

## Echolocation and Obstacle Avoidance in the Hipposiderid Bat *Asellia tridens* \*

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**Summary.** The echolocation sounds of the hipposiderid bat *Asellia tridens* consist of a constant frequency (cf) component followed by a frequency modulated (fm) terminal downward sweep of 19–21 kHz. The cf-part constitutes about 7/10 of the entire signal. In individual roosting animals the frequencies of the cf-part of consecutive sounds (resting frequency) is kept very constant but varies from bat to bat. In 18 *Asellia tridens* resting frequencies between 111–124 kHz have been measured.

The sound duration in roosting and free flying bats is between 7–10 ms. In the approach and terminal phase of bats landing on a perch or flying through obstacles, the sound duration is reduced and the repetition rate increased the nearer the bat approaches the target. At the end of the terminal phase sound durations of a minimum of 3 ms have been measured.

Flying bats lower their emission frequency in order to compensate for Doppler shifts caused by the flight movement. The echofrequency is therefore kept constant about 150–200 Hz above the resting frequency.

In flights through obstacles consisting of vertically stretched wires with different diameters, the bats were able to avoid wires down to a diameter of 0.065 mm whereas at 0.05 mm the percentage of flights without collisions is far below the chance level. The results demonstrate that the echolocation behavior of the hipposiderid bat *Asellia tridens* does not differ funda-

mentally from that of rhinolophid bats. As a result, a new suggestion for categorization of bats producing cf-fm orientation sounds is put forward.

### Introduction

The bats of the families Hipposideridae and Rhinolophidae show so many anatomical similarities that they are put together in the superfamily Rhinolophoidea. The experiments presented here were conducted to determine whether a similar close relationship could also be found in their echolocation behavior. The echolocation system of the rhinolophids has already been studied in detail (Schnitzler, 1967, 1968, 1973 a, b; Konstantinov and Solokov, 1969), but little is yet known of the hipposiderids in this respect.

The first description of the orientation sounds of a hipposiderid bat was given by Möhres and Kulzer (1955). They found in *Asellia tridens* that the echolocation pulses consist of a longer constant frequency (cf) component followed by a shorter frequency modulated (fm) component. They also claimed that the bats produce the cf-fm sounds or the cf component alone for the localization of adjacent targets and the fm component alone for the detection of more distant objects. They measured sound durations of 9–10 ms and a cf component frequency in the range of 120 kHz. They estimated that the frequency of the fm component is in the range of 50–70 kHz. Sales and Pye (1974) offered an explanation for the observation of Möhres and Kulzer, that sometimes only pure fm sounds were emitted. They suggested that strong changes of the relative amplitudes of the cf and fm components could lead to the wrong impression that no cf part is present.

Pye and Roberts (1970) studied the ear movements of *Asellia tridens* and found a correlation with sound

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**Abbreviations.** cf, constant frequency component; fm, frequency modulated component; P, probability of collision-free flights through an obstacle of vertically stretched wires; I, interval between wires; D, minimal diameter of a bat with folded wings;  $\theta$ , angle at which a bat approaches an obstacle;  $f_A$ , frequency of the cf-component of the emitted sound;  $f_E$ , frequency of the cf-component of the echo;  $f_M$ , frequency of the cf-component of the sounds recorded with the microphone; c, speed of sound

emission. They recorded only cf-fm sounds. The sound duration was assessed at 6–8 ms, the cf component frequency at 115–120 kHz and the range of the terminal downward sweep in the fm component at 15–20 kHz.

Data on duration, frequency and sound pressure level of echolocation signals of other species of Hipposideridae were given by Novick (1958) and Pye (1972, 1978).

Grinnell and Hagiwara (1972) described orientation sounds with the typical cf-fm structure in another 5 species of hipposiderids.

