated sounds occurred irregularly in sound sequences recorded from bats hanging from twigs and in flight (Figs. 7 and 4c).

#### **Discussion**

The purpose of this field study was to test the hypothesis that echolocation with long pure tone signals is an adaptation to foraging in or close to dense vegetation (Glaser 1974; Neuweiler 1976). In such an environment echolocation with a CF carrier and a narrow auditory filter tuned to the carrier frequency will render fluttering targets detectable among clutter (Neuweiler et al. 1980; Schnitzler et al. 1983; Schuller 1984). Rufous horseshoe bats indeed foraged right within forests and where vegetation was densest. The limits of the foraging sites were surprisingly clear cut, and not even the open forests on the hill tops or the galleries along the rivers in cultivated land harboured foraging horseshoe bats for more than a few minutes. These observations support the idea that movement detection by pure tone echolocation has evolved under the pressure to exploit the insect fauna active within and around canopies of trees and bushes in dense forests and jungles (Neuweiler 1984). However, this is just one way of adapting to foraging in echo-cluttering environ-

ments. Other bat species avoid echo clutter by detecting prey acoustically and/or visually (*Antrozous pallidus*, Bell 1982; *Cardioderma cor*, Vaughan 1976; *Megaderma lyra*, Fiedler 1979; *Lavia frons*, Vaughan and Vaughan 1986; *Macroderma gigas*, Guppy and Coles, to be published).

Rufous horseshoe bats are adapted by flight style and type of echolocation to the forest habitat. This might explain why in earlier days when large parts of Sri Lanka were still covered by forests, this species was the most common bat in Sri Lanka (Phillips 1980), whereas recent surveys by Rübbsamen et al. (to be published) disclosed that now hipposiderids are far more common than horseshoe bats on the widely deforested island.

We cannot offer any plausible argument for the disappearance of the bats after the first foraging period. Griffin and Simmons (1974) also report for *R. ferrumequinum*: “almost all of the horseshoe bats disappeared after the first 20–30 min of each evening’s foraging flights. We could not ascertain whether they flew away... or landed with full stomachs...” Only telemetry will help in disclosing what the horseshoe bats do and where they stay during this strange period of absence.

The horseshoe bats echolocated throughout the night without any pause, and spent most of the night hanging on twigs and searching for insects passing by. Since the bats make only short catching flights that rarely exceed 1 s, foraging in flycatcher style is a cheap but also slow way of getting food. This might explain why most of the bats stayed outside of the cave until dawn.

Individual bats returned every night to their individual foraging site where they also alighted at precisely the same spot of the same twigs of the few trees and bushes they prefer. It is, however, not clear how the individual bats recognize these same spots every night. After we had treated some of the twigs with a sticky paste, the bats no longer landed there. Since bats generally possess an excellent spatial memory (Neuweiler and Möhres 1967), they probably recollected precisely the sites of their favourite twigs.

We never observed that a bat defended its foraging area against entering conspecifics. We are therefore hesitant to call these individual foraging sites individual territories. This tolerance towards intruders might be related to the fact that the bats came from a nursery colony. During these weeks, when insects are plentiful and a female should collect as many insects as possible, it might be cheaper to tolerate intruders than to chase them away. Individual foraging sites are not specific to horseshoe bats and have been also observed in many other

species (e.g. *Hipposideros commersoni*, Vaughan 1977; *Cardioderma cor*, Vaughan 1976; *Hipposideros speoris* and *H. bicolor*, Habersetzer et al. 1984).

We made several observations of horseshoe bats flying close to the ground and briefly landing there. But we are not certain that they also caught insects in these instances. There are reports that *Rhinolophus ferrumequinum* alights on the ground and catches flightless insects (Southern 1964). The ears of horseshoe bats are sensitive in the frequency range of 20–30 kHz which includes the rustling noises made on the ground by moving insects.

There is a group of bat species which economize on flight energy expenditure and use a sit-and-wait strategy for foraging. They have individual foraging areas, scan the space by revolving their bodies through 180°–360° and make only brief capture flights. However, the prey caught and the senses used for detection differ among species: many Megadermatids perch on low branches and listen for ground-dwelling prey (*Cardioderma cor*, Vaughan 1976; *Megaderma lyra*, Fiedler 1979; *Macroderma gigas*, Guppy and Coles, to be published). They detect prey acoustically and visually and not by echolocation. Rhinolophids and some Hipposiderids (*H. commersoni*, Vaughan 1977; *H. diadema*, Brown and Berry 1983) are obligatory echolocators and only catch flying insects passing by at close range and level with or below the bats' perch. Other Hipposiderids also detect only fluttering targets by echolocation but prefer aerial or gleaned strategies (*H. ruber*, Bell and Fenton 1984; *H. speoris* and *H. bicolor*, Habersetzer et al. 1984). Interestingly, the Megadermatid *Lavia frons* also catches only flying insects from perches and pursues insects by towering flights above canopies (Vaughan and Vaughan 1986). Their brief and faint echolocation clicks are not suited for fluttering-target detection, and the authors suggest that these bats use acoustical and visual cues for prey detection.

