

Annette Denzinger · Björn M. Siemers  
Andrea Schaub · Hans-Ulrich Schnitzler

## Echolocation by the barbastelle bat, *Barbastella barbastellus*

Accepted: 19 June 2001 / Published online: 30 August 2001  
© Springer-Verlag 2001

**Abstract** When searching for insects along edges, *Barbastella barbastellus* alternated between two signal types. Type-2 signals had durations around 6 ms and were composed of an initial shallowly downward frequency modulated component, starting at about 45 kHz and followed by a shorter more steeply modulated component that ended at about 32 kHz. Type-1 signals were rather stereotyped with durations around 2.5 ms and a very short rise time. They covered an approximately 8 kHz-wide frequency band positioned just below the 12–15 kHz-wide frequency band of type-2 signals, with no or small frequency overlap. In the recordings, type-1 signals almost had always a higher amplitude than type-2 signals, at least partly caused by head movements. Assuming that signal structure reflects function, we hypothesize that type-2 signals have the same adaptive value as the signals with a broadband and narrowband component of other vespertilionids, but with a reverse arrangement of the signal elements. Like the broadband component of the type-2 signals, type-1 signals are well suited to localize background targets. Thus, the localization component may be distributed among two signals separated in time, which has the advantage that both signals can be varied independently in the direction of emission and in amplitude.

**Keywords** Echolocation · *Barbastella barbastellus* · Foraging behavior · Signal structure

### Introduction

In western and central Europe, the barbastelle bat *Barbastella barbastellus* (Schreber 1774) is considered of one

of the most endangered bat species (Stebbing and Griffith 1986; Stebbings 1988; Rydell and Bogdanowicz 1997). In many areas, populations declined rapidly or disappeared completely over the past decades (Richarz 1989; Benzal et al. 1991; Spitzenberger 1993; Zingg 1994; Sierro and Arlettaz 1997; Sierro 1999). Barbastelle bats are very specialized predators. Their diet consists almost exclusively of Lepidoptera, which makes them vulnerable to changes in the abundance of moths and may account for their drastic decline throughout many parts of Europe (Beck 1995; Rydell et al. 1996; Sierro and Arlettaz 1997; Vaughan 1997).

Little is known about the foraging behavior of barbastelle bats, and many observations are anecdotal. Several observations revealed strong evidence for an aerial-hawking strategy. Barbastelles were observed foraging for flying insects along vegetation in regular paths 4–5 m above the ground (Ahlén 1990) and around mercury-vapor street lamps (Zingg 1994). In a radio-tracking study, Sierro and Arlettaz (1997) found foraging bats flying exclusively 2–4 m above tree crowns. Single individuals were also observed while they hunted above ponds (Stebbing 1991), along low crumbling boulder-clay cliffs, and above a beach (Goldsmith, personal communication). Other authors, however, suggest that barbastelles might also glean prey from surfaces (Poulton 1929; Rydell et al. 1996; Rydell and Bogdanowicz 1997).

Comparative studies of many bat species revealed that the echolocation behavior strongly depends on the perceptual tasks that have to be performed. Foraging habitat, foraging mode, and diet are major factors that influence the structure of search signals. (Neuweiler 1989, 1990; Fenton 1990; Obrist 1995; Schnitzler and Kalko 1998, 2001; Denzinger et al. 2001). Many vespertilionids that forage in edge and gap situations emit search signals with medium duration and medium frequency. Typically, the search signals are composed of two components, a longer shallow frequency-modulated narrowband component preceded by a shorter, more steeply frequency-modulated broadband component. The narrowband

A. Denzinger (✉) · B.M. Siemers · A. Schaub · H.-U. Schnitzler  
Lehrstuhl Tierphysiologie, Universität Tübingen,  
Auf der Morgenstelle 28, 72076 Tübingen, Germany  
E-mail: annette.denzinger@uni-tuebingen.de  
Tel.: +49-7071-2972619  
Fax: +49-7071-292618

component is well suited for medium-range detection of insects flying in front of clutter-producing background targets and possibly also delivers flutter information. The broadband FM component is well suited to characterize and localize background targets. Since prey detection is less hampered by masking in the overlap-free window, signal duration depends on the distance to the background (Schnitzler and Kalko 1998, 2001). Vespertilionids that fly in narrow spaces emit short, broadband signals. These signals are well suited for spatial orientation, where a precise characterization of background targets is necessary (Schnitzler and Kalko 1998, 2001).

So far, little is known about the echolocation behavior of barbastelle bats. Several authors have published descriptions of single echolocation signals of barbastelle bats in the field (Ahlén 1981, 1990; Ahlén and Baagøe 1999; Vaughan et al. 1997; Parsons and Jones 2000) and in the lab (Konstantinov and Makarov 1981; Jones 1993), but these data were based only on single calls or one sequence. In this study, we describe the signal repertoire of the barbastelle bat and discuss the possible function of signal structure in relation to the echolocation tasks.

