

Foraging behavior and Doppler shift compensation in echolocating hipposiderid bats, *Hipposideros bicolor* and *Hipposideros speoris*

J. Habersetzer¹, G. Schuller², and G. Neuweiler²

¹ Zoologisches Institut der Universität Frankfurt am Main, Siesmayerstraße 70, D-6000 Frankfurt am Main, Federal Republic of Germany,

² Zoologisches Institut der Universität München, Luisenstraße 14, D-8000 München 2, Federal Republic of Germany
Indo-German Project on Animal Behavior Madurai Kamaraj University Madurai, India

Accepted July 16, 1984

Summary. 1. Two hipposiderid bats, *H. bicolor* and *H. speoris*, were observed in their natural foraging areas in Madurai (South India). Both species hunt close together near the foliage of trees and bushes but they differ in fine structure of preferred hunting space: *H. bicolor* hunts within the foliage, especially when *H. speoris* is active at the same time, whereas *H. speoris* never flies in dense vegetation but rather in the more open area (Fig. 1, Table 1).

2. Both species emit CF/FM-sounds containing only one harmonic component in almost all echolocation situations. The CF-parts of CF/FM-sounds are species specific within a band of 127–138 kHz for *H. speoris* and 147–159 kHz for *H. bicolor* (Tables 2 and 3).

3. *H. speoris* additionally uses a complex harmonic sound during obstacle avoidance and during laboratory tests for Doppler shift compensation. *H. bicolor* consistently emits CF/FM-sounds in these same situations (Fig. 2).

4. Both hipposiderid bats respond to Doppler shifts in the returning echoes by lowering the frequency of the emitted sounds (Fig. 3). However, Doppler compensations are incomplete as the emitted frequencies are decreased by only 55% and 56% (mean values) of the full frequency shifts by *H. speoris* and *H. bicolor*, respectively.

5. The differences in Doppler shift compensation, echolocating and hunting behavior suggest that *H. speoris* is less specialized on echolocation with CF/FM-sounds than *H. bicolor*.

Introduction

Hipposiderid and rhinolophid bats are closely related families which share some remarkable specializations in their echolocation systems: both families emit long pure tones (constant frequency=CF) terminated by a brief and shallow frequency modulated (=FM) sweep. In hipposiderid bats the CF-part does not last longer than 5–10 ms (Grinnell and Hagiwara 1972; Gustafson and Schnitzler 1979; Schuller 1980) whereas in rhinolophids signal duration may exceed 100 ms and rarely falls below 10 ms.

The auditory system in both families features narrow and sensitive tuning to the species specific range of frequencies emitted (hipposiderids: Grinnell and Hagiwara 1972; Schuller 1980; rhinolophids: Neuweiler 1970; Jen and Suthers 1982). During flight and pursuit of prey the frequencies of the echoes are increased due to Doppler effects caused by the bat's own flight speed. The compensation of such Doppler shifts is a specific feature of the rhinolophid echolocation system (Schnitzler 1973) which maintains the carrier frequency of the echo within the sharply tuned filter in the bat's cochlea (Bruns 1976a, b), effectively eliminating these Doppler shifts of the entire echo.

Schuller (1979 and in press) has presented neurophysiological evidence indicating that rhinolophids can detect fluttering targets by evaluating frequency and amplitude modulations of the constant carrier frequencies in the echoes. In rhinolophids echolocation with CF-signals was interpreted as an adaptation to foraging close to echo cluttering background (Neuweiler et al. 1980).

Abbreviations: CF constant frequency; FM frequency modulated; RF resting frequency emitted by a non-moving bat

It is not clear if hipposiderids also use the rather brief CF-part of their echo signal in the same way as rhinolophids. In a previous study, Schuller (1980) tested *H. bicolor* and *H. speoris* for their capacity to achieve Doppler compensation by an electronic playback method which was successfully used in *Rhinolophus rouxi*. From 7 *H. speoris* and 8 *H. bicolor* only one *H. bicolor* clearly performed Doppler shift compensation. The other specimen reacted only briefly or not at all to electronically Doppler shifted echoes. We therefore repeated tests for Doppler effect compensation in both species employing the pendulum method (Henson et al. 1980).

As mentioned above, in rhinolophids, which are closely related to the hipposiderids, echolocation with a CF-component is interpreted as an adaptation to fluttering target detection. It is not clear if this also applies to hipposiderids since very little is known about the foraging habits of these bats. Therefore the foraging behavior and foraging sites of these two closely related species were observed in their natural habitats in India for a period of one year by one of us (J.H.) and the results of these observations will be presented here.

Materials and methods

Field studies were made at two caves near Madurai Kamaraj University (Madurai, South India 9°58'N, 78°10'E) and three observation sites on the University campus in 1978 and 1979. Hunting bats were observed at different observation points on foraging sites close to the caves. Hipposiderid bats were caught in the evening at the cave entrance and marked with small luminescent tags (Buchler 1976). Unmarked bats were observed with a handlamp (halogen-H4).

