

Aerial hawking and landing: approach behaviour in Natterer's bats, *Myotis nattereri* (Kuhl 1818)

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Summary

We compared the flight and echolocation behaviour of a vespertilionid bat (*Myotis nattereri*) approaching a large stationary or a small moving target. Bats were trained to either land on a landing grid or to catch a moving tethered mealworm. When closing in on these two targets, the bats emitted groups of sounds with increasing number of signals and decreasing pulse interval and duration. When pursuing the mealworm, the approach phase always ended with a terminal group consisting of buzz I and buzz II. When landing, the bats emitted either a terminal group consisting of buzz I alone, with one or two extra pulses, or a group

consisting of buzz I and buzz II. In all situations, buzz I ended on average between 47–63 ms prior to contact with the target of interest, which is approximately the reaction time of bats. Therefore, the information collected in buzz II does not guide the bats to the target. The relevant part of the approach phase to reach the target ends with buzz I. The basic sound pattern of this part is rather similar and independent of whether the bats approach the large stationary or the small moving target.

Key words: *Myotis nattereri*, approach, bat, buzz, echolocation.

Introduction

All species of microchiropteran bats rely on echolocation for spatial orientation, and many of them also use it for prey acquisition (see Schnitzler et al., 2003). Both situations involve a common task: the approach to specific objects such as landing sites, obstacles or prey.

The echolocation tasks during an approach can differ. When bats perform a spatial orientation task, the target they approach is usually stationary and rather large, e.g. when landing on a wall or avoiding a tree. Aerial hawking and trawling foragers use echolocation to approach rather small prey, which are often moving and generate echoes that are usually separated from background clutter (e.g. Moss and Surlykke, 2001; Ghose and Moss, 2003). In contrast, gleaning foragers mostly use prey-generated cues to find the source of food and use echolocation only to guide their approach to the stationary and generally rather large site with prey (Swift and Racey, 2002). In this case the prey echo is buried in the background clutter.

It is evident that the echolocation task of a bat approaching a landing site and of a gleaner approaching a site with food is rather similar. In bats pursuing flying insects, however, the targets of interest move and are rather small. This raises the question whether the differences in the echolocation tasks are reflected in differences in the approach behaviour.

Most studies on the approach behaviour of bats have concentrated on aerial-hawking foragers. After detection they typically switch from search- to target-oriented flight, with head and ears pointing toward the insect. At this moment the echolocation behaviour changes from search to approach phase.

Previous studies have defined the onset of the approach phase as the first pulse emitted in reaction to the target (Griffin et al., 1960; Kalko and Schnitzler, 1989).

The approach phase is characterized by a reduction in pulse duration, pulse interval and the presence of groups containing increasing number of pulses (Griffin et al., 1960; Schnitzler et al., 1987; Schnitzler and Kalko, 2001; Schnitzler et al., 2003). Several authors also observed a decrease in the sound pressure level of the emitted calls during the approach (e.g. Hartley, 1992; Boonman and Jones, 2002).

Within the approach phase we distinguish an 'initial part' and a 'terminal part'. The terminal part varies in its pattern between species (Schnitzler and Kalko, 2001; Schnitzler et al., 2003; Denzinger and Schnitzler, 2004). In aerial hawking or trawling foragers the terminal part consists of a group of sounds that contains many pulses. In foraging vespertilionids the terminal group or buzz can be subdivided in two parts, buzz I and buzz II (Kalko and Schnitzler, 1989; Surlykke et al., 1993). In buzz II signal duration is minimal, pulse intervals remain constant at very low values around 6 ms and, in some species, frequency is also lowered (Griffin et al., 1960; Siemers and Schnitzler, 2000).

The approach behaviour to large stationary targets such as landing sites or sites with food is less studied than the approach to small moving prey. The few published studies indicate that in the approach phase, signal duration and pulse interval are reduced and signals are emitted in groups. During the approach to large targets, the repetition rate remains lower and gleaners do not produce a distinct terminal group consisting of buzz I

and buzz II (Rydell, 1990; Faure and Barclay, 1994; Tian and Schnitzler, 1997; Thies et al., 1998; Schnitzler and Kalko, 2001).

The echolocation signals of the approach phase guide the bat to the chosen target or site. The distinct increase of repetition rate and the change to shorter broadband signals found in aerial hawking bats has been interpreted as an adaptation for exact localization and tracking of moving prey in space. It was also suggested that the increase in repetition rate enhances the information flow necessary to control last instant changes in the prey's position (Schnitzler and Kalko, 2001). The lower repetition rate and the lack of a distinct terminal group in passive gleaners were explained as an adaptation to the less challenging task of approaching a stationary target (Schnitzler and Kalko, 2001).

The aim of the present study was to compare the approach behaviour within one species (*Myotis nattereri* Kuhl 1818) to small moving prey and to a large stationary landing site. Our working hypothesis was that the difficulty of the echolocation task is reflected in the echolocation behaviour. We expected that the approach phase of *M. nattereri* pursuing a small and moving mealworm should end with a distinct terminal part consisting of buzz I and buzz II, as already described (Siemers and Schnitzler, 2000; Siemers and Schnitzler, 2004) for bats catching insects. In contrast to this behaviour we assumed that landing bats would emit an approach phase having a less distinct terminal part without buzz II.

