

Echolocation in the noctule (*Nyctalus noctula*) and horseshoe bat (*Rhinolophus ferrumequinum*)

B. Vogler¹ and G. Neuweiler^{2*}

¹ Zoologisches Institut der Universität Frankfurt, 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

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Summary. 1. When catching flying prey under laboratory conditions *Rhinolophus ferrumequinum* typically emit FM-CF-FM signals (Fig. 2). Except for the last two sounds during approach and final buzz the FM-parts are fainter than the CF-component by a factor of 0.76 ± 14 (Fig. 1). The final FM-part was undetectable in some signals emitted during approach (Fig. 3).

2. In obstacle avoidance flights both, preceding and final FM-parts are prominent and louder than the CF-part by a factor of 1.14 to 1.63 (Fig. 1 and 3). Bandwidths of the FM-components increased from ca. 3.5 to 12 kHz for the starting and from 12 to 20 kHz on the average for the final FM-sweep (Table 1).

3. In the open field during cruising flights *Nyctalus noctula* emits pure tones of 22.5 to 25.0 kHz without any frequency modulated components and a duration of 10 to 50 ms (Fig. 4). Brief frequency modulated signals sweeping from ca. 50 to 20 kHz in about 1–2 ms are emitted during pursuit of prey (Fig. 4).

4. Under laboratory conditions *Nyctalus noctula* does not emit pure tones and is not able to catch flying prey in a flight chamber $10.5 \times 3.5 \times 2.15$ m in size. During flights towards a landing platform *Nyctalus noctula* invariably emits brief frequency modulated pulses. During an individual flight the structure is not changed (Fig. 5).

5. In *Nyctalus noctula* specific features of the echolocation pulses, e.g. frequency range swept through, presence of harmonics and double pulses (Fig. 6) are maintained during an individual flight. These specific characteristics of the signal may be

used to identify echoes belonging to its own emitted echolocation pulse.

Introduction

This study began by chance. In autumn/winter 1979 gardeners who had cut down a hollow tree brought a group of 10 *Nyctalus noctula*, a protected species in Germany, into our laboratory. We decided to feed the bats through the winter and release them next summer into their natural habitat. We used the time the noctule bats spent in our laboratory for comparing the echolocation behaviour of this species to that of horseshoe bats.

Both species are known to hunt insects only on the wing and both species use different signals during pursuit of prey. Schnitzler (1968) described the echolocation sounds of horseshoe bats as typically consisting of three parts, a brief frequency modulated (FM) upward sweep at the beginning, a long constant frequency part (CF) and a short FM-downward sweep at the end of the signal. When approaching an obstacle horseshoe bats increase the intensity of the final FM-sweep. Schnitzler (1968) and Simmons (1973) interpret the final FM-sweep as a signal necessary for echo ranging. However, no quantitative measurements on intensity relations between CF- and final FM-parts are available and no sound analysis exists for a sequence of echolocation signals emitted during pursuit and catch of flying prey in horseshoe bats. In the field *Nyctalus noctula* either emits a pure tone during cruising flight or frequency modulated pulses when approaching a target (Pye 1978; Ahlen 1981; Miller and Degn 1981). Under optimal recording conditions in a large flight room we hoped to get insight into the correlation of echolocation signal structure and flight situation.

* To whom offprint requests should be sent

Abbreviations: CF constant frequency; FM frequency modulated; SPL sound pressure level

Materials and methods

Two *Rhinolophus ferrumequinum* and four *Nyctalus noctula* were kept in large chambers under room temperatures of 20 to 24 °C. The room for *Rhinolophus* measured 6.75 × 3.4 × 2.15 m and that for *Nyctalus* 10.5 × 3.5 × 2.15 m. Walls and ceilings were covered with smooth plastics so that the bats could not land and had to direct their flights to specially prepared landing sites. Thus the bats had to take off from and land at distinct small areas within the room which facilitated recording of flight manoeuvres and emitted sounds.

The bats were fed with laboratory reared wax moths, flies and a variety of moths light-trapped during warm nights on the departmental campus. As supplementary food they were given mealworms. For catching prey horseshoe bats were trained to start from a distinct site under the ceiling and to return to it after prey capture. In *Nyctalus* prey catching during flight never occurred within the flight room. These bats flew from a starting site to a landing platform at the other end of the room.

Flight courses and sound emission were recorded synchronously by a 6 × 6 cm camera (Mamiya RB67) flashed by a stroboscope (8–12 flashes/s) and a high-speed Analog 7 tape recorder. Strobe flashes were recorded on a track parallel to the sound track so that the timing of sound emission could be assigned to the bat's position during the flight course documented on photograph (Fig. 1 and 5). Sounds were recorded by a 1/4" condenser microphone (Brüel & Kjaer Nr. 4135) or a QMC-condenser microphone (± 3 dB flat from 20–110 kHz).

The noise level of the recording system was 65 dB SPL from 20 to 110 kHz. Thus echolocation sounds fainter than 65 dB SPL were not detected. Echolocation sounds were analyzed as sonagrams, temporal spectra and power spectra by a Kay 72029A sonograph, Synspec-spectrograph 512 (Dr. Menne, Tübingen) and sound analyzing programs (Dr. K. Beuter, Frankfurt) on a PDP 11/40 computer.

Results

Rhinolophus

Hunting behaviour

Within the laboratory *Rhinolophus* consistently caught prey only on the wing. A horseshoe bat never caught or tried to catch non-flying moths or flies hanging from the ceiling or sitting on the floor in larger numbers. However, within their cages some horseshoe bats were frequently seen to induce take-off of resting moths by wing flapping. As soon as a moth took off it was immediately caught in flight even within the narrow cage (60 × 50 × 50 cm).

Horseshoe bats spontaneously catch flying prey in the laboratory and do not have to be trained to catch prey on the wing. When the first moth was released a bat immediately flew off, caught it and returned to its loft.

Two hundred and five catches of flying targets or prey thrown up in the air, were photographically documented by stroboscopic flashing. In 161 or 78% of these documented attacks the horseshoe

bats caught the prey in one on the wings. They flew towards the target with a speed of about 2.5 m/s and briskly reduced it to 0.5 m/s during catch. When the target was within the span on the wing, it was fished out of the air by a spread-out wing. As soon as the prey touched the wing it was folded in and drawn towards the body whereas the other 'flying' wing was maximally spread out and moved downwards. At the same time the head was bent into the catching wing and the prey seized by the teeth. Then the bat took up normal flight and returned to its loft where the prey was eaten.