The two bat species could be discriminated by their characteristic flight patterns and body shape: *H. bicolor* has long rounded ears, which are slightly bent backwards in flight and show a horn-like silhouette. It is characterized by a high-frequency wing beat and irregular flight paths close to the ground. *H. speoris* has smaller ears with pointed tips and shows stereotyped circling flight around obstacles on otherwise straight flight paths.

Quantitative studies on hunting behavior were made once a week at the three observation places on the University campus for a total period of 13, 20 and 29 weeks respectively. The bats came to feed on insects which were attracted by street lamps. To document the activity of bats, 'bat passes', i.e., the number of bat flights seen by the observer in a defined area, were counted by modifying Fenton's (1970) method. The modification consisted in a large increase of the sampling rate (bat passes were counted each minute from 18.00 to 6.30 h which yielded a high temporal resolution of behavioral changes. Activity data were plotted for 5-min mean values which were calculated as a function of a 5-point Hanning filter (Habersetzer 1983). By this procedure the temporal resolution was about 3 times higher than for simple 5-min counts. Spatial distributions of bats in the foraging grounds were measured by counting bat passes for different areas separately.

Echolocation sounds were recorded in the field and in the

laboratory with a Brüel & Kjaer condenser microphone (type 4135) and a portable Lennartz tape recorder. At Kilakuikudi cave ultrasonic calls were recorded when the bats left the cave. Another recording site was 10 m away from the cave with the microphone directed towards the open space. Sounds of foraging bats were also recorded at the hostel area on the University campus. In the laboratory ultrasonic sounds were recorded from bats resting in the cage and during passive motion in the pendulum swing experiments.

In order to test whether the bats compensate Doppler shifts by changing the emitted frequency 35 specimens were tested in a pendulum experiment (Henson et al. 1980). Each bat was sitting on a small animal holder fixed at the end of a swinging pendulum which was 2.1 m long. Sounds were recorded 10 cm in front of the bat while the pendulum was not moved (RF = resting frequency) and when it was swung for 2–3 cycles towards a plane wall at ca. 4 m distance. All swings started from the same altitude of 2 m above the floor and moved through their lowest point 0.75 m above floor. The speed of the pendulum was measured by stroboscopic photography (18 flashes/s) of 9 forward swings with an accuracy of $\pm 2.7\%$. Maximal speed of the pendulum was 4.64 m/s. The damping of the pendulum motion after two swings was estimated to be lower than 2% and it was neglected for further calculations. Shifts of echo frequencies were calculated as a function of the speed of the pendulum and compared with the frequencies of the recorded sounds.

For off-line sound analysis tape recordings were played back on a Grundig TS 1000 recorder at 1/4th of the original speed (19 cm/s) exclusively, and the sounds were heterodyned with a custom-made instrument and a mixing frequency (Wave-tek-oscillator) of 32–40 kHz for a detailed frequency analysis. The resulting low frequency was fed into a real time spectrum analyser (Symspec 512, constructed by Dr. D. Menne, Tübingen), displayed on a Tektronix storage oscilloscope, and filmed by a Recordine camera. Absolute frequency resolution of this set-up was 0.175 kHz.

Results

Behavioral studies

Common foraging areas in hipposiderid bats. Both hipposiderid species lived together in the same natural caves. The colonies were found in dark parts of the caves 5–10 m from the entrances and never in well-lit caves or cracks of rocks or in dry caves. In the evening the first bat left the cave about 10–30 min after sunset and usually *H. speoris* preceded the first *H. bicolor* by approximately 5 min. The departure flight of the colony lasted for 60–80 min and both species flew out simultaneously.

The main hunting areas of these slow flying bats were places covered with bushes and trees. Two to three hours after departing from the roosting site hunting bats were seen in the vicinity of the caves mainly as single fliers and rarely in groups of 3–4 specimens. Later in the evening and throughout the night bats were hunting with increasing activity around street lamps where insects

had gathered as patchy aggregations. Trappings of insects (at one observation site) disclosed that insect aggregations mainly consisted of Lepidoptera of 0.5–1.0 cm body size. Both hipposiderid species were observed to feed on these moths. Maximum flight activity of hipposiderids coincided with the abundant presence of Lepidoptera between 2.00 and 4.00 h (observations of 15 nights). Bats pursued Lepidoptera on their escape maneuvers by rapid changes of the flight paths. Both hipposiderid species also flew close to the ground (frequently less than 1 m altitude) and near bushes, trees, and walls (frequently less than 2 m distance).

Both species preferred foraging areas which were protected from wind. Within the Campus area tree plantations effectively decelerate winds and there the bat passes observed varied between 20 and 300 per night (29 nights in weekly intervals). In contrast, on the open unprotected grassland only 300 m away from the Campus the average bat passes counted per night were only 5 (20 nights in weekly intervals). Highest activities were observed in a hostel garden which was characterized by a variety of small spaces between hedges, walls, trees etc. The observation area was illuminated by a gate lamp 1.5 m above ground. Lepidoptera and other insects being attracted by the light accumulated not only around the lamp, but also on the leaves of the nearby bushes, and on the surface of walls. Flight activity was in the range of 1000 bat passes per night (13 nights) with a maximum of up to 4000. Most of the observations reported below are from this observation point (Table 1, Fig. 1) and from the tree area.