Materials and methods

Animals

We conducted the experiments using six adult male *M. nattereri* (Kuhl 1818), captured near Berlin (license from the Senatsverwaltung für Stadtentwicklung des Landes Berlin, Germany) and housed under standardized conditions (16:8 h light:dark cycle, $22\pm 2^\circ\text{C}$ temperature and $65\pm 5\%$ humidity). They were kept on a diet of mealworms (larvae of *Tenebrio molitor*) supplemented with vitamins (Nutrical®, Albrecht, Germany) and minerals (Korvimin®, WDT, Hanover, Germany) and had free access to freshwater. Food was given only during training and experimental sessions. We began experiments soon after the light was turned off to simulate the natural conditions of foraging time after dusk.

Experimental set-up

We conducted all experiments in a flight room ($3.6\text{ m}\times 6.0\text{ m}\times 2.8\text{ m}$) illuminated only by two infrared stroboscopic units. Two nets along the length axis separated a corridor of width 1.2 m, in which the bats either flew from a starting position to a landing grid or caught a tethered mealworm. The walls and the floor of the room were covered with acoustic foam to reduce reverberations. To exclude possible environmental influences on our results due to the order of the tasks, we trained half of the bats to perform the landing task first and the other half to catch the prey first.

Stationary target

Bats were trained to start from the hand and fly in the corridor to a vertical grid ($8.5\text{ cm}\times 10\text{ cm}$) (stationary target) on the other side of the room. The platform was always situated in the same

place during training and recording sessions. After the bats had learned the task we recorded their echolocation and flight behavior while approaching the stationary landing grid. An ultrasonic microphone was placed behind the landing platform to pick up the echolocation signals emitted by the bats in each trial.

Moving target

To study the behavior of bats approaching a moving target, we trained them to start from the hand at one end of the corridor and catch a tethered mealworm (moving target) that was hanging from the ceiling, always at the same spot, attached to a thread about 1.2 m below the ceiling, corresponding to a height of 1.6 m from the floor. It was rotated by a motor in a circle with a radius of about 10 cm and rotation period about 1 s. The microphone was mounted on a tripod approximately 40 cm behind the center of the rotation circle.

Data recording and analysis

We recorded the echolocation and flight behavior of the bats using custom-made equipment (PCTape, Department of Animal Physiology, University of Tübingen, Germany) that enables synchronization of the video and sound recordings. The echolocation signals were picked up using a custom-made ultrasonic microphone [flat frequency response ($\pm 3\text{ dB}$) between 18 and 200 kHz], digitized with a sampling rate of 480 kHz and a resolution of 16 bits, and stored as wav-files. The bats' flight behavior was recorded simultaneously with the sound recordings using two IR-cameras (Sanyo IRP, Japan; 50 frames s^{-1}) placed in two upper corners of the room. Each half frame was illuminated for 1 ms by two infrared stroboscopic units mounted on the floor. Video chunks were written onto the corresponding sound files, thus allowing the synchronization of sound and video recordings. The video images were stored on Panasonic DVC Mini videotapes using two Sony camcorders (TRV 30E).

After digitizing, the video recordings were saved as avi-files and analyzed using commercial software (Simi Motion® 6.5, SIMI Reality Motion Systems GmbH, Unterschleißheim, Germany) in order to reconstruct the bats' 3-D flight path (reconstruction error $\pm 5\text{ cm}$) and velocity. The position of the microphone, the landing platform and the mealworm were also reconstructed in a similar fashion.

The echolocation signals were analyzed using custom-made software (Selena, University of Tübingen, Germany). Signals were displayed as color spectrograms (FFT 256, Hann window) with a dynamic range of 60 dB. Due to auto-padding and interpolation in time we reached a resolution of $\Delta t=0.032\text{ ms}$ and $\Delta f=0.942\text{ kHz}$. Further analysis was conducted using a custom routine (MATLAB 6.5, MathWorks, Natick, MA, USA) written by Peter Stilz (University of Tübingen). Beginning and end of the calls were defined at -25 dB below best amplitude.

We analyzed ten trials of every animal performing each task. Ten distance classes of varying size were defined to get a homogeneous distribution of calls. The values assigned for distance corresponded to the middle of each bin (0–0.1 m, 0.05 m; 0.1–0.2 m, 0.15 m; 0.2–0.3 m, 0.25 m; 0.3–0.4 m, 0.35 m; 0.4–0.55 m, 0.475 m; 0.55–0.7 m, 0.625 m; 0.7–1 m, 0.85 m; 1–1.5 m, 1.25 m; 1.5–2.5 m, 2 m; 2.5–3.5 m, 3 m). The

distance classes were attributed to either search or approach phase. We defined the beginning of the approach phase when the averaged pulse duration of a distance class differed significantly from the averaged duration in the 3 m class.

