Ontogeny of sounds in the echolocating bat *Hipposideros speoris*

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Summary. 1. Young *Hipposideros speoris* emit multiharmonic sounds in groups of three to four notes. Newborns emit a relatively uniform pattern of FM- and FM/CF/FM-sounds. From ten days of age onwards the initial sound (first note) of a group is a FM-sound whereas the successive ones are CF/FM-sounds of consistently higher frequencies. At prevolant and volant stages of the bat's development most of the sound energy is concentrated in the second harmonic which is raised to the frequency range of the adults' CF/FM-sounds (127–138 kHz). Subsequently other harmonics disappear.

2. Harmonic components are suppressed or filtered out when they fall in a frequency range of approximately 65–75 kHz. This was found for bats of different ages regardless which fundamental frequency the suppressed harmonic components corresponded to, indicating a mechanical filtering process. These measurements coincide with the absence of the first harmonics in the same frequency range in the sounds of adults.

3. Temporal sound emission patterns were measured for bats of different ages. There was an increase in sound duration and an increase in the number of sounds (notes) per group as the bat matured to adulthood.

4. The sound emission of juveniles aids mothers in finding their young ones. Mothers located their infants even when the juveniles were displaced far from where they were left behind by their mothers. Behavioral experiments under both natural and captive conditions showed that the sound emission of young ones attracts mothers but do not give sufficient cues to allow the mother to discriminate their own from a group of young.

5. The ontogeny of the two types of sounds (CF/FM and complex harmonic FM) of adult *Hipposideros speoris* is discussed and compared with the vocalisations of other bat species.

Introduction

Hipposiderid bats echolocate with combined CF/FM-sounds (Novick 1958; Grinnell and Hagiwara 1972; Schuller 1980) consisting of a constant frequency (CF) part terminated by a brief downward modulated frequency sweep (FM). Young hipposiderids emit relatively low frequency sounds consisting of several harmonic components. As the juveniles mature, the second harmonic component of the sounds becomes prominent and its frequency is elevated to the range of adults (Gould 1979). Similar results in the ontogeny of CF/FM-signals were found for rhinolophid bats by Konstantinov (1973). Both juvenile and adult rhinolophid and hipposiderid bats emit sounds consisting of predominantly CF-parts regardless of a communicative or an echolocation context. In contrast, bat species which echolocate with short FM-sounds (e.g. *Antrozous, Eptesicus,* and *Myotis*) emit short FM-sounds and also long CF-signals when they are young (Brown and Grinnell 1980). Vocalizations of juvenile *Myotis* are characterized by audible antiphonal chirps and audible long isolation calls of a tonal character (Turner et al. 1972). The latter vocalizations are social communication calls and attract the mother which can discriminate its baby from others using only auditory cues.

Adult *Hipposideros speoris* share some acoustical properties with CF-bats and FM-bats as well. They usually echolocate with CF/FM-sounds, but under certain situations they also use complex har-

Abbreviations: CF = constant frequency; *FM* = frequency modulated

monic sounds, which are characterized by prominent FM-parts and three harmonics resulting in a broad frequency spectrum (Habersetzer et al. 1984). This speciality compared to other CF-bats was one of the reasons to consider the echolocation behavior of *H. speoris* as an intermediate stage to full CF-echolocation.

It is not known whether these two different types of echolocation sounds of *H. speoris* stem from juvenile precursors that largely differ or if they even derive from sounds which serve different purposes, e.g. echolocation or social communication. The aim of our paper is to study the ontogeny of the sounds of young *H. speoris* and the mother infant interactions under natural conditions and in captivity.

Materials and methods

Behavioral field studies were made at two caves near Madurai Kamaraj University campus (Madurai, 9°48′N, 78°10′E, South India) from 1978 to 1980. The Kilakuilkudi cave (8 km southeast from the campus) was inhabited by 500–600 *H. speoris* and 10–15 *H. bicolor*. In the Pannyan malai cave (5 km west from the campus) *Rhinopoma hardwickei, H. speoris* (300 specimens), *H. bicolor* (400 specimens), and *Megaderma lyra* roosted at different parts of the cave. Both caves were narrow but 30 m and 45 m long and featured an almost constant temperature of 27 °C and 28.5 °C, respectively, and relative humidity of about 90–95% throughout the year.

In the caves two mother-infant pairs and fifteen single infants were marked individually by cutting the nails of the hind limbs or by slits in the ears. These marked bats were regularly brought to the laboratory for measuring the development of wing size (Jones 1967) and body weight and for recording vocalizations. Sounds were recorded by a B & K microphone type 4135 providing a flat frequency response (± 3 dB) from 10 to 140 kHz for sounds at intensities higher than 65 dB SPL. The sounds were stored on tape by a Lennartz-recorder at a speed of 76 cm/s.

For comparison the same measurements and recordings were taken from captive bats. Nine pregnant bats were captured at the cave entrance while they returned from foraging. They were marked with colored celluloid bands and released into an outdoor cage ($7.5 \times 3.0 \times 3.75$ m) at the Botanical garden of the University campus. Inside the cage bats foraged on insects which were attracted from outside by a mercury lamp (125 W) mounted within the cage. A small artificial pond provided water ad libitum. All females gave birth to a young one from 5.11. to 13.12.1980. However, five of the babies died within 2 to 28 days because they were not regularly fed by their mothers. The relative humidity in the cage only reached 35–55% and the temperature rose to 31 °C during the daytime. This and outdoor noise might have caused the deficit in nursing behavior which was never observed under natural conditions within the caves. The remaining four babies grew up normally and became volant. Their sounds were recorded by using a QMC-condenser microphone.