## Materials and methods

### Field sites

We recorded the echolocation behavior of *B. barbastellus* near Ilanz (Switzerland) in the years 1995–2000. Bats roosted in a hay barn surrounded by several trees, located on a steep mountain meadow with interspersed trees above the forested slopes of the valley of the river Glenner (Lutz 1995). Recordings were made when the bats left the roost at dusk and foraged nearby above a meadow. Hunting barbastelles were also recorded along a dark forest road at the bottom of the Glenner valley and in a nearby clearing in the forest. The road was bordered by coniferous forest covering the slopes of the valley. The trees on both sides of the road were up to 15 m high and formed a gap of 10–12 m. The clearing was about 30 m wide and 100 m long. It was surrounded by coniferous forest and opened towards the forest road. All recording sites were located within a distance of about 1 km from the roost.

### Flight tent

Five individuals of *B. barbastellus* were caught close to a maternity roost in Alt Zauche, near Berlin, Germany, where the bats roosted behind the wooden planks of the outer walls of several barns. Each bat was kept between 15 min and 30 min in a flight tent (3.5 m×3.5 m×2.5 m) to record its echolocation calls.

### Sound recordings and analysis

Echolocation signals were picked up by an ultrasonic microphone, amplified, and heterodyned into the audible range by a custom-made bat detector, which also contained a digital transient recorder that continuously read the recorded signal into a ring buffer with a capacity of 3.3 s. A post trigger stored the content of the ring buffer after an adjustable delay. Afterwards, the stored sequence was read out of the memory at reduced speed (slowed down 15 times) and recorded with a Sony Walkman onto audiocassettes. Comments describing the flight behavior were registered onto the second audio channel of the cassette.

The time-expanded signals were digitized at a sampling rate of 25.6 kHz, then processed through a fast Fourier transformation

(FFT) using 256 points and a Hanning window. Signals were displayed as color spectrograms (Sona-PC; B. Waldmann, University of Tübingen) in the range of 150 kHz with a vertical resolution of 400 lines, resulting in a reading accuracy of 375 Hz (for a detailed description see Siemers and Schnitzler 2000). FFTs were calculated with 93.75% time overlap, thereby producing a new spectrum every 0.04 ms. Amplitude was color-coded with a dynamic range of –72 dB. Signal parameters were calculated from four measuring points set in the first harmonic of each signal. Time measurements in the sonagram corresponded best with those in the oscillogram if the beginning and the end of a signal were set at about –20 dB below the amplitude at peak frequency. The peak frequency is defined as the frequency with the most energy in the averaged spectrum. In 36 type-1 and 18 type-2 signals emitted above the road, we determined the rise time defined as the duration needed to reach half amplitude.

For statistical comparison of the sequences recorded from foraging bats at different recording sites, we defined two signal types: type-1 and type-2. The two signal types could be easily distinguished from the curvature, starting frequency, and amplitude and have been described by that means by other authors (Ahlén 1981, 1990; Vaughan et al. 1997; Ahlén and Baagøe 1999; Parsons and Jones 2000). Because several data sets were not normally distributed (Kolmogorov-Smirnov test under Lilliefors adaptation:  $P < 0.05$ ), we used nonparametric statistics.

## Results

### Flight behavior

At dusk, individual *B. barbastellus* left the roost one after another and flew towards the valley. The bats flew nearly horizontally and thus quickly increased their height above the ground due to the slope of the meadow. Some of the bats flew in wide circles approximately 6–8 m above the meadow before they disappeared. At the forest road, *B. barbastellus* flew straight, approximately in the middle of the gap at a height of about 6–8 m, and kept approximately 5–6 m distance from the forest edge. From regular passages at our recording sites, we infer that bats repeatedly patrolled the same section of the road. Feeding buzzes indicated that they foraged for aerial insects. In the clearing, *B. barbastellus* foraged between 2 m and 6 m above the ground. Bats either followed the edge of the forest at a distance of about 3 m, sometimes disappearing into it, or crossed the clearing. They did not forage continuously in the clearing but disappeared for several minutes, again indicating that *B. barbastellus* regularly patrolled a foraging area.

In the flight tent, barbastelle bats made short flights along the walls or crossed the tent diagonally before they landed on the wall. One bat also circled in the tent. The bats' flight was adroit, but faster and less agile than in the highly maneuverable *Plecotus* species. We never observed hovering.

### Echolocation behavior

#### *Wide edge and gap situation*

Barbastelle bats that foraged above the meadow, above the road, and in the clearing, alternated between two

**Table 1** Signal parameters of type-1 and type-2 search signals at various recording sites. To avoid pseudoreplication, only one data point per sequence was used, which is the mean of all calls of a sequence. Data are given as mean  $\pm$  SD of these data points and

maxima and minima of single calls;  $n$  indicates the number of sequences; numbers in parentheses give the absolute number of signals