Within the approach phase we distinguished an initial and a terminal part. We considered the terminal part as the last group of consecutive pulses, together with the one or two extra pulses that were emitted in some cases before contact occurred. To determine the onset of the terminal part we analyzed the interval between pulses from the end of the group to the beginning. The onset of this last group was reached when the first pulse interval was above 20 ms.

Sound parameters analyzed for the search and the initial part of the approach phase were pulse duration and interval, starting, best and terminal frequency, bandwidth, sweep rate and pulse interval within groups. The sound pressure level (SPL) of the calls was also calculated for a distance of 10 cm from the bat's mouth, corrected only for spherical spreading. We used the sweep rate to determine pulse duration in order to make this parameter independent from the quality of the sound recordings. Therefore we correlated sweep rate with pulse duration for all calls with amplitudes above -25 dB. The equation that fitted best was used to estimate the pulse duration using the sweep rate only.

Parameters analyzed for the terminal part of the approach phase were number of calls contained in buzz I and buzz II, duration of terminal part, buzz I, and buzz II time to landing at the end of buzz I and at the last call of the sequence. Further pulse duration, pulse interval, starting frequency, best frequency and terminal frequency of the echolocation signals were measured.

Statistics

For the initial part of the approach phase, we averaged signal parameters within a distance class for each animal. In order to calculate the means for all animals and conduct statistical analysis we averaged the values of the ten sequences for each animal.

We performed repeated-measures analysis of covariance (RM-ANCOVA) to test if the pattern of the pulse duration and pulse interval in relation to distance to target varies between tasks. This analysis was conducted only with the data collected from distances <0.7 m to the target, to ensure that the bats were in the approach phase for both tasks and that the distance course was linear. For estimation of emission SPL we linearized the values belonging to distance classes <0.7 m by calculating the logarithms of the distance and then also carried out RM-ANCOVA.

To address the question of how the frequency parameters change while closing in on stationary and moving targets we applied repeated-measures two-way analyses of variances (ANOVA) (Zar, 1999). For this, data were divided into two groups for each task: distances from 3.5 to 1.5 m represented the search phase, and from 0.7 to 0.1 m the approach phase. Tukey tests were used to analyze significant differences between treatments.

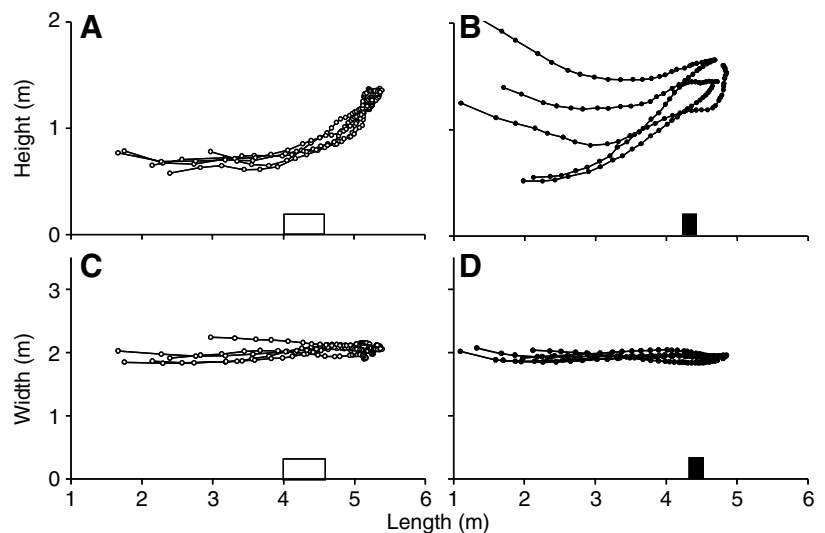


Fig. 1. Side (A,B) and top view (C,D) of the trajectories of one bat while performing the landing (A,C) and the catching task (B,D). Filled and open boxes on the x-axis represent the distance class corresponding to the beginning of the approach phase in all bats.

Results

Flight behavior

Bats that performed the landing task flew on a stereotyped trajectory towards the landing site. Except for one animal, all bats flew between 50 and 100 cm above the ground. At a distance of 1–1.5 m from the landing platform they started to fly upward until they reached the target (see Fig. 1A,C). While landing, they turned upside down and gripped the grid.

Bats that had to catch a moving mealworm flew straight towards the area in the flight room where they had encountered mealworms before. However, their trajectories were more variable (see Fig. 1B,D). The bats always used a pouch formed with their tail membrane to catch the tethered insects.

In search phase bats flew with the same velocity at both tasks but when they closed in on the target, their flight speed diminished faster in the case of the landing situation before they came to a stop (Fig. 2). Prey was caught on the wing.