Sound recordings were analysed on a Grundig TS 1000 recorder at a reduced speed of 4.75 cm/s (1/16th of original speed). Sonagrams and power spectra were obtained from a Symspec 512 frequency analyser (Dr. Menne, University of Tübingen) and photographed from a Tektronix storage oscillo-scope by a Polaroid or a Recordine-movie-camera. Sound recordings made with the QMC microphone (which picked up sounds at intensities as low as 50 dB SPL) were used to make sonagrams. The duration of single sounds and groups of sounds was measured by feeding the sounds into an envelope detector which was connected to a Watanabe xy-writer type WR 3001. The sounds emitted by infants were correlated to the known age in days after birth or to the forearm length and the body weight.

Results

Development of juveniles and behavioral observations

Young *Hipposideros speoris* were found in the caves throughout the year and a pronounced increase of parturations was observed during the rainy season from September to December. This is in contrast to *H. bicolor* which give birth only in the months from March to June. Females of *H. speoris* give birth to a single young one. The eyes of new borns are closed and the ears are folded laterally. The body is naked with a darker dorsal side and a pink ventral side. Eye slits appear after one week, and the eyes are completely opened after two weeks. The ears are raised at the tenth day and ear movements are noticeable two weeks after birth. When the bats are about one month old the fur is as dense as in adults but still of darker color. Juveniles are attached to the body of their mothers in a reverse position while firmly suckling at one of the two pubic teats.

Most of females carried their new-born with them when they flew out of the cave for foraging and the majority left their infants inside the cave when they were older than 7 days. Mothers returned regularly before midnight and retrieved their young ones. During retrieval the mother moved towards its infant, gently touched it with the forearm, and presented the ventral surface, especially the pubic region. When the infant tried to cling on the body of its mother she turned her body about an angle of 45° by partly spreading her wing membranes. This posture enabled the baby to hold the pubic teats of the mother and to release contact from the rock. Then the infant turned towards the mammary glands and after suckling it stretched either one or both of its wings repeatedly or exhibited wing fluttering by hanging from the neck of its mother. Apparently mothers spent most of the night inside the cave.

Young bats were caught in the cave after the emergence of the adult colony. To study the growth of individual and marked baby bats the lengths of the forearm, the fifth finger and the third finger were measured. Between the age of five to

ten days the wing bones grew slightly faster than during other stages of adolescence. There was no evidence for different growing rates of various bones of the wing, indicating that the forearm length alone is well suited as a measure of development. Two weeks after birth the growth rate decreased. The average forearm length of the newborn bat was 16 mm and this is 31% of the mean forearm length of the adults (52.4 ± 1.7 mm, $n = 11$). At 5–6 weeks of age the forearm length was about 70% of that of the mother. Young ones were able to fly at this time. However, these flights were uncoordinated and tentative and cover only short distances. Weaning was initiated at about two months of age, and the juveniles were able to fend for themselves at three months of age. At this time the forearm length was about 94% of that of the adults. The body weight rapidly increased during the first two weeks after birth. At birth the body weight (2.3 g) was 21% of that of adults (11.0 g) and at 15 days of age already 41% (4.5 g). However, up to the 25th day, when bats actively practiced flight and could fly for a few meters, the body weight of the juveniles did not yet exceed 50% (5.5 g) of that of adults.

Young ones became volant at an approximate age of 25–30 days (up to 35 days in the outdoor cage) and they 'practiced' flight inside the cave for short distances during the night. During daytime they hung from the neck of their mothers. Occasionally females carried their young ones even when they were large in size. The oldest juvenile carried by its mother when returning to the cave during the early morning hours between 03.00 to 06.00 h was estimated to be older than 6 weeks (forearm length of 45 mm compared to 52–55 mm of mothers). The bats born in the outdoor cage had a smaller forearm length and a slightly lower growing rate than those born under natural conditions. This might be due to less maternal care that captive babies experience compared to the bats living under natural conditions (see Methods) and probably by premature births after pregnant bats were brought to the cage. For this reason not only is the chronological age subsequently indicated but also the forearm length.

Behavioral observations on bats kept in captivity were similar to those in the field. During night hours females took their infants with them to the foraging area of the outdoor cage where insects were attracted by a mercury lamp and returned with them to the resting area of the cage during predawn hours. The resting area was a part of the cage covered with a solid roof and was the darkest area during daytime. Infants were observed to be

left for the first time at the resting area at ages ranging from two to thirteen days. Retrieving and suckling of young ones were identical to that observed in the field.

Mother–infant recognition

Four young *H. speoris* were caught in the caves together with their mothers. After separating mother and infant in the laboratory the sounds before and during reunion were recorded. Mothers exclusively emitted CF/FM-sounds of the same type as those recorded during flight (Habersetzer et al. 1984). The vocalisations of young ones were of the types described below. There was also no evidence for communication signals audible to the human ear. These observations agree with those made in the natural caves.

Vocalisations of juveniles were spontaneously emitted but were also triggered by echolocation sounds of adults. Resting juvenile bats raised their heads by approximately 30° and emitted 1–5 groups of sounds followed by pauses of a few seconds up to several minutes. This behavior could also be triggered by vocalizations of other juveniles and by ultrasonic noise such as hissing or shaking a bunch of keys.