Signal type	Recording site	Pulse duration (ms)	Pulse interval (ms)	Starting frequency (kHz)	Terminal frequency (kHz)	Peak frequency (kHz)
Type-1	Meadow; $n = 12$ (109)	2.56 $\pm$ 0.66	92.6 $\pm$ 42.97	36.5 $\pm$ 1.46	28.1 $\pm$ 0.99	32.8 $\pm$ 0.87
	Road; $n = 22$ (201)	1.33; 4.08	42.63; 287.17	33.4; 39.8	25.5; 30.0	30.8; 34.9
	Clearing; $n = 9$ (97)	2.7 $\pm$ 0.53	92.3 $\pm$ 31.21	36.2 $\pm$ 0.77	28.4 $\pm$ 0.56	33.6 $\pm$ 0.77
		1.42; 4.17	48; 320.33	33.4; 40.1	25.9; 30.8	31.5; 35.6
		2.45 $\pm$ 0.62	85.25 $\pm$ 24.36	36.1 $\pm$ 1.28	28.0 $\pm$ 0.92	33.3 $\pm$ 0.91
	1.46; 4.38	47.71; 249.0	33.8; 40.5	25.2; 30.8	31.9; 37.5	
	Kruskal-Wallis	$P = \text{n.s.}$	$P = \text{n.s.}$	$P = \text{n.s.}$	$P = \text{n.s.}$	$P < 0.05$
Type-2	Meadow; $n = 11$ (83)	4.88 $\pm$ 1.53	55.65 $\pm$ 5.80	45.2 $\pm$ 1.23	30.5 $\pm$ 2.75	40.9 $\pm$ 3.34
	Road; $n = 21$ (135)	1.71; 9.08	13.42; 112.5	42.0; 48.0	24.8; 37.1	31.9; 45.8
	Clearing; $n = 9$ (88)	6.79 $\pm$ 1.36	60.64 $\pm$ 7.41	44.6 $\pm$ 0.87	32.3 $\pm$ 1.77	40.7 $\pm$ 1.37
		2.75; 10.92	44.25; 189.92	41.62; 47.3	22.5; 37.1	32.3; 44.6
		5.18 $\pm$ 0.56	64.20 $\pm$ 10.24	45.1 $\pm$ 0.92	31.5 $\pm$ 2.71	41.7 $\pm$ 0.46
	2.88; 9.38	41.21; 134.08	42.4; 48.4	23.6; 37.5	39.0; 45.0	
	Kruskal-Wallis	$P < 0.001$	$P = \text{n.s.}$	$P = \text{n.s.}$	$P = \text{n.s.}$	$P = \text{n.s.}$

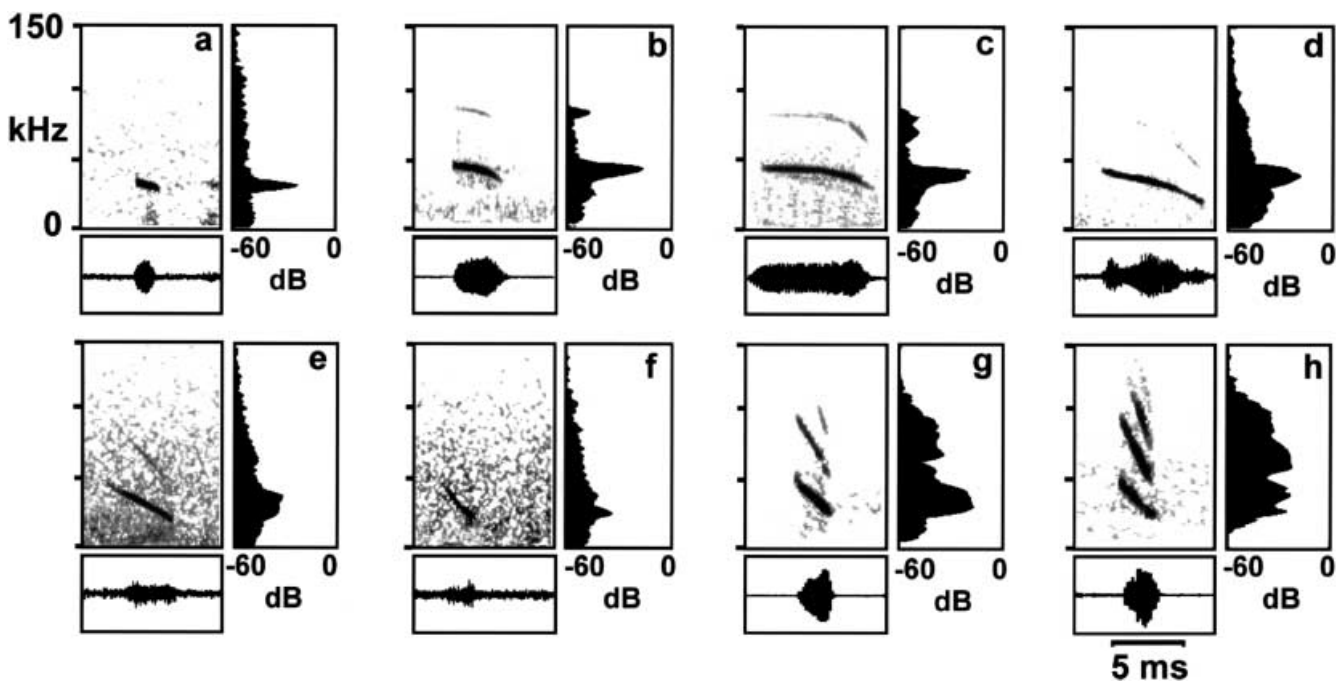
clearly distinguishable signal types. Type-1 signals were characterized by a mean duration of about 2.5 ms, and swept from about 36 kHz to about 28 kHz (Fig. 1a; Table 1). Signal parameters did not differ significantly between the recording sites except for peak frequency (Kruskal-Wallis:  $P < 0.05$ ). With a mean of 32.8 kHz peak frequency above the road and in the clearing. Type-1 signals had a rise time of 0.3 ms.