In 5 additional cases (2% of 205) the prey was caught by the tail membrane.

Catching in the wing does not require a precise target localization. As the photographs show it is sufficient that the prey moves within the span of a wing membrane. Thus the prey may be 10–15 cm away from the bat's head and still be caught.

The bats caught the prey directly by mouth in only 18 or 9% of the 205 recorded catching flights. This method of catching requires precise positioning of the head relative to the prey. Therefore the seizing of flying insects directly by the mouth was frequently accompanied by spectacular flight manoeuvres such as somersaults or rolling over. It was not clear from photographs and observations what induced the bat to catch directly by mouth.

Echolocating sounds emitted during hunting behavior

A typical sound sequence emitted during one round trip for a catch is represented in Fig. 1 and described in more detail in Table 1. This round trip only lasted slightly more than one second. Basically, sounds emitted during all catching manoeuvres reported here showed the stereotypical structure described by Schnitzler (1968). A long constant frequency part of about 83 kHz was followed by a short component which was downward frequency modulated and preceded by an even shorter upward frequency modulated part. However, relative intensities of the three components and the duration of the CF-part were variable depending on the situation.

Complete sound sequences from search phase to landing after catch were recorded and analyzed from 152 catches. The complete catching behavior may be subdivided into the following phases on the basis of the echolocation sound sequences: a) search and approach, b) final buzz, c) silent period, d) return flight, e) landing.

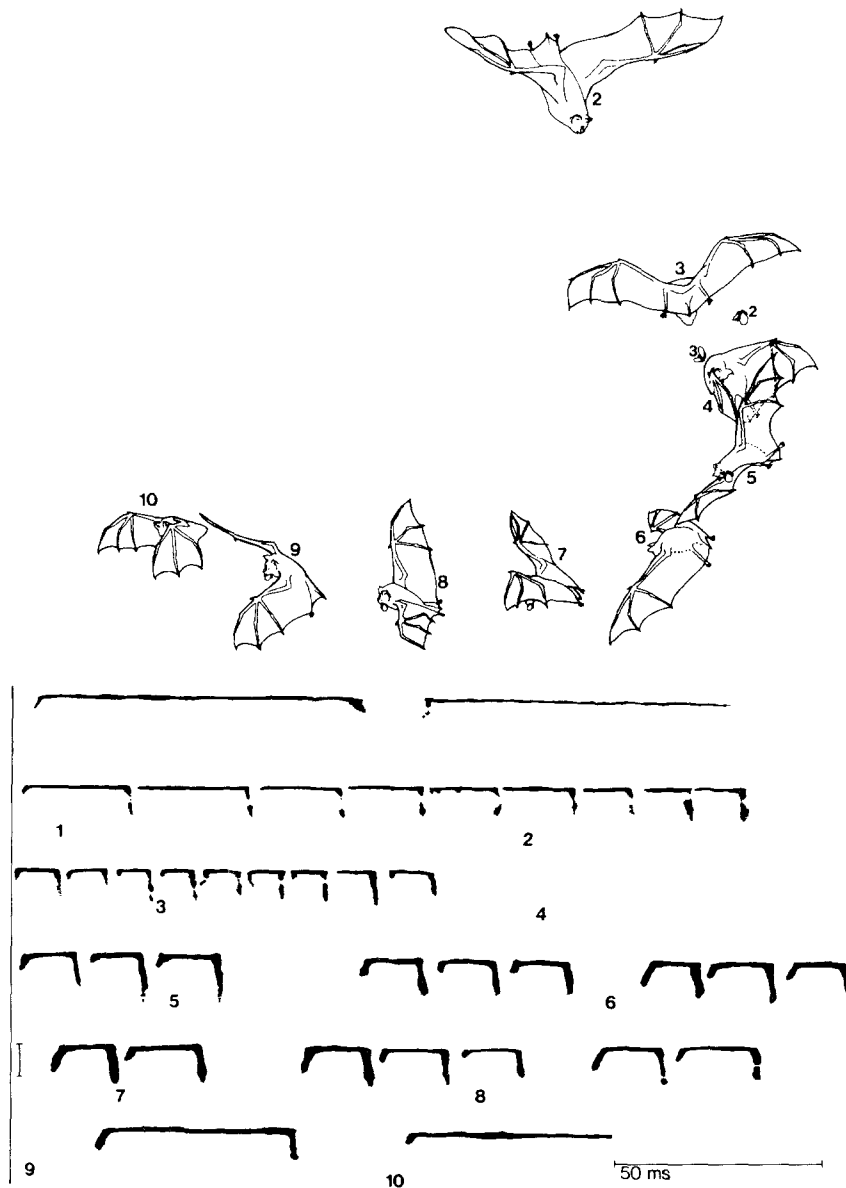


Fig. 1. An echolocating horseshoe bat catches a moth on the wing. Sonagrams of the echolocation sounds emitted during flight are shown below. Numbers indicate subsequent flight positions drawn from stroboscopic photos and identify sonagrams of echolocation sounds emitted at that position. At no. 4 the bat catches the moth. The constant frequency part of the sound is about 83 kHz; vertical bar at the left marks a frequency range of 20 kHz (Neuweiler et al. 1980)

Search and approach. Under our laboratory conditions echolocation sounds could not be clearly associated with either search or approach phase. The bats hanging in the experimental room expected prey and continuously scanned the space for prey. As soon as an insect was detected the bat took off. From sound sequences recorded before take-off no sound criterion could be found indicating the moment of detection. However, it is safe to say that all sounds emitted after take-off belonged to the approach phase of an already detected target.

Sounds emitted during search and approach phase were characterized by a long prominent constant frequency component. Duration of this CF-

component varied between 50 and 80 ms. The average sound production amounted to about 10 sounds/s with pauses between sounds varying between 15 to 20 ms. This results in a duty cycle (% of time during which sound energy is emitted) of 70–81%. During this phase of the catch the CF components were very loud, typically 105–115 dB SPL recorded by a microphone about 10 cm in front of the bat, whereas both, the beginning and the final, FM parts were considerably fainter (Figs. 1, 2).