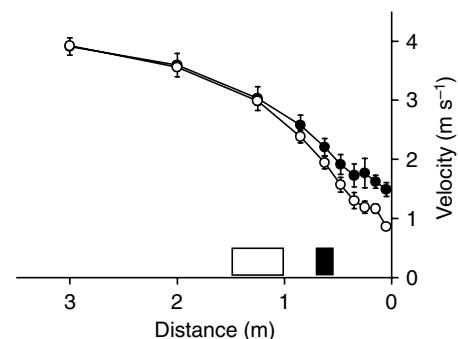
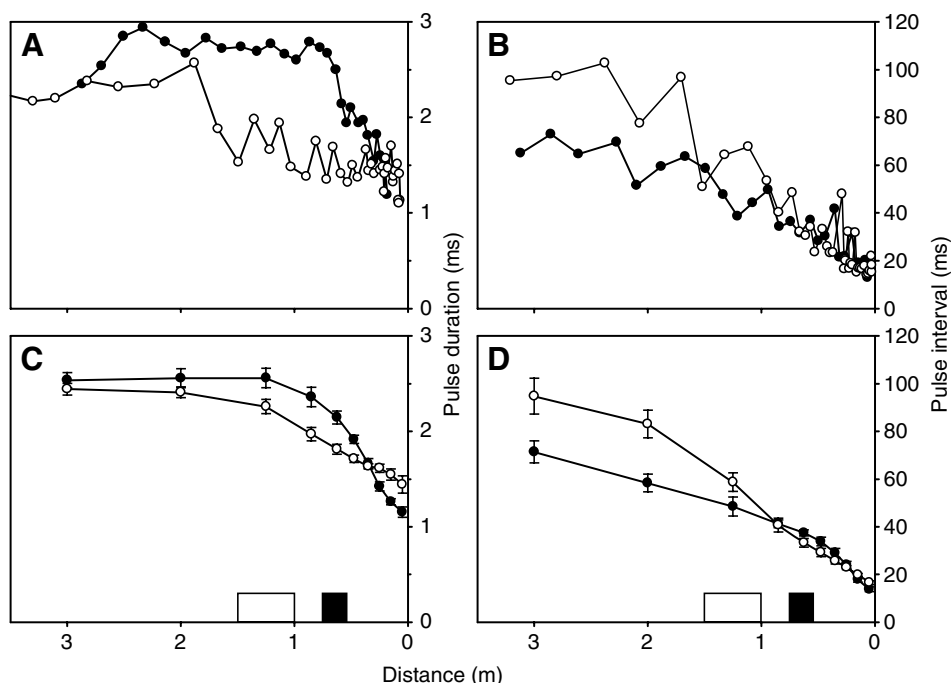


Fig. 2. Flight speed of the bats while approaching the landing platform (open circles) and the moving mealworm (filled circles). Values are means \pm s.e.m. Filled and open boxes on the x-axis indicate the beginning of the approach phase.

Fig. 3. Pulse duration and pulse interval against distance to target shown for typical single trials (A,B) and as mean \pm s.e.m. values (C,D). Open circles represent the landing task, filled circles the catching task. Filled and open boxes on the x-axis indicate the beginning of the approach phase.



Echolocation behavior

Search phase

The echolocation behavior in search phase differed significantly in pulse interval, starting frequency and emission SPL (see Fig. 3D, Fig. 4A,B, respectively). We found no differences in pulse duration between tasks (Fig. 3C). Bats flying towards the area with the moving mealworm emitted echolocation signals with an average pulse interval ranging between 71 and 41 ms, which was shorter than the averaged pulse interval (95–83 ms) emitted while flying towards the stationary landing platform. The average starting frequency of 130 ± 7 kHz when flying to the moving mealworm was significantly lower than while searching for the landing grid (140 ± 1 kHz) (ANOVA, $F_{1,15}=20.63$, $P=0.0004$, Fig. 4A). Best frequency and terminal frequency did not differ between tasks (Fig. 4A, ANOVA, $F_{1,15}=20.47$, $P=0.0004$; Tukey's test, $P>0.05$; $F_{1,15}=1.14$, $P=0.3$, respectively). Emission SPL during the search phase was much higher when bats were searching for the moving insect (111 ± 6 dB) than while looking for the landing platform (101.7 ± 0.5 dB) (Fig. 6B).

Approach phase

Initial part. The initial part of the approach phase begins with a reaction to the target of interest and ends with the last group before buzz I. In bats approaching a moving mealworm the approach phase started at a distance of 0.7–0.55 m from the target; when the animals approached the stationary landing grid it started at a distance of 1.5–1 m from the grid (Fig. 3C). The beginning of the approach phase also coincided with the onset of the change in the flight behavior, being clearer in the landing task because of the more stereotyped trajectories (Fig. 1).

Within the initial part, pulse duration (ANCOVA, $F_{1,63}=443.72$, $P<0.0001$), pulse interval (ANCOVA, $F_{1,63}=631.24$, $P<0.0001$) and emission SPL (ANCOVA, $F_{1,51}=36.10$, $P<0.0001$) were reduced as a function of distance to the target, i.e. the closer the bats got to the landing platform or moving mealworm the shorter were the calls, the higher the repetition rate and the lower was the emission SPL (Fig. 3C,D, Fig. 4B). Pulse duration changed faster (ANCOVA, $F_{1,63}=113.18$, $P<0.0001$) while approaching a moving target whereas the other parameters changed in a similar way in both tasks (see Fig. 3, Fig. 4B).