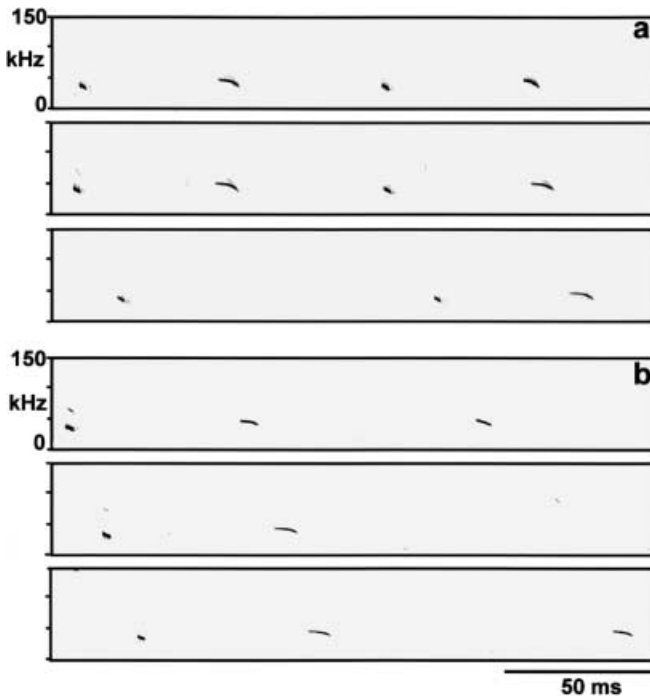
Type-2 signals (Fig. 1b, c) started with a shallowly downward frequency-modulated part at about 45 kHz, which was followed by a more steeply modulated component that ended on the average at about 32 kHz. Type-2 signals were longer than the type-1 signals, and the duration varied between the three recording sites ( $P < 0.001$ ). The longest signals, with a mean duration of

6.8 ms, were recorded above the road, compared to mean durations of 4.9 ms and 5.2 ms above the meadow and in the clearing, respectively (Table 1). The rise time in type-2 signals averaged 2.2 ms and thus was significantly longer than in type-1 signals (Mann-Whitney  $U$ ,  $P < 0.0001$ ).

In most sequences, type-1 and type-2 signals alternated regularly. In good recordings, the interval between two succeeding type-1 signals was about 115–120 ms, and the interval between type-1 and type-2 signals

**Fig. 1a–h** Echolocation signal repertoire of *Barbastella barbastellus*. Typical echolocation signals are shown as spectrograms, averaged spectra, and oscillograms. **a** type-1 signal; **b, c** type-2 signals; **d** approach signal; **e, f** buzz signals; **g** signal emitted near the roost; **h** signal emitted in the flight tent





**Fig. 2** Echolocation sequence of *B. barbastellus* searching for insects along the forest road (a) and in the clearing (b). The sequences show the alternation between type-1 and type-2 signals. Sometimes type-1 (b) or type-2 signals (a) were omitted

(about 57 ms) was generally shorter than between type-2 and type-1 (about 65 ms), indicating that a type-1/type-2 pair is emitted during each wing beat at a rate of 8.7 Hz. Sometimes the type-2 signals were omitted (Fig. 2a), and in a few sequences type-1 signals were dropped instead (Fig. 2b). Intervals twice as long between type-1 signals emitted above the road and in the clearing suggest that bats sometimes made wing beats without signal emission.

In our recordings, the type-2 signal was almost always of lower amplitude than the type-1 signal, but in a few recordings both signals had about the same recorded amplitude. Amplitude differences could either be produced by different emission sound pressure level (SPL) or could result from head movements or from a combination of both. Since type-2 signals were weaker than type-1, irrespective of whether the bat passed our

microphone to the left or the right, left-right head movements can be excluded. A stereotyped alternation of emission SPL without head movements would result in a constant amplitude difference between strong type-1 signals and succeeding faint type-2 signals, irrespective of the bat's position relative to the microphone. However, we found a change in amplitude differences, measuring 2–30 dB at peak frequency, in ten sequences when the bats passed directly above our microphone, indicating that up-down head movements at least partly explain the amplitude differences. Type-1 signals would thus be more directed towards the ground than type-2 signals.

#### *Close edge and gap situation*

While leaving the roost, *B. barbastellus* emitted short, steeply frequency-modulated echolocation signals (Fig. 1g, Table 2). Near the roost, the first harmonic swept from 49 kHz to 27 kHz in 2.8 ms. The peak frequency was 40 kHz. Bats emitted groups with two signals per wingbeat. The duration of a group measured about 115 ms, which again reflected a wingbeat rate of 8.7 Hz. With increasing distance from the background, these signals gradually changed into type-2 signals, and the bats additionally started emitting type-1 signals.

In the flight tent, signal structure was very similar to the signals emitted when leaving the roost. Calls had a mean duration of 2.3 ms. The upper frequency limit set by the vocal tract characteristics was 121 kHz (Fig. 1h). The first harmonic started at a mean frequency of 52 kHz, ended at 24 kHz, and had a mean peak frequency of 34 kHz (Table 2). Terminal and peak frequency were slightly lower than during departure from the roost (Mann-Whitney *U*:  $P < 0.05$ ). The first and second harmonic had about the same energy. *Barbastelles* emitted signal groups with mainly three steeply frequency-modulated signals. Pulse interval was thus slightly shorter than during departure (Mann-Whitney *U*:  $P < 0.05$ ). Each group again had a duration of about 115 ms. When the bats were released from the flight tent and flew away into a wide edge and gap situation, they changed signal structure from steeply frequency-modulated into alternating type-1 and type-2 signals.