These papers demonstrated that hipposiderid bats emit rather short cf-fm sounds. Systematic studies of the echolocation behavior are yet to be presented. In this paper we describe the echolocation sounds of the hipposiderid bat *Asellia tridens* in flight (both with and without obstacles) and at rest. Investigations of Doppler shift compensation and obstacle avoidance tests were also conducted for comparison with rhinolophids.

## Methods

The experiments were performed with *Asellia tridens* (Geoffroy 1812) captured in a water tunnel near the oasis Tozeur in Tunisia. The bats were kept in a flight room which was 6.20 m long, 2.40 m wide and 2.20 m in height. Five bats learned to fly from a perch at one end of the room to a perch at the other end, where they were given a mealworm and then chased back. The room was divided approximately in half by a cloth partition stretched tightly over a wooden frame. A rectangular opening of 85 cm by 118 cm near the center of the partition allowed the bats to fly from one half of the room to the other.

The echolocation sounds of single flying bats were picked up with two 6.35 mm microphones (Bruel and Kjaer type 4135) and, after amplification with measuring amplifiers (Bruel and Kjaer type 2606), and filtering (Kronbite type 3550), recorded at 76.2 cm/s on two separate channels of a tape recorder (Sangamo type 3500) with an upper frequency cut-off at 150 kHz. The sounds were played back at reduced speed on a Tektronix 502A oscilloscope and recorded on oscilloscript film with an oscilloscope camera (Tönnies recordine). The frequency analysis was done by a Ubiquitous real-time spectrum analyzer type UA 500 A.

The obstacle avoidance efficiency was measured as percentage of free flights through an array of vertically stretched wires fixed on a wooden frame which closed the opening of the partition in the middle of the room. The wires were 20 cm apart. The diameter of the wires was reduced every three days in the following sequence 1.5–0.9–0.5–0.2–0.12–0.08–0.065–0.05 mm.

In order to prevent spatial constancy the obstacle was moved after each flight through it.

The probability ( $P$ ) of a bat being able to fly through the undetected obstacle without collisions was calculated for a wire interval ( $I$ ) of 20 cm and a minimal bat diameter ( $D$ ) (3.5 cm with tightly folded wings) with an equation given by Flieger and Schnitzler (1973):

$$P = \frac{I - D}{I \times \sin \theta} = \frac{20 - 3.5}{20} = 0.82.$$

$\theta$  is the angle with which the bat approaches the obstacle. In the experiments this angle was always about 90 degrees, giving  $\sin \theta$  a value of 1. This means that a bat which reduces its diameter at the obstacle to 3.5 cm (tightly folded wings) would be able to fly through the undetected obstacle without collisions in 82% of all flights (Fig. 4, dashed line).

## Results

### *Echolocating Behavior in Resting Bats*

Active *Asellia tridens* produce echolocation sounds in a continuous flow. Undisturbed bats tend to emit single sounds with a sound duration of 9–10 ms. Pulse intervals (time interval between the beginning of two consecutive sounds) of 178–215 ms were measured in this situation.

If alerted, groups of 2–3 sounds are emitted. The group duration (time between the beginning of the first sounds in consecutive groups) is 80–145 ms, the pulse duration 7–10 ms and the shortest pulse interval 33 ms.

During a state of extreme attentiveness the bats emit groups which last 75–170 ms and contain 4–10 signals with a sound duration of 7–9 ms and a minimal pulse interval of 27 ms.

The echolocation sounds of resting bats consist of a longer constant frequency (cf) component followed by a frequency modulated (fm) terminal component. The cf component constitutes about 7/10 of the entire signal. In the terminal sweep the frequency falls approximately 19–21 kHz below the frequency of the cf component. The frequency decrease is a linear function of the time. In individual bats the cf frequency of succeeding sounds is extremely constant. Standard deviations from the average or resting frequency of 120 kHz were measured. In 18 *Asellia tridens* resting frequencies were found between 111–124 kHz.

### *Echolocation Behavior of Bats in Flight*

The echolocation sounds of five bats, trained to fly from a starting perch at the end of the room to a landing perch at the other end, were recorded and analysed over a period of several weeks.