During the initial part the echolocation calls were often arranged in groups containing increasing numbers of pulses

while approaching the target of interest. Additionally, the pulse interval within these groups decreased with increasing number of pulses per group (Fig. 3B, Fig. 5, Table 1). This was also reflected in the decreasing lower boundary of the pulse interval with decreasing distance to the target in Fig. 6. The switching between larger intervals between groups and shorter intervals

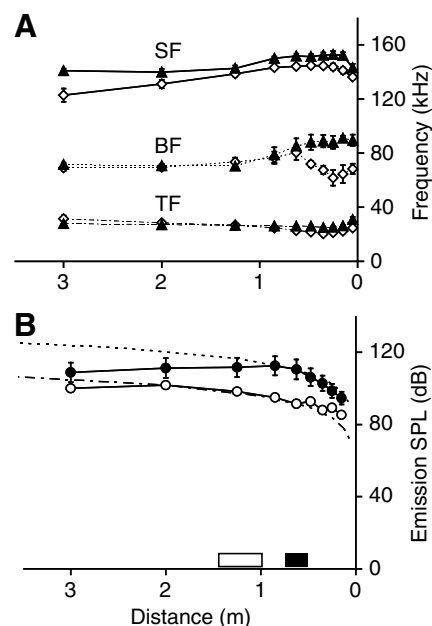


Fig. 4. (A) Starting (SF), best (BF) and terminal frequency (TF) against distance. (B) Emission SPL 10 cm in front of the bat. Values are means \pm s.e.m. Emission SPL values are represented as a function of the distance to the target. Grey lines represent the expected decrease for a reduction of 6 dB per halving of the distance. Filled and open boxes on the x-axis indicate the beginning of the approach phase. Open symbols, landing task; filled symbols, catching task.

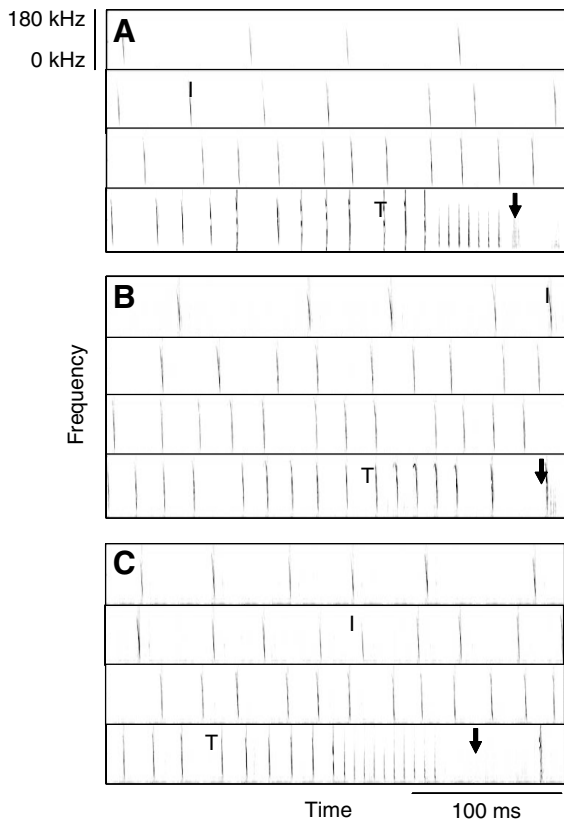


Fig. 5. Sonograms of a typical landing sequence with a buzz II (A) and without a buzz II (B), and a catch with buzz II (C). The arrow indicates the contact of the bat with the landing platform or mealworm. 'I' indicates the beginning of the initial part and 'T' the onset of the terminal part of the approach phase.

Table 1. Within-group pulse interval of different groups in the initial part of the approach phase

Groups	Landing		Catching
	Buzz I + extra pulse	Buzz I + buzz II	Buzz I + buzz II
2	33±3	30±2	35±2
3	23±1	22±1	24±1
4	17.9±0.6	17.0±0.6	20±1
More	15.6±0.5	14.2±0.6	20±0.8

Values (ms) are means ± s.e.m. (N=6).

within groups was responsible for the rather wide distribution of pulse intervals throughout the whole initial part. In the landing task the within group interval started at about 33 ms in groups containing two signals and ended at about 16 ms in the last group of the initial phase. In the prey catching task the corresponding values decreased from about 35 ms to 20 ms (Fig. 6, Table 1).

Some of the frequency parameters changed when bats switched from search to approach phase (see Fig. 4A). In the approach phase starting frequency was higher in both tasks (ANOVA, $F_{1,15}=28.96$, $P<0.0001$; Tukey's test, $P<0.05$ for both cases). Best frequency increased only in the landing task (ANOVA, $F_{1,15}=13.38$, $P=0.0023$, Tukey's test, $P<0.05$) and terminal frequency was lower in the prey catching task (ANOVA, $F_{1,15}=26.29$, $P=0.0001$, Tukey's test, $P<0.05$). Comparison between the tasks in the initial approach revealed a higher starting frequency (ANOVA, $F_{1,15}=20.63$, $P=0.0004$), higher best frequency (ANOVA, $F_{1,15}=20.47$, $P=0.0004$, Tukey $P<0.05$) in the landing task but no significant difference in the terminal frequency (ANOVA, $F_{1,15}=1.14$, $P=0.3$).