**Table 2** Signal parameters of signals emitted when leaving the roost and in the flight tent. To avoid pseudoreplication, only one data point per sequence was used, which is the mean of all calls of a sequence. Data are given as mean  $\pm$  SD of these data points and

maxima and minima of single calls; *n* indicates the number of sequences; numbers in parentheses give the absolute number of signals

Recording site	Pulse duration (ms)	Pulse interval (ms)	Starting frequency (kHz)	Terminal frequency (kHz)	Peak frequency (kHz)
Near roost; <i>n</i> = 5 (53)	2.78 $\pm$ 0.35	58.75 $\pm$ 17.30	48.7 $\pm$ 21.96	26.8 $\pm$ 0.94	39.9 $\pm$ 3.40
	1.25; 3.67	24.08; 105.17	45.4; 55.5	23.6; 30.8	30.0; 44.3
Flight tent; <i>n</i> = 5 (68)	2.31 $\pm$ 0.06	38.51 $\pm$ 6.83	52.0 $\pm$ 1.77	24.2 $\pm$ 0.87	34.05 $\pm$ 4.69
	1.58; 2.96	20.25; 69.79	46.1; 58.9	22.1; 27.4	26.3; 69.0 (2nd)
Mann-Whitney <i>U</i> -test	<i>P</i> = n.s.	<i>P</i> < 0.05	<i>P</i> = n.s.	<i>P</i> < 0.05	<i>P</i> < 0.05

## Echolocation behavior when approaching prey

To describe the approach behavior, we analyzed two complete and several incomplete sound sequences of a bat foraging and approaching prey in the clearing. Prior to an approach, the bat emitted about every 115 ms the typical pairs of type-1 (duration about 2 ms, sweeping from about 34 kHz to about 28 kHz) and type-2 signals (duration 4–8 ms, sweeping from about 43 kHz to about 34 kHz). The approach sequence always developed after type-2 signals by straightening them into broadband FM signals (Fig. 1d; Fig. 3). The starting frequency was increased to about 52 kHz, and the terminal frequency decreased to about 23 kHz, resulting in a bandwidth of about 29 kHz. Only at the end of the approach sequence was signal bandwidth reduced to about 20 kHz by a decrease in starting frequency. During approach, signals were emitted in groups, with increasing numbers of pulses and a decrease of pulse duration and pulse interval. The final buzz consisted of two distinct groups. In the example shown in Fig. 3, group I of the buzz contained 13 signals of large bandwidth (Fig. 1e). Pulse duration and pulse interval decreased and reached minimal values of 2.1 ms and 7.8 ms, respectively, at the end of group I. Group II of the buzz contained 11 signals of reduced bandwidth (Fig. 1f). Within group II, pulse duration and pulse interval were not shortened further and reached minimal values

of 1.4–0.9 ms and 6.6–4.6 ms, respectively. The buzz was followed by a type-2 signal emitted after a rather long pulse interval of 466 ms.

## Discussion

### Species identification

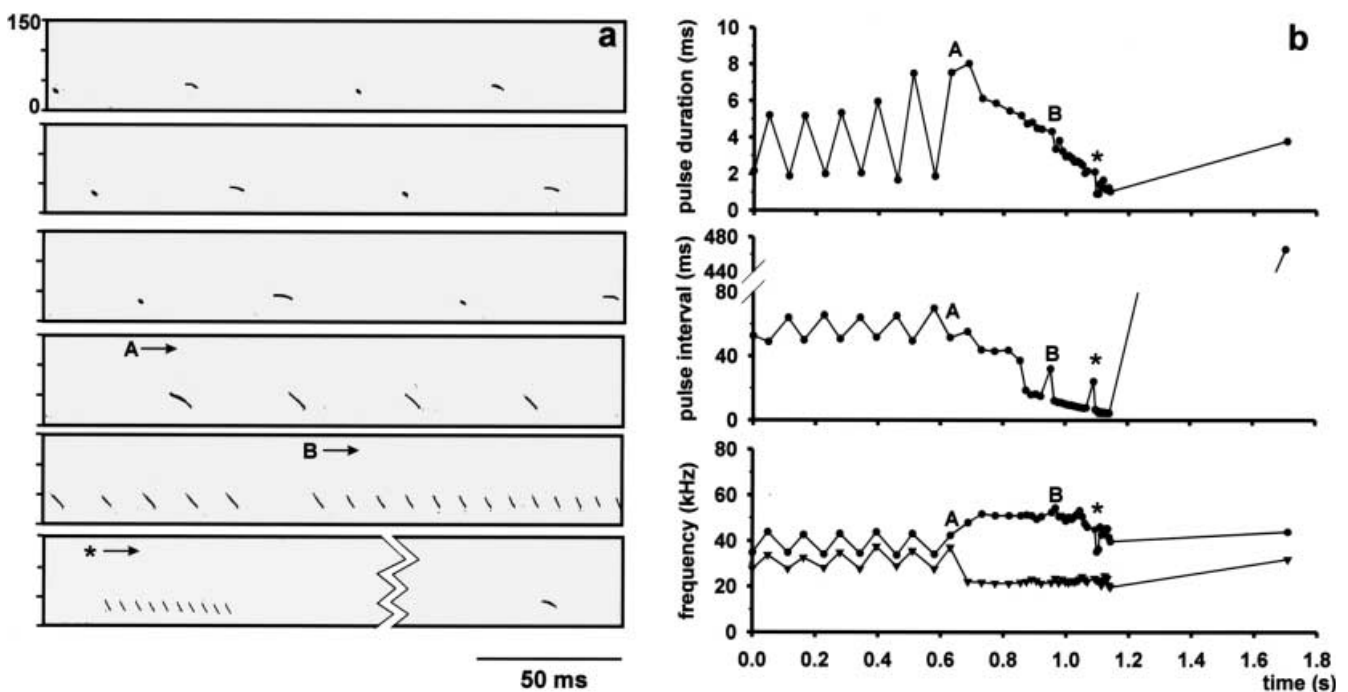
A major problem with sound recordings in the field is the identification of the bat species. Identified barbastelle bats that foraged above the meadow after leaving the roost and released individuals alternated between type-1 and type-2 signals. The two signal types also have been described by other authors (Ahlén 1981; Vaughan et al. 1997; Ahlén and Baagøe 1999; Parsons and Jones 2000) for barbastelles and are not found in any other European bat species. The bats we recorded above the road and in the clearing also emitted alternating type-1 and type-2 signals. Thus, we are confident that the bats foraging at these recording sites were *B. barbastellus*.