After the outfly of the adult colony nine young *H. speoris* were picked up in the cave at 20.45 h and placed on a rock at the cave entrance with an interindividual distance of 0.5 m. The vocalizing activity of juveniles and the retrieval behavior of mothers were observed until all but one of the misplaced young ones were carried back by their mothers between 23.00 and 5.00 h of the night. To measure the repetition rate of the vocalizations each lift of the head accompanying the emission of one or several groups of sounds are counted as one event. The juveniles emitted sounds spontaneously. Whenever echolocating adults were passing by from or to the cave entrance all isolated juveniles increased the rate of vocalisations synchronously (Fig. 1). This also occurred before 23.00 h when no mothers approached the young ones. Mothers landed on the rock after circling closer and closer to the vocalizing bats. Only in one case was a young bat taken after the first landing of the adult. All other mothers repeatedly landed on the rock close to different juveniles (e.g. to three bats of 26 mm, 37 mm, and 29 mm forearm length) and approached them. Only after making body contact did the mothers either retrieve or fly off again.

Another observation on mother-infant interaction came from the outdoor cage. Four young
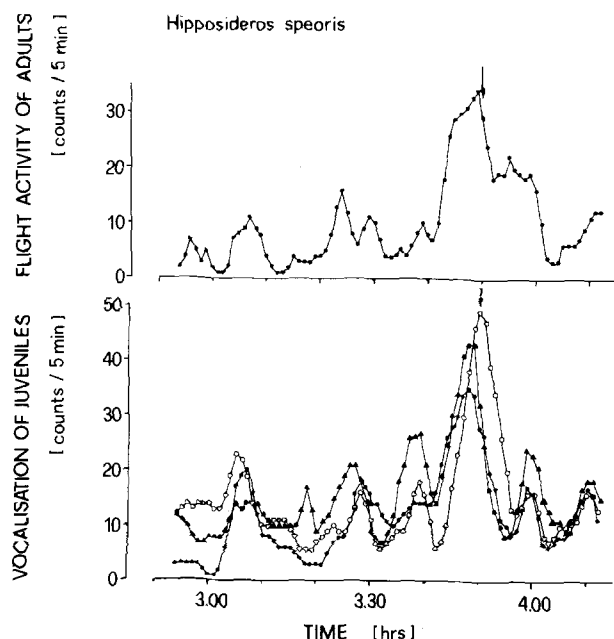
Fig. 1. Vocalising activity of young *H. speoris* and acoustical attraction of adults. The upper curve shows the flight activity of echolocating adults (bat passes/5 min) passing the cave entrance. The lower curves show vocalization of three juveniles (different symbols) which were placed on a rock near the cave entrance. The arrow marks the time when an adult landed close to the young one with the highest vocalizing activity, however, after touching this young one it was not picked up and the adult bat flew away

H. speoris (7, 13, 16, and 22 days of age, respectively) were left behind by their mothers in the resting area in a space of 1.0 m by 0.6 m and the minimal distance between individuals was 0.4 m. The roosting position of the four young bats had been experimentally interchanged before mothers returned in the morning between 4.30 and 5.44 h. All mothers picked up only their own baby but at first they landed exactly at the spots where they originally had disposed their infants irrespective of the vocalisations of the young ones. Then they nuzzled the strange bat or the wall surface before they flew to another resting spot and repeated the same behavior. They retrieved their own young ones only after two to three trials.

In both experiments vocalizing infants were of different ages. Nevertheless mothers could not identify their own young ones by acoustic cues but only after body contact. Therefore we conclude that the different types of sounds described below are not serving as identification markers but simply as a general means of attraction of mothers.

Ontogeny of sounds

Sounds were recorded from seventeen young *H. speoris* of different ages caught in the cave and were compared with sounds recorded from four bats raised in captivity. Newborn bats emit vocalisations consisting of several harmonic components but adults almost always emit pure tones with a short frequency modulated part at the end (CF/FM-type). The following data from two captive bats recorded consecutively at different ages represent the complete set of different types of sounds recorded for a total sample of 21 juvenile bats. All young *H. speoris* vocalized through the nose whether or not the mouth was open or closed, and there was no evidence that the types of sounds emitted changed in either case of the mouth open or closed.

Vocalization at two days of age. Two days after birth in the outdoor cage the bat (forearm length = 14.5 mm) emitted groups of sounds as long as it was separated from its mother. Each group consisted of three to four sounds (notes) with a fundamental frequency of about 26–28 kHz and four harmonic components with a maximum frequency of 130 kHz (Fig. 2, upper row). Sound durations varied between 5 ms and 8 ms (Table 1). Occasionally single or pairs of sounds occurred (Fig. 2, upper row). These sounds exhibited a large variation in the harmonic composition from three to five harmonic components emitted. Fundamental frequencies (= first harmonic) occurred in the comparatively broad band of 21 to 37 kHz. These fundamental components showed the highest intensies.