We also measured the pulse interval within groups for both tasks (Table 1). Within groups of the same number of signals, pulse interval was similar.

Terminal part. Before contacting the target, the bats switched to the terminal part of the approach phase, which consists of the last group of consecutive pulses together with the one or two extra pulses that were occasionally emitted, and ended with the contact of the target. The terminal part differed between the two tasks: when approaching a moving mealworm, bats produced a terminal part consisting always of buzz I and buzz II (Fig. 5C). When landing on the grid, the bats either emitted a terminal part consisting of buzz I alone and one or two extra pulses or a terminal part containing buzz I and buzz II (Fig. 3A,B). Individual bats used both strategies in different proportions, e.g. in some bats buzz I was almost

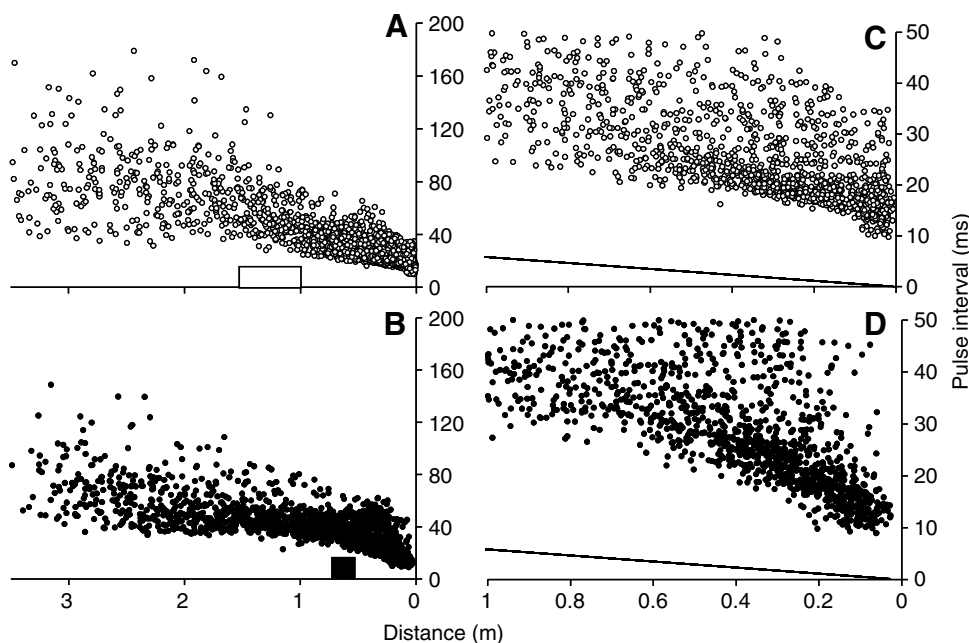


Fig. 6. Pulse interval against distance for all calls of the initial part and buzz I for the landing (open circles; A,C) and the catching task (filled circles; B,D). The black line represents the two-way travel time. Filled and open boxes on the x-axis indicate the beginning of the approach phase. B and D show a close-up of the signals during the last m travelled before contact.

always followed by a buzz II (bat 6, 74%; bat 5, 67%); others added a buzz II in about half of the cases (bat 1, 47%), and one bat almost never emitted a buzz II (bat 3: 2%, bat 2, 10%; bat 4, 13%). If buzz II was present while landing, at least part of it was emitted when the bats turned upside down to land on the platform.

The terminal parts of the three situations described differed in total duration, duration of buzz I and buzz II, and in the number of pulses emitted during buzz I and buzz II. In bats landing without buzz II but with 1–2 extra pulses, the terminal parts were rather long (142 ms), with a long buzz I (95 ms) that contained 7 pulses in average (Table 2, Table 3). In bats landing with the strategy ending with buzz II, buzz I contained fewer pulses (4±1). However, the length of the buzz I in both strategies was about the same. During landing bats always ended buzz I at a similar time interval before the contact with the landing grid, on average 47–50 ms (Table 3). However, there was a tendency for buzz I to start earlier (163±17 ms) if the terminal part lacked a buzz II compared to a buzz I followed by buzz II (138±17 ms).

For bats catching a moving mealworm the terminal part always contained both buzz I and buzz II, consisting on average of 5.3 and 8.3 pulses, respectively. The total duration of the terminal part in landing bats was the same whether or not buzz II was present (Table 3; 142 and 138 ms). In bats catching a mealworm, buzz I lasted 66 ms; this duration and the number of pulses contained in buzz I did not differ from the duration and number of signals in buzz I of animals that landed with buzz II (Table 2, Table 3). The duration (53 ms) and number of pulses (8) of buzz II in bats catching a moving mealworm were higher than in bats approaching the landing platform with buzz II (duration, 33 ms; number of pulses, 4). In both tasks the time from end of buzz I to contact was rather similar (between 47 ms and 63 ms, Table 3). The sound parameters characterizing buzz I and buzz II were rather similar except for the frequency parameters in buzz I, which were similar to the differences in the initial part (Table 2).