The basic sound pattern observed during these flights is similar to patterns found in other bats. For descriptive analysis three flight situations were selected; search-, approach- and terminal phase, as introduced by Griffin et al. (1960). The parameters of a typical flight are shown in Fig. 2.

Before take-off, *Asellia tridens* emit either single sounds or groups (group duration between 70–150 ms) of two sounds with sound duration of

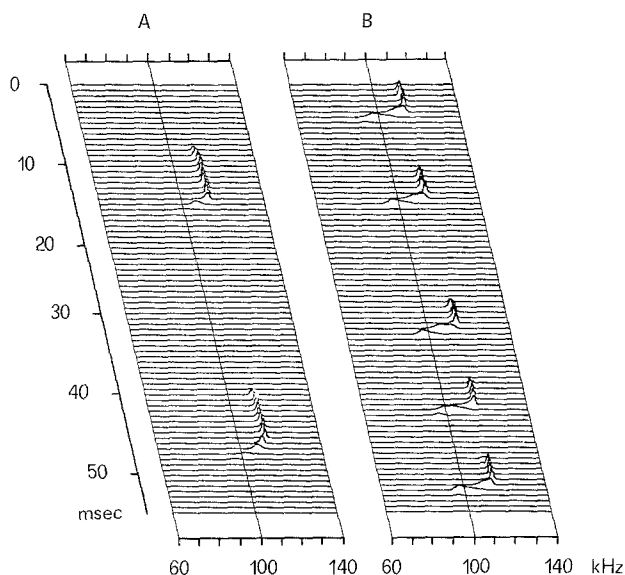


Fig. 1A and B. Real-time-spectrograms of echolocation sounds of *Asellia tridens*, emitted in free flight (A) and at the beginning of the terminal phase (B). Time interval between spectra 0.68 ms and frequency resolution 640 Hz

9–11 ms and a minimal pulse interval of 33 ms. In the search phase, during free flight far from the landing perch, groups lasting 60–110 ms and containing 2–3 sounds with a sound duration of 8–10 ms and a minimal pulse interval of 26 ms were emitted (Fig. 1A).

In the approach phase the group duration is shorter, the number of sounds per group increases and the sound duration and pulse interval is reduced the closer the bat approaches the landing perch. In this phase the arrangement of sounds in groups is not always clearly visible.

During the terminal phase, shortly before landing, 2–3 groups with a group duration of only 30–45 ms are emitted. Each group contains 3–6 sounds. The sound duration is reduced to a minimal 3 ms and the pulse interval to a minimal 8.5 ms (Fig. 1B).

Flight sounds have the same cf-fm frequency structure as the sounds of resting bats. In the long sounds emitted before take-off and in the search phase the terminal fm components have lower amplitudes whereas the fm components of the sounds in the approach and terminal phase show maximal amplitudes which are clearly higher than the amplitudes of the cf parts. When the sound duration is decreased, both the cf and fm components are shortened. The frequency drop in the fm sweep, however, remains constant. The shortening of the fm component shows a linear relationship with the duration of the entire sounds at sound durations between 5–9 ms.

### Doppler Shift Compensation

In flying bats, the frequency of the cf components of the sounds recorded with the microphones was lower than the frequency of the cf components of the sounds emitted before take-off. This microphone frequency is not the emission frequency. It incorporates a Doppler shift caused by the relative movement of the bat towards the microphone. This means that, during flight, the emission frequency ( $f_A$ ) is even lower than the measured microphone frequency ( $f_M$ ). Extrapolating from this, *Asellia* must lower its emission frequency during flight.

A lowering of the emission frequency during flight was also found in rhinolophids (Schnitzler, 1968, 1973a) and in *Pteronotus parnellii* (Schnitzler, 1970a). In these bats the emission frequency is lowered in order to compensate for Doppler shifts caused by flight movement. The echo frequency is therefore kept constant at a characteristic reference frequency.