### Adaptive value of signal structure

#### Wide edge and gap situation

In European vespertilionids, an alternation between signal types has been reported only for *Nyctalus noctula* (e.g., Miller and Degn 1981) and *B. barbastellus*. The adaptive value of such an alternation is poorly understood. In barbastelles the mean starting frequency of all analyzed type-1 signals and the mean terminal frequency of all type-2 signals overlap by only 4 kHz. In single sequences (Fig. 3) the overlap is even smaller. Peak

**Fig. 3** **a** Echolocation sequence of *B. barbastellus* recorded in the clearing including an approach sequence with buzz. **b** Pulse duration, pulse interval and starting frequency (filled circles), and terminal frequency (filled triangles) of this sequence are plotted. *A* indicates the beginning of the approach sequence; *B* the beginning of buzz; the asterisk the beginning of part two of the buzz



frequencies of type-1 and type-2 signals differ by 7–8 kHz. Assuming that differences in signal structure reflect different functions, type-1 and type-2 signals should be suited for different perceptual tasks.

The type-2 signals of *B. barbastellus* have much in common with the search signals of other edge and gap bats. They are composed of a longer, shallowly frequency modulated narrowband component and a shorter, more steeply downward modulated component of moderate bandwidth, comparable to the narrow- and broadband signal elements of other vespertilionids. Best frequencies around 40 kHz and durations around 6 ms compare to signal parameters of other edge and gap bats. *B. barbastellus*, however, emits the narrowband component before the broadband component, which so far is unique for vespertilionids but known from other families, e.g., Emballonuridae (Kalko 1995) and Mormoopidae (Schnitzler and Kalko 1998).

Type-2 signals most likely have the same function as in other bats that combine steep modulated broadband and shallow modulated narrowband components. The longer, narrowband component greatly facilitates detection of prey, and the shorter, more steeply modulated FM component delivers information for the localization and characterization of extended background targets which is necessary for recognizing landmarks and avoiding collisions (Schnitzler and Kalko 2001). Like other bats that forage in edge and gap situations (e.g., Kalko and Schnitzler 1993; Jensen and Miller 1999; Siemers and Schnitzler 2000) *B. barbastellus* varied the duration of type-2 signals with distance to background. The longest signals were emitted above the road, where bats flew highest above ground with no objects in flight direction and where they had at least 5 m distance to vertical background targets to the side. The fact that approach signals always developed from type-2 but never from type-1 signals also indicates that type-2 signals are analogous to the search signals of other edge and gap vespertilionids. Additionally, when flying from a close edge and gap situation (e.g., close to the roost) into a wide edge and gap situation, type-2 signals always developed from the steeply frequency modulated signals by reducing the starting frequency and increasing duration. Type-1 signals, however, are inserted additionally.

Type-1 signals are rather stereotyped. They are characterized by a bandwidth of about 8 kHz, medium frequency, short duration, and a short rise time or envelope onset, and they are emitted in another direction (in our recordings probably to the ground) than the type-2 signals. This signal type is not known from any other vespertilionid bat, and its function is enigmatic. Signal duration is not changed in relation to the background situation. Type-1 signals are almost always emitted together with the longer type-2 signals, which are well suited to detect flying insects. The shorter type-1 signals are less appropriate for detection, especially for the detection of glints (Rydell et al. 1996). This suggests their main function is not the perception of insects.