Discussion

The echolocation behavior of bats depends on the type of echolocation task that has to be performed (Schnitzler et al., 2003). In this study we compared the flight and echolocation behavior of *M. nattereri* when landing on a grid or catching a tethered mealworm. Our working hypothesis was that the approach to a stationary and rather large landing site would be less difficult than the catching of a moving and rather small

Table 3. Duration of the terminal part and its components

	Landing without buzz II	Landing with buzz II	Catching
Terminal part	142±9	138±20	129±8
Buzz I	95±9	88±23	66±9
Buzz II		33±4	53±5
Time to contact from the end of buzz I	47±4	50±7	63±9

Values (ms) are means ± s.e.m. (N=6).

mealworm, and that this difference between the two tasks would be reflected in differences in the search and the approach phase of the echolocation behavior.

It is important to notice that the bats had performed the tasks hundreds of times before the experimental sessions. We are aware that bats may also have used spatial memory to reach the landing site or the area in which the mealworm was presented. However, we consider that the bats need the described minimum of echolocation information when landing or catching a mealworm.

Search phase

The term ‘search phase’ was introduced to describe the echolocation behavior of foraging bats when they search for insects (Griffin et al., 1960). Strictly speaking, signals emitted during transfer flight should not be termed search signals. However, the echolocation behavior of bats in transfer flight, e.g. when they fly from their roosts to foraging areas, is rather similar to the behavior of foraging bats in search phase (Schaub and Schnitzler, 2007). Therefore, we assigned all signals in the landing task to search phase, as long as the bats did not indicate they had detected the target of interest.

During search flight to the landing grid, bats emitted single pulses more often, resulting in larger average pulse intervals than in search flight towards the mealworm, where they more often emitted groups of two calls with shorter pulse intervals. Since the available space for flying and maneuvering was the same in both situations, we infer that the bats’ expectation of either the large stationary landing site or the small moving mealworm may explain the difference. The higher repetition rate while searching for the mealworm might indicate the need for a higher information flow when searching for a moving target. Signals also differed in

Table 2. Sound parameters of the calls emitted in the terminal part

	Landing				Catching	
	Buzz I	Extra pulse	Buzz I	Buzz II	Buzz I	Buzz II
Number of calls	7±1	1.5±0.1	4±2	4±1	5.3±0.4	8.3±0.5
PD (ms)	1.33±0.03	1.18±0.06	1.16±0.04	0.61±0.02	1.25±0.06	0.53±0.04
PI (ms)	16.0±0.2		13.8±0.4	6.70±0.03	14.3±0.2	6.3±0.1
SF (kHz)	146±1	130±8	138±5	35±2	133±4	34±2
BF (kHz)	90±10	64±6	86±7	26.5±0.8	65±6	25±1
TF (kHz)	30±3	25±2	31±2	15.5±0.8	21.6±0.6	17±1

PD, pulse duration; PI, pulse interval; SF, starting frequency; BF, best frequency; TF, terminal frequency.
Values are means ± s.e.m. (N=6).

emission SPL and starting frequency between tasks. Again, these differences may reflect the properties of the different targets. As expected, emission SPL was lower when searching for the larger target, which produced echoes with a higher SPL than the smaller mealworm. This may indicate that bats keep the SPL of their echoes within an optimal intensity range, which could improve the processing of echo information.

Target detection

After the detection of a specific target, bats switch from search to approach phase. In free flying bats this switch is indicated by a distinct reduction of pulse interval and sound duration (e.g. Griffin et al., 1960; Schnitzler et al., 1987; Kalko and Schnitzler, 1989; Schnitzler and Kalko, 2001).

In our experimental conditions pulse interval was not a good indicator for the detection because its average decreased in a monotonic way along the sequence. In particular, during the catching task, bats have already emitted groups of two calls during the search phase, which explains the reduction in pulse interval. Pulse duration was a far better parameter for estimating the moment when detection of the target of interest occurred. The onset of the approach phase using pulse duration as indicator also coincided with the beginning of the decrease in emission SPL and with the change in flight behavior.

In the landing task target detection occurred at greater distances than during the catch, resulting in a longer approach phase in the former, possibly due to the louder echo of the landing grid.

Approach phase

The initial part begins with the onset of the approach phase and ends with the beginning of the terminal part. The terminal part consists of the last group of pulses and ends at contact with the target of interest. Prey-catching bats always emitted a terminal part consisting of both buzz I and buzz II that formed a unit. This result is in accordance with data in the literature that describe similar patterns for bats catching insects in the aerial-hawking or trawling mode (e.g. Griffin et al., 1960; Schnitzler and Kalko, 2001). With landing bats, however, we distinguished two patterns. Bats emitted a terminal group of pulses, consisting either of both buzz I and II or only buzz I followed by one or two extra pulses. This last pattern has not yet been described in the literature.

In the approach phase the signals were arranged in groups of increasing number of pulses. The higher the number of pulses per group, the shorter the pulse duration and within-group pulse interval. This continuous reduction of pulse duration and within-group pulse interval (Table 1) ended with the last pulse of buzz I. Pulse duration and within-group pulse interval for both tasks correlated mainly with the number of pulses within a group. Differences in frequency structure between tasks were significant, but it is questionable whether the slightly higher starting, best and terminal frequencies in landing bats influence the echolocation performance in basic tasks such as ranging and target identification.