In order to prove that the lowering of the emission frequency during flight in *Asellia* can be explained by Doppler shift compensation, the emission- and echo frequency of flying bats had to be determined.

The echo frequency ( $f_E$ ) heard by the bat and the emission frequency ( $f_A$ ) can be calculated when the flight speed of the bat ( $V_B$ ) and the frequency of the cf components of the sounds recorded with the microphone are known (Schnitzler, 1968) ( $c$  = speed of sound).

$$f_A = f_M - f_M \frac{V_B}{c},$$

$$f_E = f_M + f_M \frac{V_B}{c}.$$

In order to measure the flight speed of *Asellia*, we trained three bats to fly in a flight tunnel 50 cm wide, 50 cm high, and 50 cm long. Two microphones were positioned only 10 cm below the flight path of the bats and 1.80 m apart. When the bats passed the microphones the SPL of the recorded echolocation sounds decreased rapidly. The time interval between the bats passing microphone 1 and 2 was used to calculate their average flight speed. The sounds recorded with the second microphone were used to measure the microphone frequency  $f_M$  of the cf components. The frequency could be measured with an accuracy of  $\pm 50$  Hz.

In this situation the bats emitted groups (group duration 60–80 ms) of 2–4 sounds with a sound duration of 4–8 ms. The bats reached flight speeds between 2.1–2.7 m/s between the microphones. In all flights the bats lowered their emission frequency in order to compensate for Doppler shifts. The echo frequency