Specific foraging strategies of H. speoris and H. bicolor. The two closely related species, *H. speoris* and *H. bicolor* differed in flight characteristics and in hunting behavior. *H. bicolor* was characterized by an irregular flight which was often interrupted by hovering phases or landings on the ground from which insects were picked up. Sometimes, they captured insects from vertical walls after sustained hovering in front of the obstacle and then continued the flight after a somersault away from the wall surface. In this situation the bat regularly maneuvered in short loops closer than 0.5 m to obstacles. *H. bicolor* also hunted within the dense foliage of trees and bushes.

H. speoris, on the other hand, showed stereotyped circling flights around obstacles. These bats flew around trees and bushes but at a distance between 0.6 m and 0.8 m and they never entered the dense foliage of trees. Compared with *H. bicolor*, hovering phases were shorter and relatively

Table 1. Hunting behavior of *Hipposideros bicolor* and *Hipposideros speoris*. The two columns show the distribution of flight activity (%) of bats in different spaces

Behavioral categories		Bat passes counted	
		<i>H. bicolor</i>	<i>H. speoris</i>
I	Flight within the foliage	2.6%	0
II	Catching insects on ground and walls	6.0%	0
III	Hovering flights in front of obstacles	16.0%	0
IV	Flights within 0.5 m of obstacles	16.2%	9.5%
V	Flights more than 0.5 m away from obstacles	24.4%	26.9%
VI	Circles and slopes around the lamp	28.0%	42.2%
VII	Flights close to the ground	6.8%	21.4%
Sample size (100%) $n = 3581$		736	

rare and an individual bat pursued the same insect only for two or three catching maneuvers and rarely followed prey down to the ground. These differences in hunting behavior of *H. bicolor* and *H. speoris* (Table 1) were observed regularly at all observation points noted above.

As a consequence of overlapping hunting space of *H. bicolor* and *H. speoris*, their flight paths crossed frequently when they were active at the same time. In almost all situations when clashes among hipposiderids were likely to occur, it was the *H. bicolor* which either stopped the flight activity or evaded into dense vegetation, or flew even closer to the ground than before. *H. speoris*, which is larger in body size, invariably continued circling flights. These observations indicate that *H. bicolor* and *H. speoris* competed, at least partially, for the same food resources. In the overlapping areas *H. speoris* generally dominated over *H. bicolor*. Countings in 13 nights at the hostel area indicated a definite decline in the activity level of *H. bicolor* whenever the activity level of *H. speoris* was higher than 30 passes per 5 min. This usually occurred when 2 *H. speoris* and 4–6 *H. bicolor* were hunting at the same time.

An example of bat activity in a single night recorded at the hostel area is given in Fig. 1. Flight activity of both *H. bicolor* (Fig. 1 B) and *H. speoris* (Fig. 1 C) was maximal between 2.30 and 3.40 h. Between 2.45 and 3.10 h a maximum of activity of *H. speoris* (Fig. 1 C) coincided with a minimum of that of *H. bicolor* (Fig. 1 B). The sudden decline