The rate that the bats decrease the pulse interval depends on the distance to the target at the beginning of the approach phase. At the onset of the initial part they emit groups of two pulses

with a within-group pulse interval of about 30–35 ms. At the end of the initial part they often produce groups of four, or sometimes even more, pulses with a within-group pulse interval of 14–20 ms. These values are slightly higher than the within-group pulse intervals of buzz I, which are 14–16 ms (Fig. 6, Table 1). If the bats detect the target of interest at greater distances, e.g. when landing, the decrease in pulse interval from the beginning to the end of buzz I will be less steep than if detection occurs at shorter distances e.g. when catching a mealworm.

The arrangement of pulses in so-called 'strobe groups' and the pulse intervals within groups (strobe intervals) have been studied in *Eptesicus fuscus* approaching a tethered insect close to background vegetation (Moss et al., 2006). Moss et al. found a higher incidence of groups and also a prolongation of the strobe interval with increasing clutter interference. The higher incidence of groups reflects the longer duration of the approach phase. That is similar to our results where landing bats had a longer approach phase with more groups. However, we could not find any dependence of pulse interval within groups on the type of the echolocation task. In both situations it was reduced in a similar way and depended on the number of pulses emitted per group.

Buzz I ended on average between 47 and 63 ms prior to the contact with the target, both when catching a moving mealworm and when landing on the stationary grid (Table 3). The time between the end of buzz I and contact corresponds approximately to the reaction time of bats, as estimated from the time lag between the last narrowband search pulse and the succeeding first broadband approach pulse in bats foraging in open space (A.D. and H.-U.S., unpublished data) (Webster, 1967). Thus, information delivered from echoes of buzz II and extra pulses reach the bat too late to be used for the completion of landing or catching.

We therefore conclude that, independent of the echolocation task, the relevant section of echolocation signals controlling the approach to targets of interest starts with the beginning of the approach phase and ends with the last pulses of buzz I. In both tasks, the basic pattern of this relevant section is rather similar, except that in the landing task the approach started earlier. This is an unexpected result as the basic pattern of the relevant part of the approach phase is less different than assumed.

There may be other situations that influence the approach pattern, however. Moss et al. reported differences, depending on the clutter situation (Moss et al., 2006). If the prey was near vegetation the approach phase ended with groups having fewer pulses than when the prey was further away.

The addition of buzz II found in all aerial-hawking vespertilionids makes a big difference in the pattern of the approach signals but is no more relevant for guidance to the target of interest. The information delivered by the signals emitted after buzz I (buzz II signals or extra pulses) may help the bat to understand what went wrong if it missed the moving prey or did not hit the landing grid. Our results contradict the hypothesis that buzz II would facilitate safe landing (Russo et al., 2007), since the bats can no longer react to information provided by these last calls before they contact the landing site. With the information delivered by buzz II the bats may control their actions after missing the prey or the landing site.

Harbor porpoises commuting through a pool from a starting point to a reward position regulate the pulse interval to keep the processing time constant between the reception of an echo from the destination area and the emission of the next pulse (Verfuss et al., 2005). It is assumed that the processing time is necessary to extract the information contained in the pulse echo pairs. In our experiments the processing time was not kept constant. If we use the within-group pulse intervals (Fig. 6) and subtract the corresponding two-way travel time to calculate the processing time, we obtain values of about 19 ms for the beginning of the approach phase in the landing bats and 21 ms in the prey-catching bats. At the end of buzz I the processing time was about 10 ms in both situations. This could mean that at the beginning of the approach the bats' information processing system does not work at its limit, but that might be reached at the end of buzz I.

After detection, emission SPL decreased with a rate of about 6 dB per halving of distance. This result is comparable to results obtained from other species. We are aware that we used only one microphone to estimate the emission SPL. Nevertheless we assume that our measurements of the SPL are rather accurate as bats direct their signals to the landing site when approaching it (J. Koblitz, personal communication). Indeed, our results are comparable to those found in other studies. Intensity compensation during the last part of the approach was about 4 dB per halving of distance in *Myotis daubentonii* (Boonman and Jones, 2002). In a 2-AFC paradigm the gain control slope for *Eptesicus fuscus* was 6.7 dB per halving of distance, and for *Noctilio leporinus* it was 7.2 dB (Hartley, 1992).

Lowering of the emission SPL during an approach with about 6 dB per halving of the distance keeps the SPL at the target constant so that the SPL of a returning echo increases only according to the reduction in distance between target and bat on the way back. The SPL decrease reduces the range of possible echo intensities. Again, this may indicate that bats keep the SPL of their echoes within an optimal intensity range, which could improve the processing of echo information.

In conclusion, the approach controlled by echolocation ends with the last signal of buzz I, and the echolocation behavior during the approach to a moving or a stationary target is rather similar. With the beginning of the approach phase, bats decrease the pulse interval by emitting calls grouped in clusters of increasing number of pulses. All signals emitted after buzz I may help the bat evaluate how it missed the moving prey or did not hit the landing grid.

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