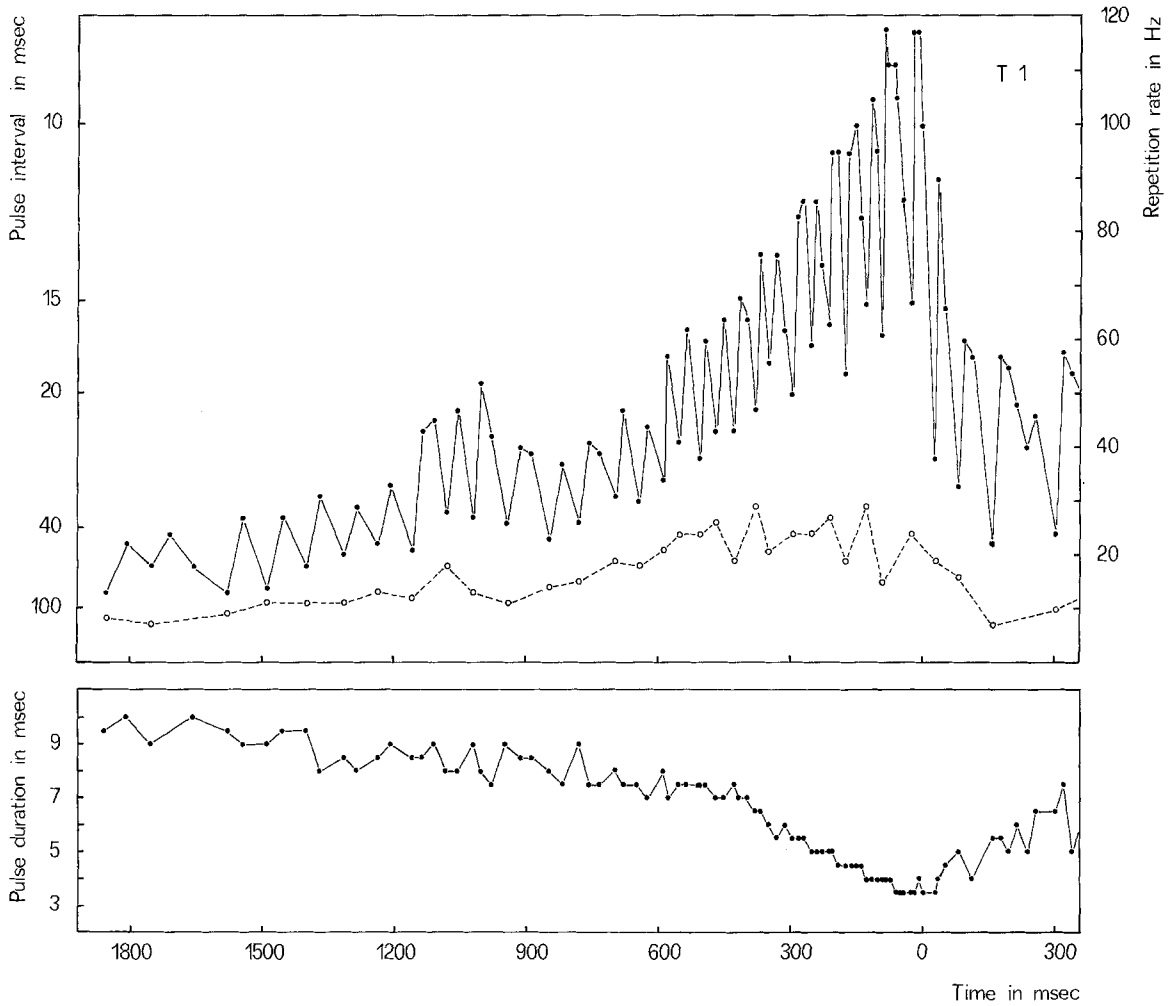


Fig. 2. Echolocation parameters for a flight from the starting to the feeding perch and after landing (after 0 ms). Upper graph: ● Pulse interval and repetition rate, ○ group duration. Lower graph: ● Pulse duration

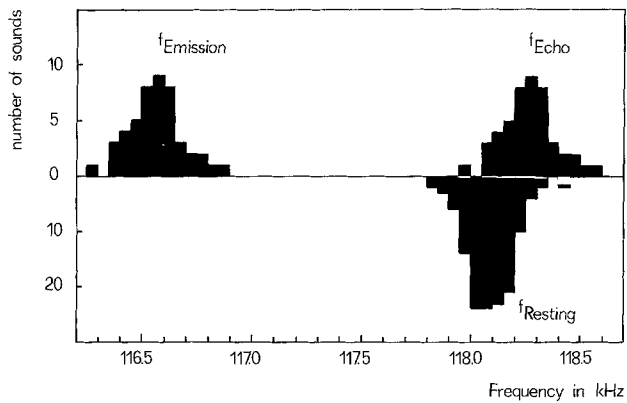


Fig. 3. Compound histogram of the frequencies of the cf-parts in a resting *Asellia tridens* (lower part), and of the echo and emission frequencies of the same bat in flight (upper part)

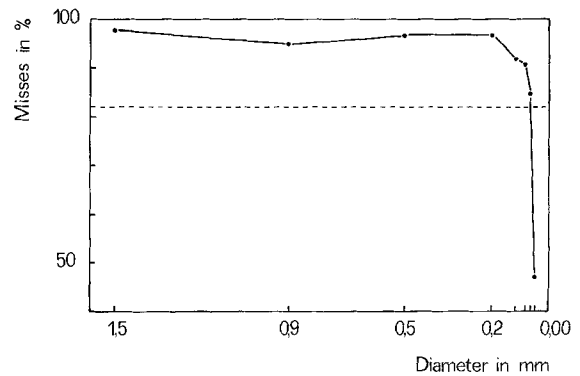
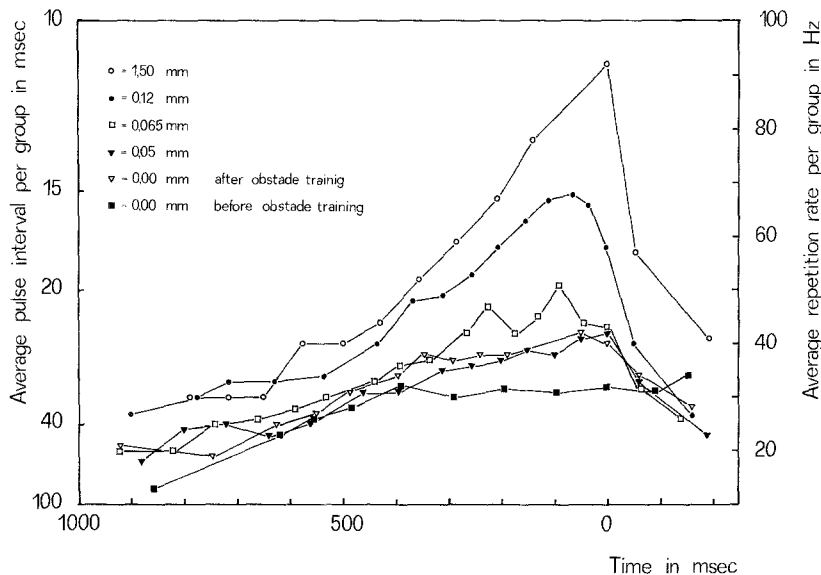