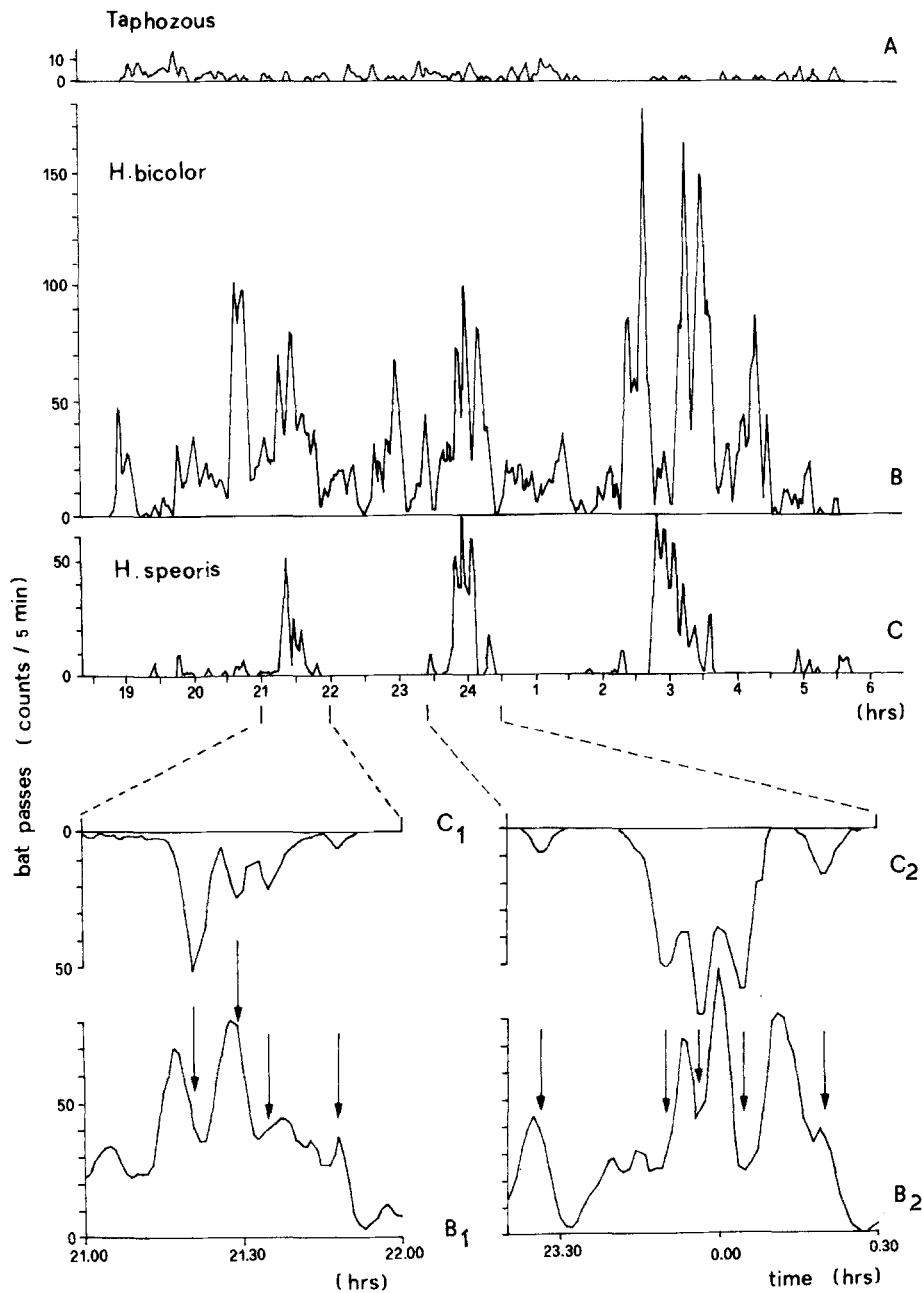


Fig. 1A–C. Flight activity of *Hipposideros bicolor* (B) and *Hipposideros speoris* (C) at the hostel observation site during one night. For comparison the simultaneously recorded flight activity of *Taphozous kachhensis* (A) is shown. Note that at 3.00 h a maximum of activity in *H. speoris* coincides with a minimal one in *H. bicolor*. Blown up representations of activity bouts in *H. speoris* (C₁ and C₂, inverted plots) and *H. bicolor* (B₁, B₂) disclosing complementary activity patterns (arrows) of the two species

of the activity of *H. bicolor* was not due to a paucity of prey and avoidance of interference with *H. speoris* as described above may be a reason for this behavior. Similar interference of activity during the same night becomes obvious when the data are plotted by an expanded time axis as shown in the lower curves of Fig. 1.

Echolocation sounds

Ultrasonic sounds of *H. bicolor* consisted of a constant frequency (CF) component of 3–6 ms fol-

lowed by a frequency modulated (FM) component in the last 2 ms. This type of CF/FM-sounds was recorded in all echolocation situations (Fig. 2, lower graph). The frequencies of the CF components ranged from 147 to 159 kHz with a mean of 154 kHz. The individual CF-frequencies of resting specimens are given in Table 2. In almost all situations *H. speoris* echolocated with sounds of the same CF/FM-type as *H. bicolor* (Fig. 2, upper graph, left sonograms) but with CF frequencies within a band of 127–138 kHz (mean: 133 kHz). CF-frequencies of individual bats are given in Ta-

Table 2. Doppler effect compensation of *Hipposideros bicolor*. Maximal frequency change of emitted sounds (given in kHz and % of full compensation) during consecutive pendulum swings (maximum speed: 4.64 m/s, max. Doppler shift: 4.1 kHz). No frequency response to Doppler shifts or cessation of sound emission are indicated by dashes

No. of bat	Resting frequency kHz	Maximal frequency change of emitted sounds during motion					
		1. forward swing		1. backward swing		2. forward swing	
		kHz	% full comp.	kHz	% full comp.	kHz	% full comp.
1	151.2	-2.4	60	+0.5	12	-2.4	60
2	149.2	-1.4	35	+0.5	13	—	—
3	147.6	-1.6	41	+0.5	13	-0.5	13
4	156.4	-2.3	55	+0.3	7	-1.0	24
5	146.8	-2.6	67	—	—	—	—
6	158.4	-2.3	55	—	—	-2.3	55
7	158.4	-2.1	50	—	—	—	—
8	149.6	-2.6	65	—	—	-1.7	43
9	154.8	-2.6	63	+1.0	24	-1.0	24
10	159.2	-2.4	57	+0.5	12	-0.5	12
11	156.8	-2.4	58	+0.9	22	-0.9	22
12	156.0	-2.6	63	+0.3	7	-2.1	51
13	149.6	-2.6	65	—	—	-2.4	60
14	158.0	-2.6	62	—	—	-2.4	57
15	153.2	-1.9	47	+0.5	12	-0.8	20
16	156.4	-2.4	58	+0.9	22	—	—
17	148.8	-1.9	48	+0.5	13	-1.2	30
Ideal Compens.	154.0	-4.1	100	+4.1	100	-4.1	100
Mean sample (SD)		<i>n</i> =17	55.7 (±8.7)	<i>n</i> =11	14.2 (±5.5)	<i>n</i> =13	36.1 (±17.8)

ble 3. Consequently the frequency bands of the CF components in the two hipposiderid species do not overlap. The frequencies of sounds in individual bats varied in a narrow range around the resting frequencies with standard deviations of 0.3% in both species (sample size: 20 to 50 echolocation pulses in each of 35 individuals).