Type-1 signals cover an approximately 8-kHz-wide frequency band positioned just below the approximately 12- to 15-kHz-wide frequency band of type-2 signals, with no or only small frequency overlap. Together, both signals cover in the mean a bandwidth of 16–17 kHz. It is assumed that, in the signals of edge and gap bats, the more steeply modulated signal part serves to localize and characterize background targets (Schnitzler and Kalko 1998, 2001). In *B. barbastellus*, this function may be distributed between two signals separated in time, the more steeply modulated portion of the type-2 signal and the type-1 signal. The short rise time of the type-1 signals favors localization accuracy. Because of the abrupt signal onset, the frequencies are spread out, thus increasing the effective bandwidth at the start of the signal. By that means, a sharp on-response is generated that may allow precise range measurements of background targets and thus deliver additional spatial information (Simmons et al. 1984). The distribution of a function onto two signals separated in time has the great advantage that these signals can be varied independently of each other in the direction of emission and in SPL. Indeed, the type-1 signals are emitted in another direction than the type-2 signals, which favors to characterize complex background contours separately. This is especially necessary when barbastelles exploit gaps, e.g., when foraging in clearings, like in this study, and between tree tops, a behavior described by Sierro and Arlettaz (1997) and Sierro (1999), who found *B. barbastellus* foraging exclusively 2–4 m above tree crowns and pursuing insects in dives. Besides, the emission SPL of type-2 signals might also be weaker than that of type-1 signals. This could be interpreted in terms of a clutter-rejection strategy.

The alternation between signal types also has been described by other authors (Ahlén 1981, 1990; Vaughan et al. 1997; Ahlén and Baagøe 1999; Parsons and Jones 2000), but data were based only on single calls. The values given for the type-1 signals by Parsons and Jones (2000) match our type-1 values very well. This is also true for the frequency parameters of the type-2 signals but not for signal duration. The longer durations emitted by the bats in our study are most likely due to a more open habitat structure.

#### *Close edge and gap situation*

When flying close to the background, e.g., when departing from the roost and when flying in the flight tent, bats emit short, steeply frequency-modulated signals consisting of two to three harmonics. The energy is almost equally distributed, thus increasing the effective bandwidth of the signal. The narrowness of the flight tent accounts for the shorter signal duration, pulse interval and the lower terminal frequency in this recording situation. Similar signals have been described from recordings of *B. barbastellus* in the lab (Ahlén 1981; Konstantinov and Makarov 1981; Jones 1993). Short broadband signals are well suited for spatial orientation

where an exact description of the background is necessary (Schnitzler and Henson 1980; Schnitzler and Kalko 1998) and are also found in other bat species confronted with the same perceptual task.

### Approaching prey

When approaching and closing in on a flying insect, aerial insectivorous bats face a similar challenge in localizing the constantly moving prey. The approach sequences of *B. barbastellus* are thus similar to those of other vespertilionids and are characterized by a distinct change in signal structure (e.g., Griffin et al. 1960; Kalko and Schnitzler 1998). In contrast to the species of the genera *Pipistrellus* and *Myotis*, barbastelles do not lower the terminal frequency in the second group of the buzz.

### Conclusion

Signal structure and foraging behavior indicate that barbastelle bats forage mainly in edge and gap situations and therefore belong to the guild of background-cluttered space aerial insectivores. The emission of two different signal types has the great advantage that both signals can be varied independently of each other in the direction of emission and in SPL. Type-2 signals most likely have the same function as in other edge and gap foragers that combine steep modulated broadband and shallow modulated narrowband components. Additionally, type-1 signals might facilitate the characterization of complex background contours, as necessary when foraging in clearings, above tree crowns, or above steep, crumbling cliffs.

**Acknowledgements** We are most grateful to Miriam Lutz and Fabio Bontadina for their help in Switzerland. We also wish to thank Ingrid Kaipf for technical assistance and Elisabeth Kalko for comments on an earlier draft of the manuscript. This research was supported by grants from the Deutsche Forschungsgemeinschaft to H.-U. Schnitzler (SFB 307 and Forschergruppe: Wahrnehmung und Agieren im Raum). The research reported here complies with the current laws of Switzerland and Germany. Investigations were carried out under the license of the Landesumweltamt Brandenburg.