Fig. 4. Average percentage of flights without collisions (misses) of 3 bats through vertical wire obstacles of different diameters (distance between wires 20 cm). Dashed line represents the chance level



**Fig. 5.** Average pulse interval per group and average repetition rate per group of flights through obstacles of different diameters, and of flights without an obstacle before and after obstacle training

was therefore kept constant at a characteristic reference frequency. This reference frequency was about 150–200 Hz above the resting frequency of the individual bat. Figure 3 demonstrates the Doppler shift compensation for a bat flying with a speed of 2.5 m/s. This bat had a resting frequency of 118.25 kHz, the emission frequency was found to be lowered to 116.55 kHz.

#### Obstacle Avoidance

The percentage of collision-free flights through an obstacle consisting of vertically stretched wires was above 95% down to a diameter of 0.2 mm, above 90% at 0.12 mm and 0.08 mm and still above the chance level of 82.5% at 0.065 mm. At 0.05 mm the percentage of free flights dropped far below the chance level to 47% (Fig. 4). These results indicate that *Asellia tridens* detects and avoids wires down to a diameter of 0.065 mm.

The analysis of the echolocation sounds emitted during the obstacle flights leads to the same conclusion. The greater the diameter of the obstacle wires, the earlier the bats reacted to the obstacle by increasing the number of pulses per group and by decreasing the sound duration and the pulse interval.

At a wire diameter of 1.5 mm the minimal sound duration was 3.5 ms and the minimal pulse interval 10 ms. At 0.065 mm only a few short pulses with a minimal pulse interval of 20 ms were emitted. At 0.05 mm the sound pattern could not be differentiated from the one produced by an obstacle-trained bat when no obstacle wires were present.

In bats trained for obstacle avoidance the pattern emitted with no obstacle present still showed slightly shorter pulse durations and pulse intervals compared with bats with no obstacle experience. This difference was also found in *Rhinolophus ferrumequinum* (Schnitzler, 1967). It demonstrates that bats trained to avoid obstacles have an “obstacle expectation”.

The calculated average pulse interval per group demonstrates the reaction of the bats to the different wire diameters and the difference in the echolocation pattern in experimental animals with no obstacle before and after obstacle training (Fig. 5). At 0.05 mm the average pulse interval does not differ from that recorded with no obstacle wires whereas the average at 0.065 mm is clearly below the one at 0.05 mm. This confirms the result that at 0.065 mm the bats still detect the wires and respond to them.