In specific situations *Hipposideros speoris* deviated from this stereotyped sound emission. When flying or being fastly moved (in the laboratory) towards a solid target like a wall in a novel surrounding *H. speoris* emitted complex multiharmonic echolocation sounds (Fig. 2, upper graph, right sonagram) whereas *H. bicolor* continued to emit CF/FM-sounds. It is interesting to note that in a familiar situation, e.g. flights close to rock walls inside their caves, *H. speoris* only emitted CF/FM-sounds. The complex harmonic sounds had a broad spectrum of about 120 kHz in contrast to the narrow band CF/FM-signals (15–25 kHz bandwidth). Frequencies of CF-components of complex harmonic sounds varied unsystematically by 2–16% within 0.2 s and the frequency of the second harmonic was up to 45 kHz lower than the CF-frequency of typical CF/FM-sounds.

Doppler shift compensation

As described in Methods in both species tests for Doppler shift compensation were performed by moving the bat on a pendulum towards a wall. Maximal frequency change of emitted sounds during consecutive pendulum swings was evaluated as the mean value of emitted CF-frequencies during a 0.2 s time interval at the moment when the pendulum was moving with maximal speed (4.64 m/s). By this averaging procedure random variations of sound frequencies were eliminated.

The maximal Doppler shift of echofrequencies reached at the highest pendulum speed was $\pm 2.7\%$ of the individual emitted (RF = resting frequency). The sinusoidal variations of the pendulum speed between 4.64 m/s and zero results in corresponding sinusoidal changes in echofrequencies (dashed lines in Fig. 3) with a maximum shift of 3.5 kHz in *H. speoris* and 4.1 kHz in *H. bicolor* (Tables 2 and 3).

During the first forward swing of the pendulum all 17 *H. bicolor* responded to an increase of echo frequency by lowering the emitted frequencies by 1.4–2.6 kHz (Table 2 and Fig. 3). This corresponds

Table 3. Doppler effect compensation of *Hipposideros speoris*. Maximal frequency change of emitted sounds (given in kHz and % of full compensation) during consecutive pendulum swings (max. speed: 4.64 m/s, max. Doppler shift: 3.5 kHz). No frequency response to Doppler shifts or cessation of sound emission are indicated by dashes

No. of bat	Resting frequency kHz	Maximal frequency change of emitted sounds during motion					
		1. forward swing		1. backward swing		2. forward swing	
		kHz	% full comp.	kHz	% full comp.	kHz	% full comp.
1	135.8	-0.9	25	+0.7	19	-1.7	47
2	126.8	—		complex harmonic and CF/FM-sounds		—	—
3	134.0	-1.7	48	—	—	—	—
4	129.2	—		complex harmonic and CF/FM-sounds		—	—
5	130.8	-1.7	49	—	—	—	—
6	137.6	-1.8	49	—	—	-1.5	41
7	132.8	-2.6	74	+0.3	8	-0.3	8
8	134.8	-1.9	53	—	—	-0.3	8
9	134.8	-1.9	53	—	—	-0.2	6
10	133.2	-2.6	73	—	—	—	—
11	134.0	-1.9	53	+0.3	8	—	—
12	131.2	-2.1	60	—	—	-1.9	54
13	130.0	-2.5	72	+0.3	9	-0.8	23
14	134.4	-1.9	53	—	—	-1.5	42
15	132.8	-1.6	45	+0.5	14	—	—
16	133.2	-2.3	65	—	—	—	—
17	130.0	—		complex harmonic and CF/FM-sounds		—	—
18	136.8	-2.1	58	—	—	-0.5	14
Ideal Compens.	133.0	-3.5	100	+3.5	100	-3.5	100
Mean sample (SD)		<i>n</i> =15	55.4 (±12.3)	<i>n</i> =5	11.8 (±4.4)	<i>n</i> =9	27.1 (±18.0)

to 35–65% (average 56%, SD 8.7%, *n*=17) of complete compensation of the Doppler shifts in the echoes. Thus full compensation was never achieved in contrast to *Rhinolophus rouxi* which compensates Doppler shifts to a level of 95% (Schuller 1980). Interestingly for the second forward swing, compensation for Doppler shifts of the echofrequencies was reduced to an average of 36% of full compensation (SD 17.8%, *n*=13) or occasionally the bats stopped sound emission.

During backward swings, when echo frequencies were shifted below the resting frequency *H. bicolor* either did not react at all or slightly increased the emitted frequency by a mean of 14.2% of a full compensation (SD 5.5%, *n*=11).