In most sounds the upward frequency sweep at the beginning of the signal was very faint or missing on the recordings. The final FM-part was present in most sound records and undetectable

Table 1. Sound emission of a horseshoe bat during a catching flight (shown in Fig. 1)

Flash no.	Flight phase	Sound no.	Complete sound duration (ms)	FM-sweeps				Pause between sounds (ms)	Repetition rate (sounds/s)	Duty cycle
				Start		Final				
				Duration (ms)	Band width (kHz)	Duration (ms)	Band width (kHz)			
	Approach	1	77.8	2.4	7.8	2.4	7.8	14.5	10.8	81%
		2	60.0	2.4	13.0	1.4	5.2	17.8	12.8	
1		3	27.1	2.0	5.2	2.4	20.8	1.0	35.58	
		4	27.6	1.5	4.0	2.0	20.8	1.4	34.50	
		5	20.1	—	—	2.0	20.8	1.4	46.50	
		6	18.2	—	—	2.4	19.5	1.4	51.00	
		7	16.8	—	—	2.0	20.8	1.4	54.90	
2		8	17.3	—	—	2.0	18.0	1.4	53.50	
		9	12.2	—	—	2.0	20.8	1.4	73.50	
	Final buzz	10	12.2	—	—	2.4	20.8	1.4	73.50	90%
		11	11.3	—	—	2.0	20.8	1.4	78.70	
		12	11.7	1.4	5.2	2.0	19.5	1.4	76.30	
		13	9.8	1.4	5.2	2.0	19.0	1.4	89.30	
		14	9.3	1.4	4.0	2.0	20.8	1.4	93.40	
3		15	9.3	1.4	4.0	2.0	22.1	1.4	93.40	
		16	9.3	1.4	5.2	2.0	19.5	1.4	93.40	
		17	8.4	1.4	5.2	1.4	20.8	1.4	102.40	
		18	8.4	1.4	5.2	2.0	20.8	1.4	102.40	
		19	10.5	1.4	5.2	2.4	23.4	2.4	77.10	
		20	11.7	1.4	4.0	2.0	17.0			
4				Pause 73 ms						
		21	15.4	2.9	13.0	2.0	23.5	1.4	59.50	
		22	13.6	1.0	4.0	2.0	26.0	2.4	62.50	
		23	16.0	2.0	9.0	2.4	29.0			
5	Flight home			Pause 32.5 ms						
		24	15.9	2.3	12.0	2.4	26.0	1.8	56.50	
		25	15.4	1.8	8.0	2.4	25.4	1.9	57.80	
		26	15.9	1.8	12.0	2.3	21.0			
6				Pause 15 ms						
		27	15.0	2.8	14.0	2.3	25.0	1.8	59.50	
		28	16.4	1.8	12.0	2.8	26.0	1.8	54.90	
		29	15.5	2.3	12.0	2.3	21.0			
	(Obstacle avoidance)			Pause 15 ms						
		30	16.6	3.8	17.0	2.5	26.0	1.6	54.90	
		31	19.0	2.1	12.0	2.5	26.0			
7				Pause 22.5 ms						67%
		32	16.9	3.0	18.0	2.8	26.0	1.6	54.00	
		33	16.7	2.1	12.0	2.6	23.5	2.6	49.20	
8		34	15.2	1.8	5.0	2.1	18.0			
				Pause 15.5 ms						
		35	17.5	3.0	14.0	2.3	23.0	2.3	50.50	
		36	20.1	2.3	12.0	2.3	22.0			
9				Pause 32.1 ms						
		37	48.8	3.0	15.0	2.3	21.0			
				Pause 25.3 ms						
10		38	50.1	3.0	6.5	—	—			

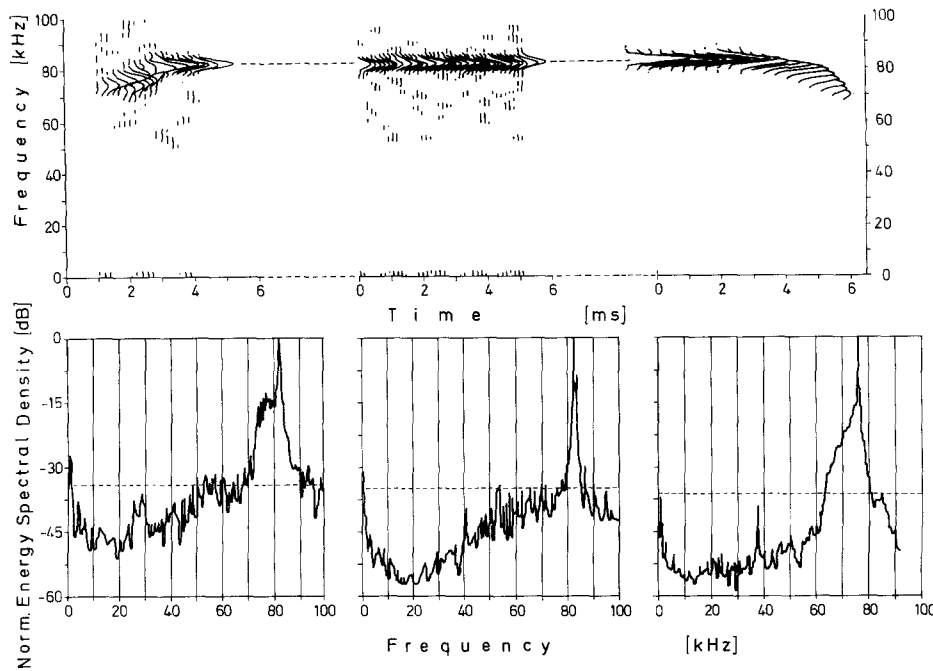


Fig. 2. Temporal (*upper graph*) and power spectra (*lower graph*) of a typical FM-CF-FM echolocation sound in a horseshoe bat. *Left:* Frequency modulated upward sweep at the beginning of a sound. *Middle:* part of a pure tone component lasting from 10 to 80 ms. *Right:* Frequency modulated downward sweep at the end of the echolocation sound. Dashed horizontal line marks level 35 dB below maximal energy density. This level was used for bandwidth measurements