Despite these large variations in harmonic composition and a large variation in the occurrence of FM- and CF-segments we cannot discriminate clearly between different types of sounds at the age of two days. To follow the details in the composition of sounds the time axis was expanded by the factor of 4 compared to the sonagrams in Fig. 2. There was a continuous change from sounds with prominent FM-parts with a band width of 15–20 kHz in the intense high frequency components (hyperbolic FM- or FM/CF-type) to sounds with downward swept frequency modulated components at the beginning and at the end and a constant frequency segment (FM/CF/FM-type). The bat did not emit pure tone (CF-) or CF/FM-sounds at this age. Interestingly, sound components in the frequency range of 65–75 kHz were emitted with very low intensities (−25 to −35 dB compared to other components) or they even disappeared in the recordings. These effects occurred independently of the type of sounds emitted.
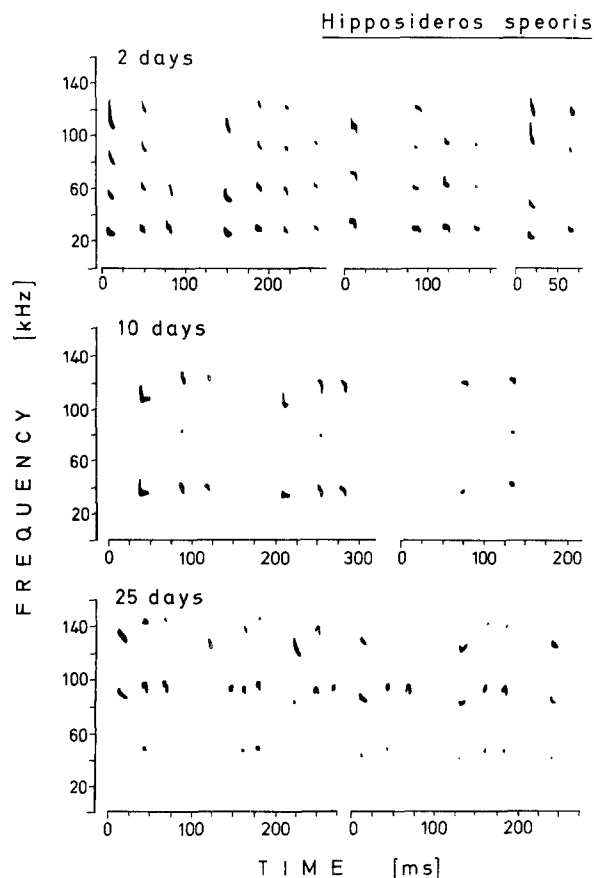
Fig. 2. Sonagrams of sounds of *H. speoris* emitted two days (upper row) ten days (middle row), and twenty five days (lower row) after birth when the bat was not yet able to fly

Fig. 3. Sonagrams of sounds of volant *H. speoris* emitted thirty days (upper and middle row), forty four days (lower row, left), and fifty five days after birth (lower row, right)

Vocalization at 10 days of age. At the 10th day after birth (forearm length = 20 mm), sounds were emitted in groups of three to four. Compared to the recordings of the two day old bat the harmonic content of the sounds was reduced to three harmonic components and the mean fundamental frequency was raised from 26 kHz to 33 kHz (for standard deviations see Fig. 4). In contrast to the earlier recordings the signal structure of the first note now differed clearly from the consecutive notes of a group. The first note was lower in frequency and more intense than the following sounds. The initial part of this first sound was downward frequency-modulated and was followed by a CF-part (FM/CF-type, Fig. 2, middle row). All subsequent notes of a group, as well as single sounds and pairs of sounds, were pure tone (CF-) and CF/FM-sounds. The first (33 kHz) and the third (109 kHz) harmonics of these sounds were prominent. At this age of the bat the frequencies of the second harmonics now fell in the range of 55 to 85 kHz and were emitted at faint intensities or were not present in the recordings.
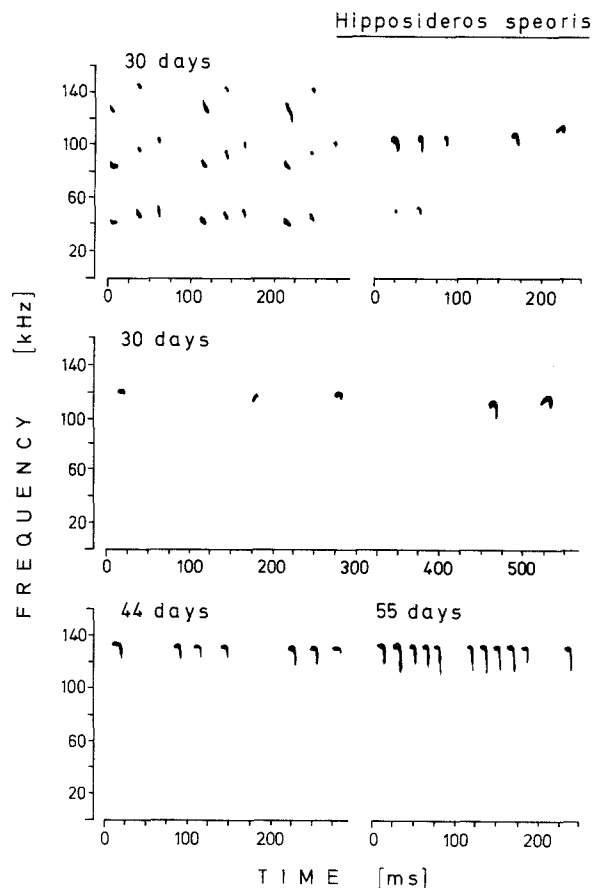
Vocalization at 25 days of age. At the age of 25 days (forearm length = 29 mm) the frequencies of the sounds were further increased. The second harmonic now ranged from 86 kHz to 98 kHz (s.d.) and regained prominence. The first harmonic was lower in intensity than on earlier recordings. The sound structures of the first note remarkably differed from the succeeding notes of a group. The first note was a downward swept FM-signal, while the second and third notes were CF- or CF/FM-sounds which never showed initial downward modulated components. The latter sounds were emitted with consistently higher frequencies compared to that of the first note (Fig. 2 lower row).