In *H. speoris* Doppler shift compensation is basically the same as described above for *H. bicolor* (Table 3). However, *H. speoris* compensates less consistently than *H. bicolor*. Three of 18 *H. speoris* tested did not respond to Doppler shifts of the echo frequencies. These three bats occasionally emitted groups of complex harmonic sounds (Fig. 3 and Table 3) of various durations instead of CF/FM-sounds. Doppler shift compensation of the other bats reached 55% of full compensation

on the average (SD 12.3%, *n*=15) during the first forward swing. Among these bats there were another three *H. speoris* (No. 5, 10, 18) emitting a single brief group (0.2 s) of complex harmonic sounds. In subsequent forward swings nine of the bats failed to respond and the other nine *H. speoris* compensated by 6–54% of full compensation (average 27%, SD 18.0%, *n*=9). During the backward swings most *H. speoris* did not respond to the decrease of the echo frequencies below RF in contrast to *H. bicolor*. Thus *H. bicolor* generally compensates for Doppler shifts more consistently than *H. speoris*.

Discussion

The present study showed that ‘swinging’ hipposiderids responded to positive Doppler shifts of echo frequencies. However, in contrast to the almost perfect (95%) compensation in *Rh. rouxi*, the compensations were less consistent and only partial in *H. bicolor* (56%) and in *H. speoris* (55%).

Incomplete compensation is not due to imprecise control of emitted frequencies since individual non moving hipposiderids may maintain the rest-

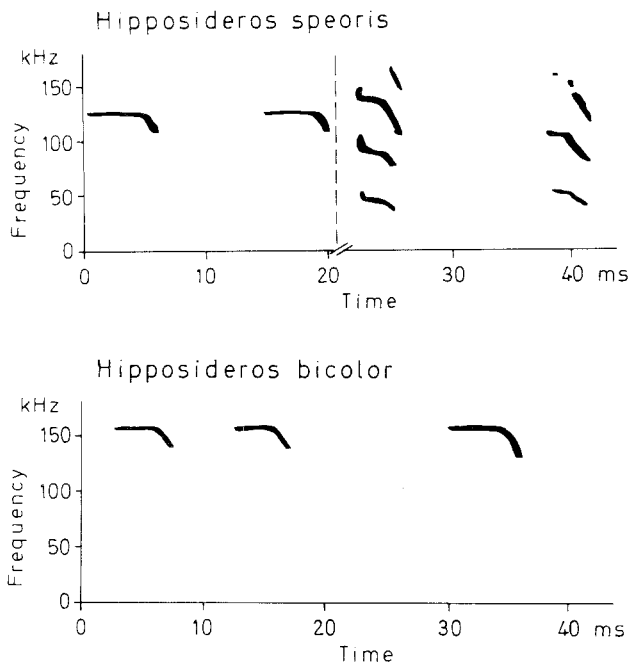


Fig. 2. Echolocation sounds of hipposiderid bats: *H. bicolor* (lower graph) consistently emits CF/FM-sounds in all situations tested. *H. speoris* emits CF/FM-sounds (upper graph, left side) while leaving the cave and during flight in the open. During flights towards a wall and passive motion in the pendulum experiment complex harmonic sounds occasionally occur (upper graph, right side). CF-components of complex harmonic sounds are shorter and the second harmonic is 15–45 kHz lower than in CF/FM-sounds. FM-components are prominent and first and third harmonics are intense

ing frequency (RF) in short sound sequences with similar accuracy as rhinolophids (Schuller 1980). There may be other reasons for this variability of performance. First of all the poor compensation response to Doppler shifts in the echoes might be due to the restraining conditions of a bat sitting in a swing whereas bats in free flight may well be able to Doppler compensate as Gustafson and Schnitzler (1979) showed in the hipposiderid bat, *Asellia tridens*.

Due to the dimensions of the swing, the speed of change of Doppler shift in the echoes was a fixed parameter which was not experimentally manipulated. The oscillating frequency of the pendulum was about 0.3 Hz thus inducing a Doppler shift transition from 0 to 4 kHz within 0.75 s. In rhinolophids the dynamic response of the Doppler shift compensation system was limited to very low modulation frequencies (Schuller et al. 1975). The response was reduced to 50% of full compensation when a Doppler shift of 4 kHz was presented within 5 s. If this restriction also applies to hipposiderids they might have been unable to compensate the highest shifts, when the pendulum went