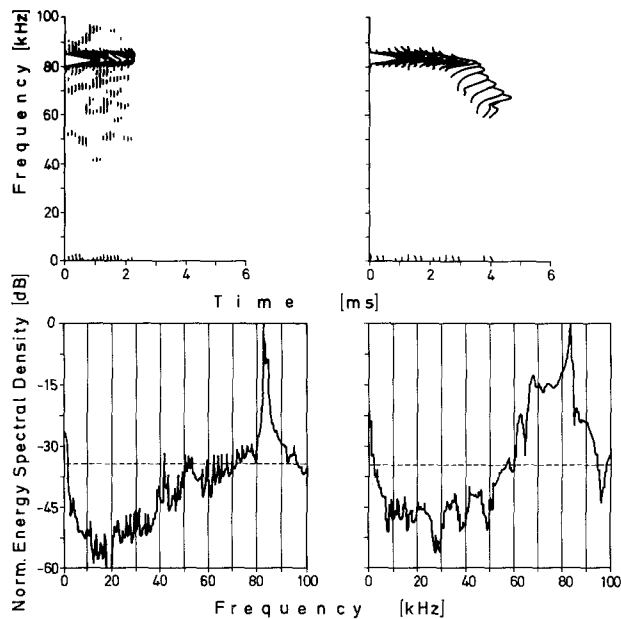


Fig. 3. Variability of sound termination in horseshoe bats. *Upper graphs* show temporal, and *lower ones* corresponding power spectra of the last 4 ms of two echolocation sounds. *Right row:* Typically the echolocation sound ends with a downward FM sweep. Bandwidth and intensity of the final FM-part are variable. In this example bandwidth is 33 kHz, the largest recorded in this study. *Left row:* end of a sound emitted during approach to prey. In this sound no detectable final FM-sweep is present

in a few sounds (Fig. 3). In any case it was always fainter than the CF-component as estimated from sonagrams. In 41 randomly chosen sounds which were analyzed in detail by computer analysis the pressure ratio between FM-end sweep and CF-part

(FM/CF) varied between 0.25 and 0.96. The final FM sweep was never louder than the CF-component (Fig. 1, 2 and 4 left row).

Final buzz. The final buzz is a very fast sequence of sounds emitted just prior to the catch (Griffin et al. 1960). In horseshoe bats it was characterized by a shortening of the CF-component and by a minimal pause of only 1.4 ms between subsequent echolocation sounds (Fig. 1, No. 3 and Table 1). This minimal pause was the most invariant parameter of the final buzz and the duty cycle rose to 90%.

In contrast to the constant minimal pause, duration of the final buzz and duration and number of sounds varied considerably. The final buzz may last from 130 to 400 ms with an average of 290 ms ($n=38$) and it may consist of 11 to 23 sounds (average 17–18).

Within the first 5–6 sounds duration was shortened from 30 to 15 ms and in the following main group of sounds duration continued to decrease from 15 down to 8.4 ms. Shortening always referred to the CF-component whereas the final FM-part remained unaltered (see Table 1). The upward frequency modulated part at the beginning of the sound was negligible throughout the final buzz.

Within the complete sequence of echolocation sounds emitted from take off to landing those of the final buzz were the faintest, ranging from 70 to 90 dB SPL. Within the final buzz sound pressure may continuously decrease or remain more or less constant. However, in most records the last two

sounds of the final buzz were the loudest ones, and their duration was always a few milliseconds longer than the previous ones. As during approach, in the final buzz phase the CF-component of most sounds was still the most prominent part even though its duration was considerably reduced. 33 final buzz sounds were analyzed in detail. In 26 sounds the final FM-sweep was fainter than the CF-component (FM/CF-pressure ratio varied from 0.44 to 0.99 with an average of 0.76 ± 0.14). The FM-part was louder than the CF-component (FM/CF pressure ratio 1.14–1.73) only in the seven analyzed sounds which were among the last two sounds emitted in final buzzes.

Silent period. During the brief catch period no echolocation sounds were emitted (Fig. 1, No. 4). Since the sounds of the final buzz are emitted during one expiration (Schnitzler 1968), the catching time of 50–90 ms simultaneously serves for inspiration. During catching the head of the bat was faced towards the wing membrane containing the prey and echolocation would be rather meaningless in this posture.

Flight towards landing. After the catch the horseshoe bat resumed sound emission. On their way home the bats had to by-pass the microphone. The proportion of the three sound components emitted after catching was markedly different from that of approach or final buzz sounds. Now both beginning upward frequency sweep and final downward frequency modulation were very prominent and sonagrams of the sounds have a trapezoid shape (Fig. 1, No. 5–8). The FM parts are usually louder than the pure tone component by a factor of up to 1.63 or 1.14 on the average (Fig. 3, right row). During each expiration a group of 2–3 sounds are emitted with pauses of 1.5–5 ms in between. The intergroup pause lasted about 15–80 ms. The duty cycle dropped to 60–67% mainly due to these pauses. Sound duration, i.e. duration of the CF-component increased from 13 to 30 ms during obstacle avoidance.

Landing. Immediately before landing at their loft the horseshoe bats again emitted a final buzz with the same sound parameters and sequences as described for the final buzz prior to catch.

Nyctalus noctula

Even in the largest flight room available ($10.5 \times 3.5 \times 2.15$ m) this species could not be induced to catch flying prey in spite of intensive,

careful training for several weeks. This is in striking contrast to the behaviour of horseshoe bats which spontaneously catch insects on the wing in much smaller confinements.

Nyctalus quickly learned to start from their cages and flew in wide circles through the flight room but they never tried to catch flying prey, which they immediately accepted as food when offered by forceps in the cage or on a special landing post. They also continuously produced echolocation sounds during flight. Evasive flight manoeuvres also indicated that they detected mealworms thrown into their flight path.

On the other hand noctules had great difficulties to avoid obstacles put into their flight path such as vertical or horizontal rods. Vertical rods (diameter 1 cm) were only avoided when spaced more than 50 cm apart and horizontal ones when spaced more than 1 m apart. With obstacles spaced more narrowly the bats frequently hit the rods and got hurt. From all these experimental observations it became obvious that the fast flying noctule lacks the manoeuvrability for catching prey on the wing within a room of $10.5 \times 3.5 \times 2.15$ m, although they clearly detected the target by echolocation.

Analysis of echolocation sounds was therefore restricted to flights of *Nyctalus* from the cage over a distance of 6.60 m to a landing platform where it was rewarded by a mealworm and to free field recordings.