#### Discussion

The results of our experiments demonstrate that the echolocation behavior of the hipposiderid bat *Asellia tridens* does not differ fundamentally from that of the rhinolophids *Rhinolophus ferrumequinum* and *Rhinolophus euryale*. All these bats emit cf-fm sounds, change the main parameters of their echolocation sounds in comparable orientation situations in a similar way, reach approximately the same efficiency in obstacle avoidance tests and use Doppler shift compensation. The main difference to the rhinolophids is that *Asellia tridens* emits shorter sounds. Sound durations of 11–3 ms were measured whereas *Rhino-*

*phus ferrumequinum* reaches 70–10 ms and *Rhinolophus euryale* 45–7 ms.

Simmons et al. (1975) divided cf-fm bats into two categories according to pulse duration. Bats which produce sounds shorter than 5 ms belong to the category short cf-fm and bats with pulse duration above 6 ms to the category long cf-fm. They suggested that these two categories represent different strategies of exploiting the information-bearing properties of the cf-component.

All rhinolophids investigated so far emitted long cf-fm sounds, whereas in hipposiderids and mormoopids some species belong to the long cf-fm and other to the short cf-fm category. In the hipposiderid *Asellia tridens* we measured sound durations between 11–3 ms. That means that the categorisation of Simmons et al. (1975) cannot be used for this bat. Another exception is *Hipposideros diadema* (Grinnell and Hagiwara, 1972). When hand-held this bat emitted sounds which lasted between 4.8–9.1 ms. This raises the question as to whether we should keep the categorization “long and short cf-fm sounds” in future or not. We think that the proposed separation is rather artificial for the following reason:

The echolocation sounds of only a few species of cf-fm bats have been recorded so far and most of these recordings have been made under very limited conditions (mostly hand-held). On the other hand, we know from the echolocation behavior of well studied cf-fm species that they can vary their sound duration within a wide range, e.g. *Rhinolophus ferrumequinum* 10–192 ms (Schnitzler and Flieger, in preparation). This makes it likely that not only *Asellia tridens* and *Hipposideros diadema*, but also other cf-fm bats so far put into the category of short cf-fm bats have sound durations longer than 6 ms. The possibility that the separation into the categories of long and short cf-fm sounds as proposed by Simmons et al. (1975), is thus based on a sampling artifact is very high.

We therefore propose another categorisation for bats with cf-fm sounds:

1. Bats with cf-fm sounds and Doppler shift compensation as *Rhinolophus ferrumequinum*, *Rhinolophus euryale*, *Asellia tridens*, *Pteronotus parnellii*, and probably all other rhinolophids and hipposiderids.

2. Bats with cf-fm sounds and no Doppler shift compensation as probably some molossids and some of the mormoopid bats (except *Pteronotus parnellii*).

The two categories may reflect different adaptations of the echolocation systems to the ecologically determined orientation problems of the two groups of bats. The cf-fm bats with Doppler shift compensation use their constant echo frequency as a carrier for frequency and amplitude modulations created in

the echo by the moving wings of their insect prey (Schnitzler, 1970a, b, 1973b, 1978; Goldmann and Henson, 1977). These modulations not only contain information about the nature of the located target (size, wingbeat-frequency, angle of target relative to the bat, etc.), but may also help to discriminate the modulated target echo from nonmodulated background clutter. This means that these bats are very well equipped to hunt in an obstacle rich area. Field observations by Brosset (1966) for *Rhinolophus ferrumequinum* and Bateman and Vaughan (1974) for *Pteronotus parnellii* demonstrate that this is the case, at least in these two species.

The short cf components in bats with no Doppler shift compensation are not as suitable as the long ones of Doppler compensating bats for the detection of fluttering target movements due to the limited frequency resolution and the short duration. Since the signal energy of the short cf component is still higher than that of the following fm sweep, it may help the initial detection of weak echoes, as proposed by Grinnell and Hagiwara (1972). This would increase the detection range of these bats, which mainly hunt in the open air.

For the consolidation of categories proposed in this paper much work is still to be done. We hope that further laboratory and field work on echolocation and feeding behavior of cf-fm bats will lead us to better understanding of the functional adaptations of their echolocation systems.

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