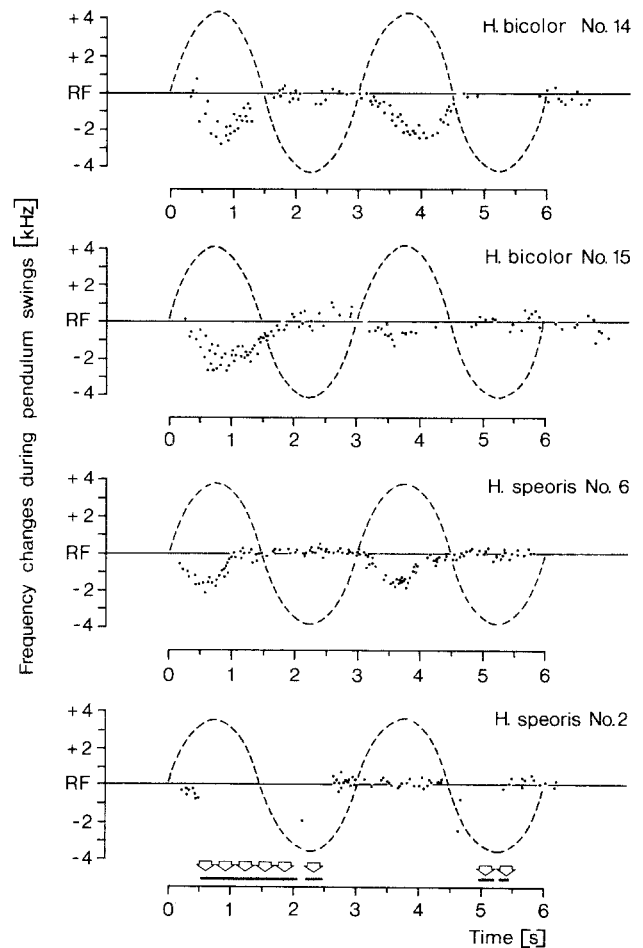


Fig. 3. Doppler shift compensation in *Hipposideros bicolor* and *H. speoris* when swinging on a pendulum. Each dot represents the CF-frequency of a single sound in relation to the individual resting frequency (RF). RF is 158.0 kHz for No. 14, 153.2 kHz for No. 15, 137.6 kHz for No. 6 and 126.8 kHz for No. 2. The broken lines show positive (+) and negative (–) Doppler shifts of echo frequencies caused by forward and backward pendulum swings. During forward swings bats decrease sound frequencies but compensations for previous echo frequency shifts remain incomplete. Negative Doppler shifts cause no (No. 14 and 6) or only little (No. 15) increase of sound frequencies. Emitted sound frequencies of No. 2 (*H. speoris*) are not affected by Doppler shifts. Black lines at bottom of the graph represent emission of complex harmonic sounds, and arrows indicate that frequencies of these sounds are far below the range of the individual CF-band of bat No. 2

through the maximal speed. Therefore it remains possible that incomplete compensation might have been attributed to the rapidly changing velocity of the swing.

In all experiments *H. bicolor* displayed more consistent Doppler shift compensation than *H. speoris*. Moreover, one third of the *H. speoris* bats occasionally emitted complex harmonic sounds instead of CF/FM-signals when they were swung to-

wards the wall. *H. speoris* can not compensate for Doppler shifts when emitting these broad band signals most probably due to the large frequency variations in complex harmonic sounds. This transition to broad-band signal emission was also observed under natural situations when *H. speoris* flew close to a large target, whereas *H. bicolor* never emitted such broad band signals under any circumstances. Interestingly a similar reaction is also reported for the mormoopid bat *Pteronotus p. parnellii* (Kobler, personal communication), another bat compensating inconsistently and incompletely. Apparently in *H. speoris* sound configuration can be adapted more flexibly to different target situations than in *H. bicolor* and rhinolophids which invariably emit CF/FM-sounds.

It is suggested that due to poor Doppler shift compensation *H. speoris* might give up fluttering target detection in a novel situation and probes the targets by a broad band signal which might result in a good target texture differentiation (Habersetzer and Vogler 1983). In this respect they resemble several other species from the Madurai study area, e.g. *Pipistrellus mimus* (Habersetzer 1983) and *Rhinopoma hardwickei* (Habersetzer 1981), which gradually change their echolocation signals from long narrow-band sounds to brief broad-band signals when approaching a prey or a target.

CF/FM-echolocation is commonly interpreted as a specific adaptation to fluttering target detection in an echo-masking environment, i.e. close to vegetation or other cluttering background (Neuweiler et al. 1980). Therefore one might speculate that in a phylogenetic context *H. speoris* appears to be less strictly specialized for fluttering target detection than *H. bicolor* or rhinolophids. Assuming that this trend towards exclusive specialization for fluttering target detection really exists the incomplete and less consistent Doppler shift compensation in hipposiderids might be interpreted as an intermediate step between less specialized and fully specialized CF-echolocation as it exists in rhinolophids.

In our study area in Madurai both species, *H. speoris* and *H. bicolor*, always forage close to or within vegetation or other large objects surrounded by insects. They do not share this foraging niche with any other bat species. *Pipistrellus* also forages at vegetation level but prefers to hunt in open spaces and keeps distance to foliage and obstacles (Habersetzer 1983). *Megaderma lyra* only scans the ground for larger insects and vertebrates and *Taphozous* and *Tadarida* prefer to forage in higher altitudes above tree level (Habersetzer 1983).