Echolocation sounds

Free field. Around Frankfurt *Nyctalus* comes out of the woods and preferably hunts over open meadows or along forest or bush borders. They fly in fast swings several meters above ground and occasionally dip down to 1–2 m in pursuit of a prey. The results of Pye (1978) and Miller and Degn (1981) were confirmed. *Nyctalus* emits two types of sounds:

1. During cruising flight long pure tones of about 10 to 50 ms duration and a frequency of about 22.5 to 25 kHz (Fig. 4) were emitted. No harmonics were present in the recordings and no frequency modulation could be detected anywhere in the signal. This is also demonstrated by the narrowly peaked energy density spectrum in Fig. 4.

2. During pursuit of prey *Nyctalus* emits a short frequency modulated sound with or without harmonics (Fig. 4). These FM sounds were identical to those recorded under laboratory conditions.

Laboratory recordings. Within our flight room all noctule bats invariably emitted only short, frequency modulated pulses.

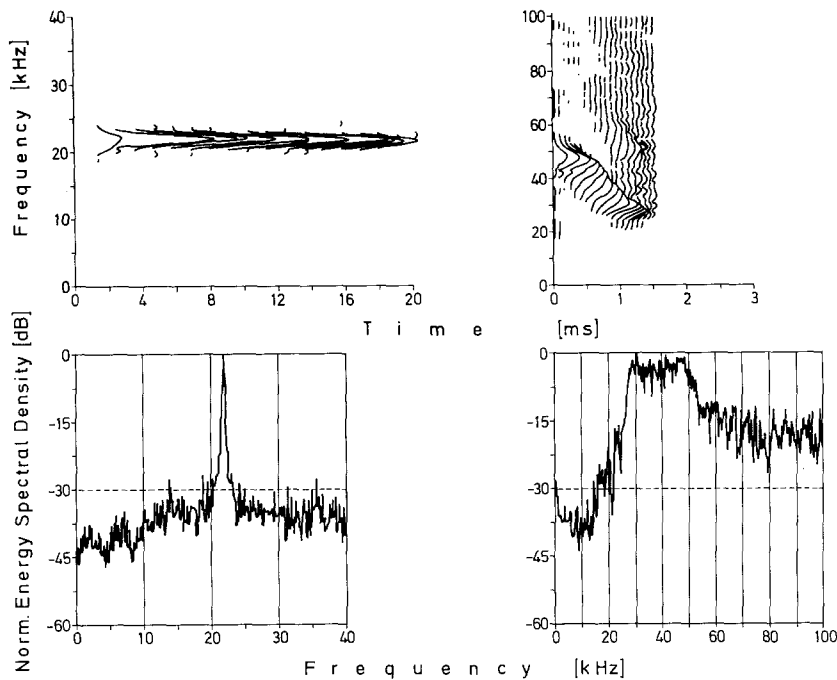


Fig. 4. Echolocation sounds of *Nyctalus noctula* (upper graphs temporal, lower ones corresponding power spectra). *Left row:* During cruising flight in the open field only pure tones of ca. 20 ms duration and without any frequency modulated part are emitted. *Right row:* During approach to a target or within the laboratory *Nyctalus* emits various frequency modulated downward sweeps of a few ms duration. Here a hyperbolically modulated sound is shown with a weak second harmonic

Under our laboratory conditions three types of pulses occurred:

1. A hyperbolically downward modulated sweep from about 60 to 20 kHz was emitted with weak or no harmonics. The sweep lasted for about 1.8 to 4.7 ms (Fig. 4, right).

2. A pulse swept more linearly downward from 70 to 20 kHz with one harmonic ranging from about 85 to 42 kHz. These pulses may last as long as the sweeps without harmonics or be as short as 1.7 ms (Fig. 5).

In both vocalization types the frequency range swept varied considerably from sound to sound. Both types of echolocation sounds have been also recorded under natural conditions by us as well as by Pye (1978), Ahlen (1981) and Miller and Degen (1981).

3. Double-pulses (Figs. 5 and 6).

This echolocation sound consisted of a frequency sweep and one harmonic, as in type 2, with a total frequency range of 85 to 20 kHz. After a pause of 2.3 to 2.8 ms, a second steep pulse occurred, sweeping commonly from about 60 to 20 kHz. The complete double sound lasted for 4.0 to 5.7 ms (Fig. 6).

One might argue that the second pulses were echoes and not sound emissions. However, the following arguments exclude this interpretation:

a) The time relation between first and second pulse remained fixed during a recording sequence of sound emission from start to landing even

though the relative distance between directional emitter (bat), microphone and possible reflectors changed considerably.

b) Double pulses were recorded in some flights whereas in others recorded under the same conditions they never occurred.

c) Shifting the positions of possible reflectors around the recording site did not alter the structure, occurrence or non-occurrence of double pulses. We therefore considered the double sounds as to be genuinely emitted echolocation pulses.

When a *Nyctalus* bat took off and flew to the landing post, it only emitted one of the three sound types throughout the flight path. In none of 30 recorded complete sound sequences emitted during such flights did the bat switch to different sound types (e.g. Fig. 5).

When the bat took off 6.60 m from the landing site it emitted a few pulses of about 10 sounds/s. After 600 ms (3.5 m from the target) the bat started to emit 2 echolocation sounds per expiration. The occurrence of such twin sounds with larger pauses in between defined the approach phase (Fig. 5). Throughout the approach phase, lasting about 800 ms, the pauses between groups are progressively shortened and the last group may even consist of 3–4 sounds. The average emission frequency was about 26 sounds/s.