Vocalization at 30 days of age. At this age (forearm length = 31.5 mm) the bat flew for a few meters inside the cage and the frequency distribution of sounds still consisted of three harmonic components. However, the frequency differences of subsequent sounds of a group became higher. The most intense component (second harmonic) of the first sound remained at a frequency of about 95 kHz

as it also occurred at earlier stages of life, but the second and the third sound of a group were tuned to progressively higher frequencies in steps of 10 kHz and 7 kHz respectively (Fig. 3 upper row, left sonagram).

At some sections of the recordings the initial FM-sound was missing and only CF- or CF/FM-sounds were noticed with intense second harmonic components ranging from 104 kHz to 120 kHz (Fig. 3 upper row, right sonagram, and middle row). While the sound frequency (2nd harmonic) was raised to 120 kHz the corresponding first harmonic component increased to 60 kHz and promptly faded (Fig. 3 middle row) as did third and second harmonics in the earlier vocalizations when they were in this frequency range. However, these sounds were emitted infrequently and at a low repetition rate compared to the sounds with three harmonics which were emitted in groups and always at lower frequencies.

Vocalization at 44 days of age. Sounds of a second volant *H. speoris* raised in the outdoor cage were recorded 44 days after birth (forearm length = 41 mm). Again sounds were emitted in groups of three to four. At this age sounds consisting of second harmonics of 133 ± 3 kHz were emitted and the first harmonic components completely disappeared (Fig. 3 lower row, left sonagram). Thus the frequency of CF/FM-sounds had now reached the frequency range of adults which is between 127 and 138 kHz. The relatively low repetition rate of CF/FM-sounds observed earlier (5–20 kHz) was now increased to 30–50 Hz, but this was still lower than in adults. Low intensity first harmonic components were found on the sonagrams only when the second harmonics of the sounds were lower than 125 kHz, which rarely occurred when the bat emitted sounds at a high repetition rate of about 60 Hz.

Vocalization at 55 days of age. When sounds were recorded from the same bat eleven days later (forearm length = 44 mm) it emitted the same type of CF/FM-sounds as recorded before. The repetition rate of sounds was further increased (see also Table 1). Groups of three to five and sometimes up to a maximum of seven notes were recorded. These vocalisations could no longer be discriminated from those of adults.

All data regarding frequency distribution of sounds during the growth of young *H. speoris* are summarized in Fig. 4. Mean sound frequencies and standard deviations were calculated separately for each detectable harmonic component from intensi-
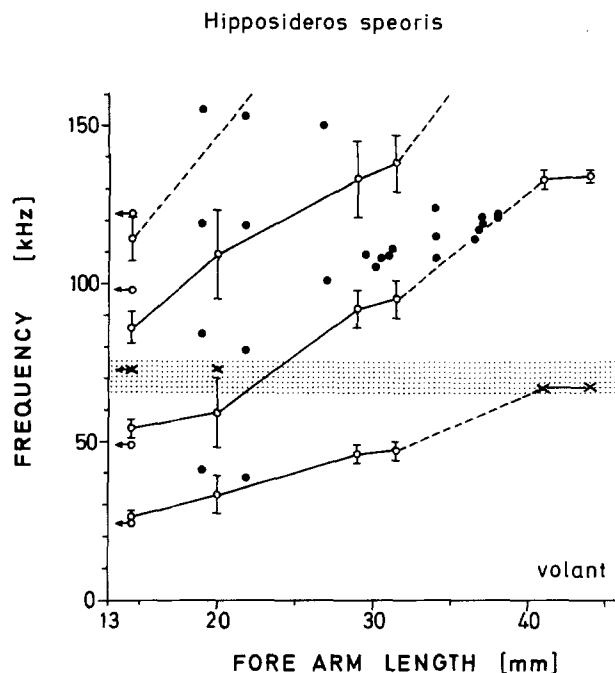

Fig. 4. Frequencies of sounds emitted by adolescent *H. speoris* with forearm lengths as indicated. Mean frequencies of harmonic sound components (circles) and standard deviations (vertical bars) were calculated from power spectra of 30–150 sounds of individual bats. Open circles connected by solid (same bat) and dotted (extrapolated) lines are measurements on bats recorded consecutively in the cage. Filled circles represent sounds of 17 bats grown up in their natural caves. The missing third harmonic component at 73 kHz in the sounds consisting of five harmonics (marked by arrows for the bat of 14.5 mm forearm length), and the missing second harmonic and first harmonic components in the three and two harmonic sounds are indicated by crosses. Note that the frequency range of attenuated or missing harmonic components (shaded area) remains constant during the ontogeny of sounds

ty maxima in the power spectra of 30–150 sounds. The interpolated sections (dashed lines, Fig. 4) between the data from the two bats (open circles, Fig. 4), which were presented above in detail, are confirmed by the raise of sound frequencies found for the other 17 bats raised in their natural caves (Fig. 4, filled circles). As previously mentioned, the same types of sounds were recorded from captive bats and from those in the caves. This was checked by comparing sonagrams, which were stored on an oscilloscope screen with the sonagrams of Figs. 2 and 3. However, sound frequencies of the 17 bats from the cave are about 8 kHz higher during the prevolant stages than in bats recorded in the cage (Fig. 4). This again indicates an accelerated development of bats in a natural surrounding. The range of the frequency variation was smaller when the bats emitted sounds in the frequency range of adults. The standard deviations of individual sound frequencies (absolute values in Fig. 4)

decreased from 13% (forearm length 20 mm) to only 1.5% and 2% when the bats kept in the cage had become volant. A similar relation was found for bats raised in the natural cave: the standard deviations (not indicated in Fig. 4, for comparison see Table 1, No. 2–No. 4) of the mean sound frequencies decreased continuously from 9% (forearm length 21.8 mm) when the bats emitted mainly sounds with three harmonics, to 1.1% (forearm length 38.1 mm) when the volant bats exclusively emitted CF/FM-sounds. These results demonstrate that during adolescence accuracy of tuning the sound frequencies is improved as the emitted sound frequencies are raised closer to the frequency range of adult sounds.