In horseshoe bats the CF component was emitted under all circumstances. It is the signal used for detecting flying insects by flutter, and typically CF signal duration was invariably prolonged in the last moments before take-off. During catching flights the bats invariably add a final FM sweep to the CF component. This makes sense since for distance discrimination the composite CF/FM signal is mandatory (Roverud, pers. comm.) in horseshoe bats. These results corroborate with earlier findings in *Rhinolophus ferrumequinum* catching flying insects in the laboratory (Vogler and Neuweiler 1983). Only when the bats had caught the

prey and returned to their vantage points did they emit very prominent initial and final FM sweeps which had intensities higher than the pure tone. Vogler and Neuweiler (1983) therefore concluded that the initial and final FM sweeps might be important parts of the signals for obstacle avoidance in flight. This is what we observed in the field (Table 2).

As shown in Table 2 in most sounds emitted during flight an initial FM sweep was present and in two-thirds of the samples it was as broad or even broader than the final one (Table 3). This indicates that the initial FM sweep has to be considered as an integral part of the echolocation signal. It is therefore misleading to call horseshoe bats CF/FM bats. The nomenclature for structures of echolocation signals is descriptive and never indicates the possible importance of a sound component for echolocation. Therefore, the correct label for horseshoe bats may then be FM/CF/FM bats. Our field data seem to be at odds with the statement of Schnitzler et al. (1985) that in their recordings from one rufous horseshoe bat the CF component only "sometimes is preceded by an upward FM sweep". However, an inspection of the sonograms from catching flights shown in their Figs. 1 and 2 shows that from 189 sonograms, 119 (i.e. 67%) feature an initial FM sweep.

In most sounds from horseshoe bats we monitored in the forests of Sri Lanka, the first harmonic of the CF component could be clearly detected at about 40 kHz. Surprisingly in some occasions the first harmonic was as loud as the second one, and in a few instances we were able to monitor horseshoe bats only when the bat detector was set at 40 kHz. This observation is corroborated by recent neurophysiological and behavioural experiments. O'Neill et al. (1985) have shown that in cortical distance-ranging neurons of rufous horseshoe bats, the first harmonic is mandatory in the first signal (emitted sound) for the responsiveness of the neurons in a manner similar to that already shown in *Pteronotus parnellii* by O'Neill and Suga (1982). In addition, Roverud (pers. comm.) found that in rufous horseshoe bats the performance in distance discrimination is disrupted by interference signals in the frequency range of the first harmonic. All these data from the field and from the laboratory unequivocally show that the first harmonic is an important part for information analysis in echolocation of horseshoe bats.

There also was a sex-specific difference in the frequency range of the CF part emitted by adult males and females. Since there is only a minor overlap between the male and female frequency

band the CF signal may not only subserve echolocation but might also carry communicative information. Of course, the lower frequencies emitted by males might be only a side effect of the different androgen levels between males and females during adolescence, which might result in small structural changes of the larynx as shown in other mammals and in man.

Strangely enough we also observed several horseshoe bats flying over us or hanging on twigs which we could only monitor at a dialsetting of the QMC bat detector at 50 kHz or others at 65 kHz. A misreading or miscalibration of the bat detectors can be ruled out since the 50 kHz sounds were also recorded on videotape. There is a disagreement among the authors as to how to interpret these data. Some of us suggest that these were sounds from other horseshoe bat species. However, according to Phillips (1980) only one other horseshoe bat species occurs in Sri Lanka, *Rhinolophus luctus beddomii*, emitting 42 kHz (Roberts 1972), which still leaves one frequency band unexplained. Adolescent horseshoe bats emit sounds either through the nose or through the mouth. The sounds emitted through the mouth also show the typical FM/CF/FM pattern but are shifted to lower frequencies and contain strong harmonics (unpublished data). Thus sounds recorded at 50 and 65 kHz might come from horseshoe bats which occasionally vocalize through the mouth instead of through the nose as they usually do.

This brief but intense field study has settled some open questions in echolocation of horseshoe bats.

(1) The observed foraging behaviour strongly supports the hypothesis that specific adaptations in pure-tone echolocation for fluttering prey detection evolved under the pressure of detecting prey within dense vegetation.

(2) The pure tone component is primarily a detection signal and usually is emitted with no FM components added while searching for prey.

(3) The initial FM sweep and the first harmonic of the echolocation sounds are integral and important parts of the echolocation signals.

(4) The FM components are most important for obstacle avoidance and when approaching a target (see also Vogler and Neuweiler 1983).

The study has also brought up new questions to be solved. Do horseshoe bats discriminate prey before leaving their vantage points? Are the foraging strategies governed by insect abundance? Are the individual and sex-specific frequencies also of communicative significance? What kind of information may the initial FM sweeps carry, and why

might bats sometimes emit very loud first harmonics? This wide range of new problems can be best addressed in the future by combined field and laboratory investigations.

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