The final buzz was invariably separated from the approach phase by an inspiration pause of about 30 ms (Fig. 5B, between No. 4 and 5). Then

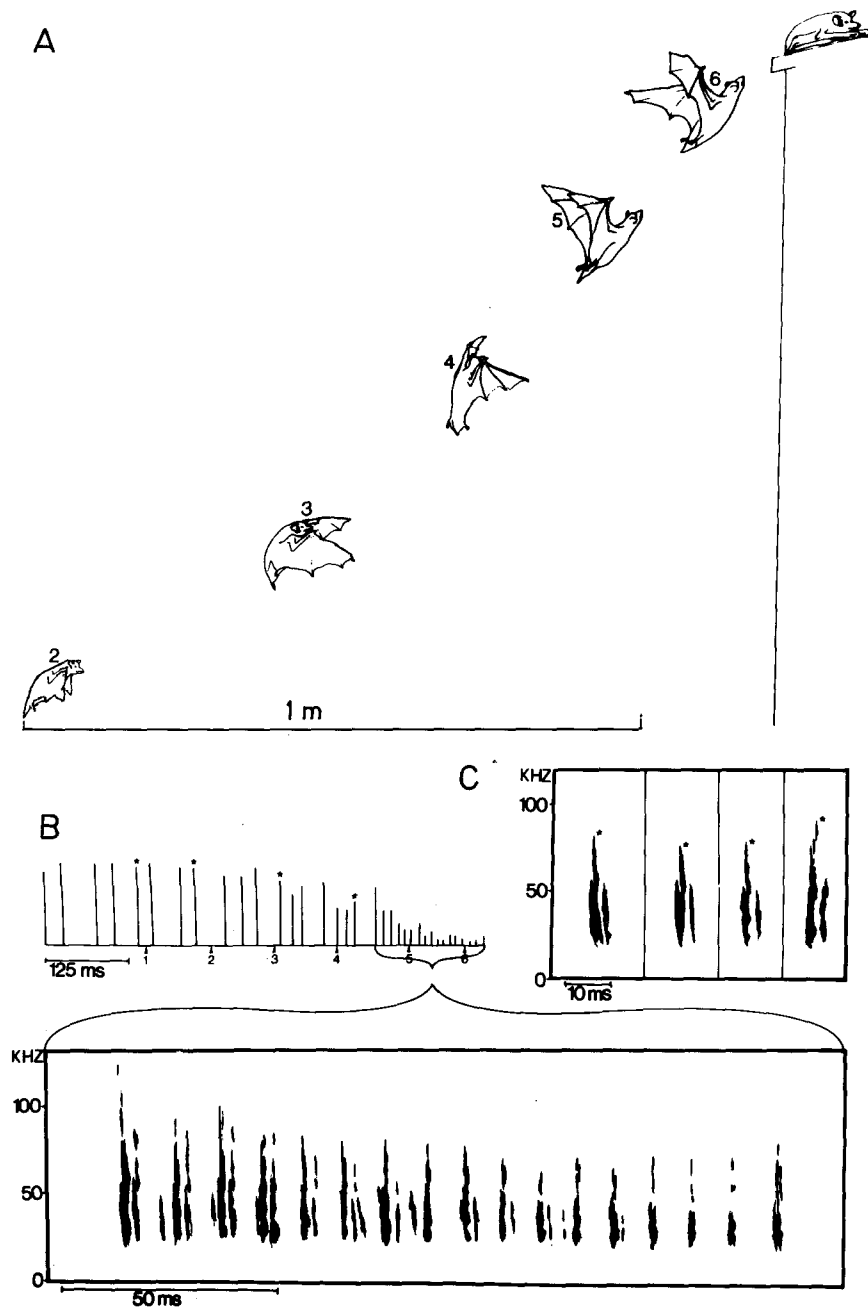


Fig. 5 A–C. An echolocating *Nyctalus noctula* flies to a landing platform (A). Sound sequence emitted during flight in A is shown in B. Each vertical line represents a sound. Length of the line corresponds to sound intensity. Numbers on abscissa refer to flight position marked by the same number in A. In C sonagrams are shown of those sounds marked in B by an asterisk. Lowest line shows sonagrams of sounds of the final buzz sequence. Throughout this flight the bat emitted so-called double pulses

the echolocation sounds of the final buzz were emitted during one expiration lasting about 200 to 250 ms. This contained about 16 to 20 sounds with an emission frequency of about 90 sounds/s.

Echolocation sounds of *Nyctalus* are very intense and reach 124 dB SPL when recorded a few cm in front of the mouth. As in horseshoe bats the final buzz was faintest. Even though the bat was only 1 m or less from the microphone, the final buzz recordings were about 12 dB fainter than those of preceding sounds recorded from a much greater distance (Fig. 5).

As already mentioned a bat will emit only one sound type during one flight path. Additionally the frequency range swept through and the time course of the sweep may differ from flight to flight as well as between individuals. Echolocation sound emission was influenced by conspecifics. For instance the rate of sound emission by a flying bat was increased when another vocalizing bat sat on the landing platform. Interestingly, when several bats flew at the same time, the individual sounds emitted by each bat differed in frequency range or time course of sweep or in sound type. However,

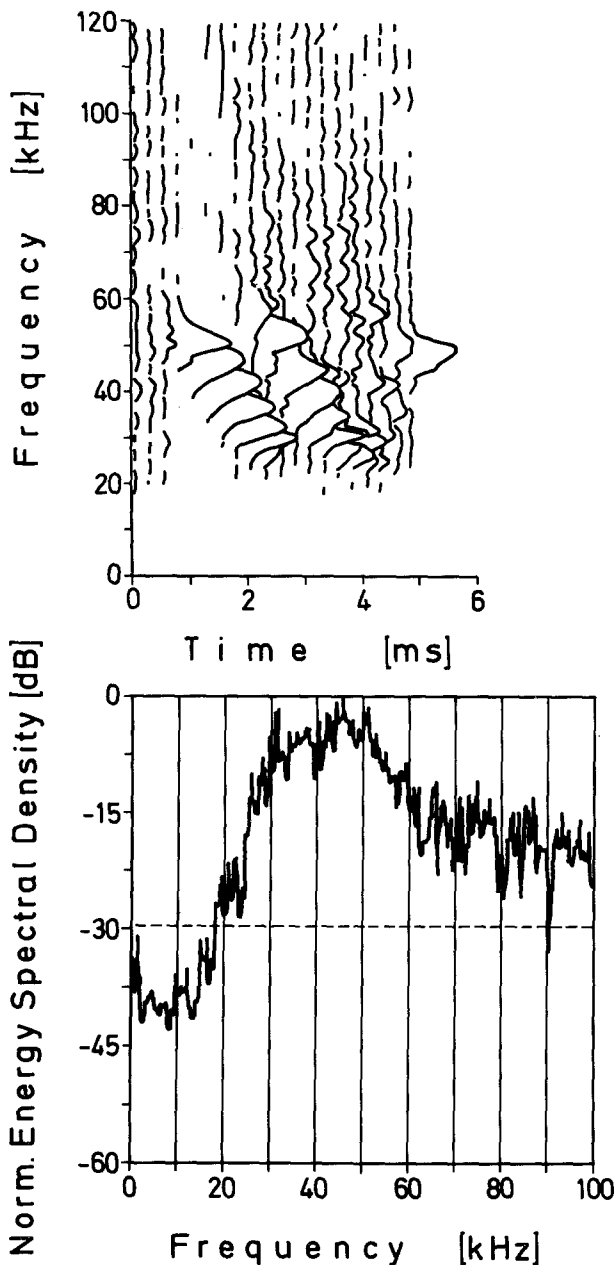


Fig. 6. Double pulse, a type of echolocation sound frequently emitted by *Nyctalus noctula* in the laboratory. (Upper graph temporal, lower one corresponding power spectrum)