As already shown in some sonagrams (Figs. 2 and 3) certain harmonic components were attenuated or they disappeared in the recordings. This effect always occurs whenever sound components fell into the range of 65–75 kHz whether they belong to the third, second, or first harmonic (indicated by cross symbols in Fig. 4). Interestingly, the frequency band in which sound components are suppressed is rather narrow (shaded area in Fig. 4). This is demonstrated by harmonic components having frequencies just outside the narrow suppressed band which are not suppressed. For example in the power spectra from the bat with a forearm length of 20 mm (10 days after birth) only in 16 of 39 sounds a second harmonic component was detectable with a mean frequency of 59 kHz. The second harmonics of 13 sounds were lower than 65 kHz, 2 were higher than 75 kHz and only one weak trace in the power spectra was found at 74 kHz. However, for the total sample ($n = 39$) of sounds the second harmonic component (which was recalculated from the intense third harmonic components) was 73 kHz. Thus, the measured frequency distribution at 59 kHz represents mainly sounds with frequencies below the suppressive frequency band of 65–75 kHz.

Similar effects were found for a bat from the cave (dots in Fig. 4 at a forearm length of 22 mm), which emitted sounds mainly above the suppressed frequency band. Again, the mean frequency of the second harmonics (77.8 kHz $\pm$ 3.5 kHz, $n = 94$) deviated from the expected value (76.8 kHz $\pm$ 3.6 kHz, $n = 122$) recalculated from higher sound components. The difference of only 1 kHz was much smaller than in the previous measurements (14 kHz) and this is due to 14 sounds of which the second harmonics fell in the frequency range of 72–75 kHz but were not fully suppressed. In all cases these second harmonics were of much lower intensities compared to the third harmonic

components. It is interesting to note that just above the suppressive frequency range the intensity relations of harmonics drastically changed. 60.4% of the second harmonics above 75 kHz ($n = 80$, max. 83 kHz) were more intense than the strong third harmonics of the sounds.

These examples also demonstrate that for sounds emitted during early stages of development the suppression of harmonic components is inconsistent due to the sporadic variations of the frequencies emitted. On the other hand, the first harmonics are persistently suppressed in sounds of volant and adult bats since they always fall in the suppressed frequency band since the emitted frequencies now vary by no more than 1% to 2%.

The frequency analysis of juvenile sounds disclosed that different types of sounds and large frequency variation occur. These large variations might be one reason why mothers were not able to discriminate acoustically between their own young one and others. However, there might be a possibility that juveniles were acoustically identified by the temporal pattern of their vocalizations. Temporal patterns of series of sounds from five young bats of different body size and age were analyzed. The temporal characteristics of juvenile vocalisations are given in Table 1 for three individual non-flying bats (No. 1–3) and for two volant bats (No. 4, No. 5). As long as sounds with several harmonics or FM-sounds were emitted the repetition rate of sounds and groups (series of sounds) was considerably higher in larger and older bats (Table 1, No. 1, No. 2, No. 3). The duration of sounds emitted in a group were systematically shortened from sound to sound. In contrast durations of CF/FM-sounds emitted consecutively in a group by the two volant bats varied only in a very small range between 7.1 ms and 8.6 ms (Table 1, No. 4, No. 5). There was no evidence for significant individual differences. Although there were sometimes groups with five notes in the older juvenile, temporal characteristics were almost identical between these two individuals. The repetition rate of CF/FM-sounds and the repetition rate of groups of these CF/FM-sounds were lower than those of the three harmonic sounds emitted by the considerably younger bat (No. 3). However, both bats (No. 4, No. 5) occasionally emitted harmonic sounds of lower frequencies with a repetition rate of 50–70 Hz. Obviously a high repetition rate can be achieved more easily and at an earlier age with low-pitched sounds of a harmonic composition.

Figure 4 and Table 1 show that frequency, harmonic composition, and temporal characteristics of sounds change systematically in correlation to

Table 1. Ultrasonic sounds of 5 juvenile *Hipposideros speoris*. *Upper part:* Properties of groups of sounds, the duration was measured from the beginning of the first sound to the end of the last sound. *Middle part:* Duration of the first to the fifth sound of a group and mean repetition rate of sounds. *Lower part:* Frequency of the second harmonic component of single sounds and number of harmonic components which occur regularly (rarely). All data are means; standard deviations are indicated by ± symbols

Bat number	1	2	3	4	5
Forearm length (mm)	14.5	21.8	30.5	38.3	44.0
Age (days after birth)	2	11	17	32	55

Properties of emitted series of sounds (groups):

	1	2	3	4	5
Group duration (ms)	$n=14$ 85.3±19.4	$n=16$ 64.4±18.7	$n=35$ 43.5±8.4	$n=22$ 66.0±15.5	$n=19$ 66.7±16.9
Group interval (ms)	$n=14$ 72.5±9.4	$n=15$ 79.8±23.4	$n=28$ 62.4±8.6	$n=18$ 61.5±24.4	$n=17$ 63.1±34.3
Repetition rate of groups (Hz)	6.3	5.2	9.4	7.8	7.7

Mean duration of ultrasonic sounds emitted in a group:

	1	2	3	4	5
First note (ms)	$n=15$ 8.5±0.9	$n=17$ 8.4±1.2	$n=38$ 7.1±1.0	$n=22$ 7.7±1.0	$n=19$ 8.2±1.3
Second note	$n=15$ 6.6±0.8	$n=17$ 5.7±1.1	$n=37$ 6.1±0.6	$n=22$ 8.2±0.7	$n=19$ 8.6±1.0
Third note	$n=14$ 5.3±1.0	$n=11$ 4.6±0.7	$n=30$ 4.1±0.8	$n=18$ 7.8±0.8	$n=16$ 8.1±0.8
Fourth note	$n=1$ 6.25	$n=6$ 4.6±1.3	$n=6$ 2.6±0.5	$n=12$ 7.5±0.5	$n=8$ 7.4±0.5
Fifth note	–	–	–	–	$n=5$ 7.1±0.5
Repetition rate of sounds (Hz)	25.6±3.3	36.1±3.7	50.8±4.6	41.9±7.2	49.2±11.9

	1	2	3	4	5
Frequency of the 2nd harmonic (kHz)	54±5.2	79±7.1	108±3.9	122±1.3	134±2.0
Number of harmonic components	4 (5,3)	3 (4)	3 (2)	1 (2)	1

the growth of young bats. However, the large variation of these parameters in individual bats does not allow a prediction of a particular age of a bat based on acoustic measurements.

Discussion

Young *H. speoris* which are left in the cave during night hours by their mothers are retrieved by them without audible communication calls from either the mothers or the infants. This is in contrast to other bat species of the study area. Young *Rhinopoma hardwickei* and *Megaderma lyra* emit audible isolation calls and in both species mothers also emit tonal audible calls when they return to the cave. Young ones reply to these calls and mothers find their babies by repeatingly evoking their vocalisations, e.g. when they had fallen down from their resting places. Similar mother infant commu-

nication was reported for other bat species (Brown and Grinnell 1980; Gould 1971; Kulzer 1962; Schmidt 1972). It is not clear why *H. speoris* do not use special communication signals. In contrast to other sympatric species hipposiderids also roost in small humid caves and humid cracks, but they leave these roosts when they become dry in the summer. The absence of low frequency social calls in these temporary shelters may probably protect the colonies from discovery by predators.

Myotis discriminates between its young one and others only by auditory cues (Turner et al. 1972). Our observations disclosed that *H. speoris* mothers can not discriminate ultrasonic vocalizations of its own infant from those of others even when strange juveniles were much older or younger than its own. Therefore we conclude that the types of sounds emitted during adolescence in *H. speoris* mainly serve for acquiring the sound repertoire of

adults and do not play a specific role in a communicative context, except for simply attracting the mothers (Fig. 1). Nuzzling on the resting spot and on the infant during retrieval might indicate that identification of individuals is aided by olfaction.

Studies of the ontogeny of ultrasonic sounds in FM-bats and CF-bats revealed a general increase of sound frequencies and a reduction in the number of harmonics as the bats mature (Brown and Grinnell 1980; Gould 1975a, b). This is in accordance with our results on *Hipposideros speoris* (Figs. 2, 3). Young ones emit sounds consisting of several harmonics in groups of three to four notes. At an early stage of life a relatively uniform pattern of FM/CF/FM-sounds occurs. At prevolant and volant stages of a bat's development sound frequency is raised to the range of adults and harmonic components are step by step eliminated until only the strong second harmonic component is left in the CF/FM-sounds. The phenomenon of emphasizing the second harmonic component also occurs in some other hipposiderid species (Gould 1979). However, the emission of different types of sounds even within one group of sounds seems to be a unique characteristic of *H. speoris*. From ten days of age onwards the initial sound (first note) of a group is a FM-sound whereas the subsequent ones are CF/FM-sounds with several harmonics. Occasionally, these vocalizations were also recorded even from volant bats which typically emitted CF/FM-sounds of the adult type.

The suppression of sound components in the 65–75 kHz range occurs independently of the type of sound emitted by *H. speoris* and regardless to which fundamental frequency the suppressed harmonic component corresponds. This strongly indicates that a passive mechanical filtering process in the nasopharyngeal tract causes this gap in sound frequencies. The fact that the band of the filter range remains almost constant during the growth of young bats (Fig. 4) is most likely due to the large size of the head at the time of birth and its very low growth rate compared to that of the body or the wing. The width of the suppressed frequency band, only 10 kHz, is sufficient for an effective suppression of the first harmonic of adult CF/FM-sounds since the CF-frequencies of the second harmonic vary only from 127 kHz to 138 kHz interindividually and ± 0.4 kHz individually. Doppler shifts caused by the flight speed (4.6 m/s) may shift the echo frequencies returning to the bats by up to $+3.5$ kHz (Habersetzer et al. 1984). Therefore we consider the frequency gap which helps to generate a pure tone signal to be an adaptation to CF/FM-echolocation.