### References

- Ahlén I (1981) Identification of Scandinavian bats by their sounds. Swedish University of Agricultural Sciences, Department of Wildlife Ecology, Report 6, Uppsala
- Ahlén I (1990) Identification of bats in flight. Swedish Society for Conservation of Nature and the Swedish Youth Association for Environmental Studies and Conservation, Stockholm
- Ahlén I, Baagøe HJ (1999) Use of ultrasound detectors for bat studies in Europe: experiences from field identification, surveys, and monitoring. *Acta Chiropterologica* 1:137–150
- Beck A (1995) Fecal analyses of European bat species. *Myotis* 32/33:109–119
- Benzal J, Paz O de, Gisbert J (1991) Los murciélagos de la Península Iberica y Baleares, patrones biogeográficos de su distribución. In: Benzal J, Paz O de (eds) Los murciélagos de España y Portugal. Ministerio de Agricultura, Pesca y Alimentación, Madrid, pp 37–92
- Denzinger A, Kalko EKV, Jones G (2001) Ecological and evolutionary aspects of echolocation in bats. In: Thomas J, Moss C, Vater M (eds) Advances in the study of echolocation. University of Chicago Press, Chicago (in press)
- Fenton MB (1990) The foraging behavior and ecology of animal-eating bats. *Can J Zool* 68:411–422
- Griffin DR, Webster FA, Michael CR (1960) The echolocation of flying insects by bats. *Anim Behav* 8:141–154
- Jensen ME, Miller LA (1999) Echolocation signals of the bat *Eptesicus serotinus* recorded using a vertical microphone array: effect of flight altitude on searching signals. *Behav Ecol Sociobiol* 47:60–69
- Jones G (1993) Flight morphology, flight performance and echolocation in British bats. In: Kapteyn K (ed) Proceedings of the 1st European bat detector workshop. Netherlands Bat Research Foundation, Amsterdam, pp 59–78
- Kalko EKV (1995) Echolocation signal design, foraging habitats and guild structure in six Neotropical sheath-tailed bats (Emballonuridae). *Symp Zool Soc Lond* 67:259–273
- Kalko EKV, Schnitzler H-U (1993) Plasticity in echolocation signals of European pipistrelle bats in search flight: implications for habitat use and prey detection. *Behav Ecol Sociobiol* 33:415–428
- Kalko EKV, Schnitzler H-U (1998) How echolocating bats approach and acquire food. In: Kunz TH, Racey PA (eds) Bat biology and conservation. Smithsonian Institution Press, Washington DC, pp 197–204
- Konstantinov AI, Makarov AK (1981) Bioacoustic characteristics of the echolocation system of the European wide-eared bat *Barbastella barbastella*. *Biophysics* 26:1112–1118
- Lutz M (1995) Erste Wochenstubenkolonie der Mopsfledermaus *Barbastella barbastellus* im Kanton Graubünden. *Fledermausanzeiger* 44:11
- Miller LA, Degn HJ (1981) The acoustic behavior of four species of vespertilionid bats studied in the field. *J Comp Physiol A* 142:67–74
- Neuweiler G (1989) Foraging ecology and audition in echolocating bats. *Trends Ecol Evol* 4:160–166
- Neuweiler G (1990) Auditory adaptations for prey capture in echolocating bats. *Physiol Rev* 70:615–641
- Obrist MK (1995) Flexible bat echolocation: the influence of individual, habitat and conspecifics on sonar signal design. *Behav Ecol Sociobiol* 36:207–219
- Parsons S, Jones G (2000) Acoustic identification of twelve species of echolocating bats by discriminant function analysis and artificial neural networks. *J Exp Biol* 203:2641–2656
- Poulton EB (1929) British insectivorous bats and their prey. *Proc Zool Soc Lond* 19:227–303
- Richarz K (1989) Ein neuer Wochenstubennachweis der Mopsfledermaus *Barbastella barbastellus* (Schreber, 1774) in Bayern mit Bemerkungen zu Wochenstubenfunden in der BRD und DDR sowie zu Wintervorkommen und Schutzmöglichkeiten. *Myotis* 27:71–80
- Rydell J, Bogdanowicz W (1997) *Barbastella barbastellus*. *Mamm Species* 557:1–8
- Rydell J, Natuschke G, Theiler A, Zingg PE (1996) Food habits of the barbastelle bat *Barbastella barbastellus*. *Ecography* 19:62–66
- Schnitzler H-U, Henson OW Jr (1980) Performance of airborne animal sonar systems: I. Microchiroptera. In: Busnel RG, Fish JF (eds) Animal sonar systems. Plenum Press, New York, pp 109–181
- Schnitzler H-U, Kalko EKV (1998) How echolocating bats search and find food. In: Kunz TH, Racey PA (eds) Bat biology and conservation. Smithsonian Institution Press, Washington DC, pp 183–196
- Schnitzler H-U, Kalko EKV (2001) Echolocation by insect-eating bats. *Bioscience* (in press)
- Siemers BM, Schnitzler H-U (2000) Natterer's bat (*Myotis nattereri*, Kuhl 1818) hawks for prey close to vegetation using echo-

- location signals of very broad bandwidth. *Behav Ecol Sociobiol* 47:400–412
- Sierro A (1999) Habitat selection by barbastelle bats (*Barbastella barbastellus*) in the Swiss Alps (Valais). *J Zool (Lond)* 248:429–432
- Sierro A, Arlettaz R (1997) Barbastelle bats (*Barbastella* spp.) specialize in the predation of moths: implications for foraging tactics and conservation. *Acta Oecologica* 18:91–106
- Simmons JA, Kick SA, Lawrence BD (1984) Echolocation and hearing in the mouse-tailed bat, *Rhinopoma hardwickei*: acoustic evolution of echolocation in bats. *J Comp Physiol A* 154:347–356
- Spitzenberger F (1993) Die Mopsfledermaus (*Barbastella barbastellus* Schreber, 1774) in Österreich – *Mammalia Austriaca* 20. *Myotis* 31:111–153
- Stebbins R (1988) Conservation of European bats. Helm, London
- Stebbins R (1991) Genus *Barbastella*. In: Corbet GB, Harris S (eds) *The handbook of British mammals*, 3rd edn. Blackwell Scientific Publications, Oxford, pp 128–130
- Stebbins R, Griffith F (1986) Distribution and status of bats in Europe. Institute of Terrestrial Ecology, Monks Wood Experimental Station, Huntingdon, Great Britain
- Vaughan N (1997) The diets of British bats (Chiroptera). *Mammal Rev* 27:77–94
- Vaughan N, Jones G, Harris S (1997) Identification of British bat species by multivariate analysis of echolocation call parameters. *Bioacoustics* 7:189–207
- Zingg PE (1994) Neue Vorkommen der Mopsfledermaus (*Barbastella barbastellus* Schreber, 1774) im Berner Oberland. *Mitt Naturwiss Gesell Thun*:121–132