Detailed observations of their foraging behavior revealed that the foraging areas of *H. bicolor* and *H. speoris* are not identical (Table 1). From our data presented and Fig. 1 we conclude that *H. bicolor* retreats to the narrow and complicated foraging spaces within the canopies of bushes and trees when both species happen to be active in the same area at the same time. *H. speoris*, the larger of the two species, was never observed to enter the foliage and prefers to circle around the trees, branches or other objects whereas *H. bicolor* displays highly sophisticated flight maneuvers including long lasting hovering and peering its way skilfully through thorny bushes. This retraction into the foliage and more secluded spaces when *H. speoris* is present might explain why bats show a complementary activity pattern of the two species.

This pressure exerted by activities of *H. speoris* to *H. bicolor* forcing it to limit its foraging area to spaces within foliages might also explain why masking echoes will be a more serious problem for *H. bicolor* than for *H. speoris* and hence the former might have to rely more heavily on fluttering target detection with CF-echolocation. These arguments would then imply that at least *H. bicolor* should detect a prey insect only or more easily when it is moving. Whether or not this is really the case is currently being tested in another series of experiments.

Acknowledgements. As a part of the "Indo-German Project on Animal Behaviour" this study was supported by the University Grants Commission of India, Government of India Scholarship, and Alexander-von-Humboldt-Stiftung, Deutsche Forschungsgemeinschaft (SFB 45, SFB 204) and the Deutscher Akademischer Austauschdienst. We thank Professor S. Krishnaswami for offering the facilities of the School of Biological Sciences, Professor M.K. Chandrashekar for supporting the fieldwork, Dr. D. Uma and M.K. Sripathi for assistance in sound recordings, and H. Tschardt and Mr. Grommet for technical help. We are grateful to Dr. A. Feng who made many helpful suggestions and revised the English.

References

- Bruns V (1976a) Peripheral auditory tuning for fine frequency analysis by the CF/FM bat, *Rhinolophus ferrumequinum*. I. Mechanical specializations of the cochlea. *J Comp Physiol* 106:77-86
- Bruns V (1976b) Peripheral auditory tuning for fine frequency analysis by the CF/FM bat, *Rhinolophus ferrumequinum*. II. Frequency mapping in the cochlea. *J Comp Physiol* 106:87-97
- Buchler ER (1976) A chemiluminescent tag for tracking bats and other small nocturnal animals. *J Mammal* 57:173-176
- Fenton MB (1970) A technique for monitoring bat activity with results obtained from different environments in Southern Ontario. *Can J Zool* 48:847-851
- Grinnell AD, Hagiwara S (1972) Adaptations of the auditory

- nervous system for echolocation. Studies on New Guinea bats. *Z Vergl Physiol* 76:41–81
- Gustafson Y, Schnitzler H-U (1979) Echolocation and obstacle avoidance in the hipposiderid bat *Asellia tridens*. *J Comp Physiol* 131:161–167
- Habersetzer J (1981) Adaptive echolocation sounds in the bat *Rhinopoma hardwickei*. A field study. *J Comp Physiol* 144:559–566
- Habersetzer J (1983) Ethoökologische Untersuchungen an echoortenden Fledermäusen Südindiens. PhD thesis Fachbereich Biologie, Universität Frankfurt
- Habersetzer J, Vogler B (1983) Discrimination of surface-structured targets by the echolocating bat *Myotis myotis* during flight. *J Comp Physiol* 152:275–282
- Henson OW Jr, Henson MM, Kobler JB, Pollak GD (1980) The constant frequency component of the biosonar signals of the bat, *Pteronotus parnellii parnellii*. In: Busnel R-G, Fish JF (eds) Animal sonar systems. Plenum Press, New York, pp 913–916
- Jen PH-S, Suthers RA (1982) Responses of inferior collicular neurons to acoustic stimuli in certain FM and CF/FM paleotropical bats. *J Comp Physiol* 146:423–434
- Neuweiler G (1970) Neurophysiologische Untersuchungen zum Echoortungssystem der Großen Hufeisennase *Rhinolophus ferrumequinum*. *Z Vergl Physiol* 67:273–306
- Neuweiler G, Bruns V, Schuller G (1980) Ears adapted for the detection of motion, or how echolocating bats have exploited the capacities of the mammalian auditory system. *J Acoust Soc Am* 68:741–753
- Schnitzler H-U (1973) Control of Doppler shift compensation in the greater horseshoe bat, *Rhinolophus ferrumequinum*. *J Comp Physiol* 82:79–92
- Schuller G (1979) Coding of small sinusoidal frequency and amplitude modulations in the inferior colliculus of CF/FM bat *Rhinolophus ferrumequinum*. *Exp Brain Res* 34:117–137
- Schuller G (1980) Hearing characteristics and Doppler shift compensation in South Indian CF/FM bats. *J Comp Physiol* 139:349–356
- Schuller G, Beuter K, Schnitzler H-U (1974) Response to frequency shifted artificial echoes in the bat *Rhinolophus ferrumequinum*. *J Comp Physiol* 89:275–286
- Schuller G, Beuter K, Rübsamen R (1975) Dynamic properties of the compensation system for Doppler shifts in the bat, *Rhinolophus ferrumequinum*. *J Comp Physiol* 97:113–125