the double pulse sound was never recorded from bats flying in groups. These individual differences in signal characteristics might help the bat to recognize their own echo signals when several bats fly at the same time.

Discussion

In the laboratory the difference in echolocation behaviour between horseshoe and noctule bat is

striking. Whereas a horseshoe bat spontaneously catches flying prey even in narrow confinement, the noctule bat will never do so even in large flight rooms and even after long and intense training. The main reason for this difference is a lack of manoeuvrability in the noctule during rather slow flight. These bats have long, slender wings and in their natural habitat hunt in fast swings interrupted by quick dips. Apparently our flight room was still too small for the bat to pick up the speed necessary for full manoeuvrability. In contrast horseshoe bats are slow flyers and in their natural habitat hunt flying prey close to bushes and trees. In flight this bat is able to turn around within a narrow space and may even hover for a few seconds. Thus the difference in hunting behaviour of these bat species which only catch prey on the wing most probably result from the different flight capacities adapted to their different foraging areas.

The echolocation signals used by both species are again markedly different. Horseshoe bats in any environment invariably emit pure tones with the preceding and succeeding short frequency modulated sweep, whereas noctules emit pure tones without any additional modulated component while cruising in open air and switch to short frequency modulated broad band signals when pursuing prey or when flying in confinements.

Depending on the situation horseshoe bats vary the length of the pure tone and relative intensity of the three components of the stereotypic echolocation sound. In natural habitats horseshoe bats might widely apply this variability between the three echolocation sound components. However, no quantitative data on a possible correlation between emitted sound structure and type of foraging areas are available. In our laboratory during search and approach of flying prey they preferably emit very long 30 to 80 ms pure tones frequently without a preceding FM upward sweep. The final FM sweeps are quite faint and range only over a short frequency band of about 17 kHz. In some recordings of sounds during search and approach phase the final FM sweep is below the recording noise level or even missing (Fig. 3, left row). Apparently the echo information needed for detecting and focusing on the prey during search and approach is best transmitted by the long echo pure tone carrier. As is well known by signal analysis (Schnitzler and Henson 1980) and neurophysiological data of audition (summary see Neuweiler et al. 1980), horseshoe bats may detect fluttering targets by frequency and amplitude modulations and narrow side bands induced onto a pure tone echo by the periodic wing beats of prey. A long pure tone

signal is best adapted for carrying this kind of movement-correlated information, and horseshoe bats have special filters in their ears tuned to the carrier frequency of the echo and capable of extracting the prey movement-correlated modulations of the pure tone echo.

During the final buzz phase immediately prior to seizing the prey the bat may need a maximum of precise information about the locality of the target. In this phase horseshoe bats emit a fast sequence of short echolocation sounds with the smallest possible pause of 1.4 ms. The duty cycle rises to 90%, but apparently a continuous uninterrupted flow of pure tone echo information is not what the bat wants, otherwise it would emit one or two echolocation sounds of 150–200 ms duration, sounds which they are capable of producing. Instead they emit short pulses in fast sequence, which suggests that in the final buzz horseshoe bats need either the final FM-sweep or the rise and fall slope of the envelope or both.

It is generally believed that the final FM-sweep is that component of the signal which carries ranging information, i.e. time lapse between sound emission and echo arrival at the ear. According to optimal filter theory, a short broad band signal would be best adapted for precise timing information (Simmons 1973). However, our analysis of the final buzz sounds in horseshoe bats disclosed:

a) that the frequency bands of the final FM-sweeps are narrow and never reach the maximal band the bat is capable of emitting, such as those FM-sweeps emitted during the return phase; and b) that the maximal intensity of the sound is still concentrated in the pure tone component, whereas the final FM-sweep is fainter than the pure tone, with the exception of the last two sounds of the final buzz. The last sounds, however, are emitted only a few milliseconds before the catch, so that they certainly can not guide the hunting strategy of the bat and thus may be irrelevant for prey localization.

Within the final buzz most sound energy is still within the pure tone component and this casts some doubts onto the assumption of the final FM-sweep being the carrier of range information. It might as well be assumed that the envelope, i.e. the rising slope of the echolocation sound carries range information. This possibility is rendered feasible by neurophysiological studies on binaural hearing in echolocating bats which showed that binaural onset time differences in pure tone pulses are neurally codable down to at least 20 μ s (Harnischfeger 1980).

On the other hand in *Pteronotus parnellii*, O'Neill and Suga (1982) described a specialized ranging area in the auditory cortex which is specifically sensitive to FM-components emphasizing the final FM-sweep as carrier of time information. If the horseshoe bats indeed have to rely on the FM-sweep for range finding or, as our analysis of final buzz sounds suggests, may use the signal envelope for that purpose, or if they use both parameters has to be decided by behavioural experiments. We expected the final buzz sounds to contain the most prominent FM-components within the sound sequence emitted during the catch. To our own surprise very strong preceding and succeeding frequency modulated components did not occur during the final buzz, but only after a catch when the bat flew back to its loft and had to avoid recording devices. During this flight course both preceding upward and final downward frequency modulated sweeps are louder than the pure tone component.

So far the FM-sweep at the beginning of the echolocation signal has attracted little attention. It was considered as an unavoidable by-product of intonation since it was frequently observed in the first sound of an expiration and was less obvious or missing in subsequent sounds (Schnitzler 1968). The data reported here comprise many first sounds of an expiration without a beginning FM sweep, whereas after a catch several subsequent sounds invariably contain a very loud and about 20 kHz broad FM upward sweep. This suggests that horseshoe bats may emit this component at will and the beginning FM-upward sweep has to be considered as an information carrying part of the echolocation signal.