H. speoris increases the sound frequency not only during growth but also stepwise in subsequent sounds of a group 25 and 30 days after birth (Figs. 2, 3), as if it intends to reach the adult frequency. Interestingly, the upper frequency limit of the species specific CF-band was never exceeded by the second harmonic of the juvenile sounds. The question arises, how do young ones 'know' when they have hit the adult CF-frequency and thus make no further increase in frequency. We suggest that the passive suppression of the first harmonic component described above indicates to the bat that it has reached the specific adult frequency range of 127 kHz to 138 kHz, because the change from a two harmonic sound to a one harmonic sound appears to be easily recognized by the bat. However, the accuracy of ± 40 kHz at which adult bats keep sound frequencies around their individual CF-frequencies, requires a more sophisticated mechanism. Neuweiler et al. (1984) found sensitive frequency ranges in the audiograms of adult *H. speoris* corresponding to the individual CF-frequencies of sounds. If we assume that this sensitive filter has been almost completely established when the bats become volant this could explain the decrease in the variation of sound frequencies as the bats mature (Fig. 4). However, it is important to note that the accuracy at which volant bats keep the sound frequencies within their individual CF-band (from ± 1.3 kHz to ± 3 kHz) is less than in adults (± 0.4 kHz) although the bats catch insects and fend for themselves at that time. This may indicate a delayed development of fine adjustment in the tuning of CF-frequencies in *H. speoris* after the ontogeny of sounds has been completed.

Rhinolophid bats use ultrasonic CF/FM-sounds similar to the sounds of hipposiderid species but of much longer duration. For *Rhinolophus ferrumequinum* it has been shown that its ultrasonic system is extremely specialized for the constant frequency (CF) part of the adult CF/FM-sounds (Neuweiler et al. 1980). Young *Rhinolophus hipposideros* emit variable low frequency sounds, the frequency of which rises with age (Kay and Pickvance 1963). Recent studies on juvenile *Rhinolophus rouxi* show that the rise of sound frequencies is accompanied by a simultaneous shift of the sensitive filter range from low frequencies up to the frequency range of adults (Rübsamen, pers. comm.). A similar correspondence between lower emitted frequency and lower center filter frequency has been noted in a juvenile *H. calcaratus* (Grinnell and Hagiwara 1972) indicating the same principle of ontogeny in rhinolophid and hipposiderid bats. At

7–10 days of age *Rhinolophus ferrumequinum* emits multiharmonic sounds through the mouth and the frequency of the first harmonic component is lower than 20 kHz (Konstantinov 1973). When sounds are emitted through the nose the first harmonic is higher than 20 kHz. While bats are growing up the sound frequencies are raised and the second harmonic component becomes prominent and reaches the adult frequency range of 83 kHz after 30 days (Konstantinov 1973). In *Rhinolophus ferrumequinum nippon* is has been shown that the development of noisy (oral) to pure-tone (nasal) sounds goes along with a protruding growth of the epiglottis. This causes tightening of the nasopharyngeal junction which is perfectly closed in adults. At four weeks of age this species emits nasal sounds of an emphasized second harmonic at 71 kHz which is in the range of frequencies emitted by adults (Matsumura 1979).

In *H. speoris* sounds were emitted through the nose at all stages of development. The same type of sounds were recorded when the bats vocalized with the mouth open and closed, indicating that the position of the jawbone does not affect sound emission through the nose. In contrast to rhinolophid bats, vocalizations of *H. speoris* were always in a frequency range higher than 20 kHz and never of a 'noisy' multiharmonic type. One exception was when an adult *H. speoris* was injured while being caught at the cave entrance. In this case the bat uttered shrieking audible sounds which demonstrated that *H. speoris* can emit low frequency sounds through the mouth. However, we found no evidence that such vocalizations play a role in a behavioral context and they never occurred during mother-infant interaction.

The temporal sound emission patterns of young *H. speoris* in this study showed trends of increasing the sound duration and increasing the number of sounds (notes) per group when the bats were older (Table 1). Interestingly, bats can also achieve high repetition rates of sounds even at early stages of development if they emit sounds with several harmonic components, whereas (CF/ FM-) sounds with one harmonic component can be emitted in a high repetition rate only after the bats have become volant (Fig. 3, Table 1). Comparative studies on two Indian species, *H. speoris* and *H. bicolor* (*fulvus*) show that their auditory systems are not as specialized to the CF-part of the sounds and that they do not respond to Doppler effects as regular as rhinolophid bats. Moreover, compared to *H. bicolor* (*fulvus*), *H. speoris* responded less frequently to Doppler effects and it was the only species which emitted

broadband complex harmonic (FM/CF/FM-) signals under certain echolocation situations (Habersetzer et al. 1984). In this aspect *H. speoris* resembles bats which do not compensate for Doppler effects and echolocate with FM-sounds and CF-sounds consisting of several harmonics, e.g. *Rhinopoma* (Habersetzer 1981), *Taphozous* and *Pipistrellus* (Neuweiler 1983; Habersetzer 1985).

If *H. speoris* wants a broadband signal it must increase or lower the frequency of sounds to avoid the frequency gap of 65–75 kHz. The latter case was actually observed in volant bats in our study and in an earlier study in adults (Habersetzer et al. 1984). The common characteristic of FM/CF/FM-signals (complex harmonic sounds) of adults and FM-, FM/CF-, and FM/CF/FM-signals of juveniles of *H. speoris* is the initial downward modulated FM-part causing a considerable broadening of the spectra. In contrast to this broadband sound of relatively low frequencies, other type of juvenile sounds, the frequencies of which are consecutively raised to the species specific (CF-) frequencies of adults, exclusively show upward modulated (or no FM-) components (Fig. 3). It is interesting to note that the closely related *H. bicolor* (*fulvus*) only shows upward modulated FM-segments in the beginning of all juvenile sounds (Marimuthu and Habersetzer, in prep.). These initial upward modulations are regularly found in rhinolophids (Brown and Grinnell 1980) and also in hipposiderids (Gould 1979), which echolocate exclusively with CF/FM-sounds. Considering these facts we interpret the juvenile FM-sounds of *H. speoris* as precursors of the adult complex harmonic sounds.

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