Then why after a catch does a horseshoe bat emphasize both FM components in its echolocation signals? During a catch the bat emits no sound so that it flies 'blind' for about 100 ms. After this critical phase general reorientation and redefinition of the bat's own position relative to the environment may be necessary. Therefore loud sounds with a maximum of different information bearing elements may be optimal. As indicated by behavioural experiments in *Myotis myotis* and *Megaderma lyra* (Habersetzer and Vogler 1983), frequency modulated signals may carry echo information on target and obstacle structures apart from ranging and directional information. Obtaining all possible information for reorientation after the silent period might be the reason for emitting all three sound components at about equal intensity.

In noctule bats the long, pure tone emitted in

open spaces is most easily interpreted as a high energy, narrow band signal covering long distances and detecting potential prey within a large range of about 20 to 30 m. Of course one might also consider the pure tone to be a fluttering prey detector as in horseshoe bats. For audition this would also require a narrow filter tuned to the carrier frequency as in horseshoe bats. Since noctules are a protected species we did not experiment on the auditory system of noctules. However, it seems unlikely to us that noctules possess such a filter system. Horseshoe bats hunt in an echo-cluttered area and flutter encoding may be the only way to detect prey in noise, whereas noctules hunt in open spaces at high speed. In this situation cluttering rarely occurs but detection of prey at greater distances may be important for this fast flying predator. Thus pure tone emission in echolocation may be adapted for two different functions: fluttering prey detection in noise and detection of targets at long range.

In noctules the broad band FM-signals appear to be obligatory for pursuing prey and obstacle avoidance. The noctules could not be induced by any means to emit pure tones in our laboratory. Apparently the presence of walls, even at distances of several m, is interpreted as an environment with obstacles. Recently it has been shown that not only noctules, but also other species emit only FM-pulses under laboratory conditions, while in the natural habitat during cruising flight pure tones are emitted (e.g. Habersetzer 1981). Apparently approach to obstacles, landing sites or prey requires a broadband signal. Yet, the reasons for this are not clear. Again it is commonly argued that FM-sweeps allow for precise ranging information. However, there exists no unequivocal experimental proof to this notion. So the FM-signal may as well be preferred in close-up echolocation for detecting and differentiating target structure such as, e.g., the roughness of a landing site, by spectral analysis of the broadband echo (Habersetzer and Vogler 1983).

During flights the noctule bats did not vary the fine structure of their echolocation sounds from start to landing in any conceivable systematic way. Once a single bat started emitting a certain pulse type it continued to do so until landing. Apparently the fine structure of the signal, such as frequency band emitted, time course of modulation, presence of harmonics, is not critical for echolocation in our laboratory condition. One should not draw general conclusions from this fact since the echolocating bats had become familiar with

the flight room and flight path for many weeks of training and detailed echolocational information on the flight path may not be necessary.

Even though the fine structure of the emitted signal did not differ during an individual flight course, it varied markedly between individuals especially when flying simultaneously. From several recordings of group flights we got the impression that each individual bat retains its own individual sound structure marked by a certain frequency range swept or by the presence or prominence of an additional harmonic and so on. These observations certainly deserve more detailed studies especially in the natural habitat. Each bat may mark its own signal with a unique time structure and thus retrieve all echoes caused by its own echolocation signal from a cluster of echo signals belonging to different bats. Radar receivers also identify the emitted signal from alien ones by an individual structural marker. Thus variability of the fine structure may not express adaptation of the signal to specific echolocation performances, but may serve more as a marker or identifier of the individual signal. Interestingly when flying in small groups *Rhinopoma hardwickei* shift the emitted pure tone frequency into three distinct frequency bands (Habersetzer 1981). Similar observations have been made by other authors in other bat species (Pye 1972). The observations reported here and the data from the literature suggest that identification of an individual's echo may be a critical point in echolocation for bats. This aspect has never been analyzed and certainly deserves detailed further studies.

Unfortunately we cannot offer any explanation whatsoever for the occurrence of double pulses. We have put forward our arguments why we do not consider the second pulse as an echo. However, before speculating on the meaning of this signal, it should be verified whether the signal is also emitted under natural conditions or if it only occurs in the laboratory. In the latter case these conditions have to be defined experimentally.

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References

- Ahlen I (1981) Identification of Scandinavian bats by their sounds. Swed Univ Agricult Sci Dept Wildlife Ecol Report 6, Uppsala
- Griffin DR, Webster FA, Michael CR (1960) The echolocation of flying insects by bats. *J Anim Behav* 8:141-154
- Habersetzer J (1981) Adaptive echolocation sounds in the bat *Rhinopoma hardwickei*. *J Comp Physiol* 144:559-566
- Habersetzer J, Vogler B (1983) Discrimination of surface-

- structured targets by the echolocating bat *Myotis myotis* during flight. *J Comp Physiol* 152:275–282
- Harnischfeger G (1980) Brainstem units of echolocating bats code binaural time differences in the microsecond range. *Naturwissenschaften* 67:314–315
- Miller LA, Degn HJ (1981) The acoustic behaviour of four species of vespertilionid bats studied in the field. *J Comp Physiol* 142:67–74
- 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
- O'Neill WE, Suga N (1982) Encoding of target range and its representation in the auditory cortex of the mustached bat. *J Neurosci* 2:17–31
- Pye JD (1972) Bimodal distribution of constant frequencies in some hipposiderid bats. *J Zool* 166:323–335
- Pye JD (1978) Some preliminary observations on flexible echolocation systems. In: Olembo RJ, Castelino JB, Mutere FA (eds) *Proc Fourth Int Bat Res Conf, Lit. Bureau Nairobi, Kenya*, pp 127–136
- Schnitzler HU (1968) Die Ultraschallortungslaute der Hufeisenfledermäuse in verschiedenen Ortungssituationen. *Z Vergl Physiol* 57:376–408
- Schnitzler HU, Henson OW (1980) Performance of airborne animal sonar systems: I. Echolocation of microchiropteran bats. In: Busnel RG, Fish J (eds) *Animal sonar systems*. Plenum Press, New York, pp 109–179
- Simmons JA (1973) The resolution of target range by echolocating bats. *J Acoust Soc Am* 54:157–173