

Echolocation call intensity in the aerial hawking bat *Eptesicus bottae* (Vespertilionidae) studied using stereo videogrammetry

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Summary

Aerial hawking bats use intense echolocation calls to search for insect prey. Their calls have evolved into the most intense airborne animal vocalisations. Yet our knowledge about call intensities in the field is restricted to a small number of species. We describe a novel stereo videogrammetry method used to study flight and echolocation behaviour, and to measure call source levels of the aerial hawking bat *Eptesicus bottae* (Vespertilionidae). Bats flew close to their predicted minimum power speed. Source level increased with call duration; the loudest call of *E. bottae* was at

133 dB peSPL. The calculated maximum detection distance for large flying objects (e.g. large prey, conspecifics) was up to 21 m. The corresponding maximum echo delay is almost exactly the duration of one wing beat in *E. bottae* and this also is its preferred pulse interval. These results, obtained by using videogrammetry to track bats in the field, corroborate earlier findings from other species from acoustic tracking methods.

Key words: bat echolocation, source level, flight paths, videogrammetry, flight speed.

Introduction

Understanding the echolocation behaviour of free-living bats has been advanced in recent years by simultaneously recording echolocation calls while monitoring three-dimensional flight paths. In particular, the intensity of the sonar signal, which is of pivotal relevance for any echolocator as it sets the range of 'view' achieved by echolocation, can only be assessed correctly when distance, direction and orientation of the sound source relative to the recording microphone are known (Holderied and von Helversen, 2003). Several methods are available for linking echolocation behaviour to flight patterns. Differences in arrival times of calls can be monitored by microphone arrays, so that flight positions of calling bats can be reconstructed from acoustic data (Holderied and von Helversen, 2003; Jensen and Miller, 1999; Rydell et al., 1999; Surlykke et al., 1993). Stereophotogrammetry using still cameras and multiframe illumination allows visual tracking of flight paths, and has been synchronised with recording of echolocation calls (Britton and Jones, 1999; Britton et al., 1997; Kalko and Schnitzler, 1993; Kalko et al., 1998; Schnitzler et al., 1994; Siemers and Schnitzler, 2000). In this study, we employ stereo videogrammetry using two digital video cameras for reconstructing flight paths of bats in the field. We use the method to describe the flight and echolocation behaviour of a bat species that forages in open 'uncluttered'

space where the majority of echoes returned to the bat come from potential prey items (Schnitzler et al., 2003).

There have been few measurements of call intensities from bats flying in open spaces, due to the technical difficulties of implementing such methods in the field (Holderied and von Helversen, 2003; Surlykke et al., 1993; Jensen and Miller, 1999). Recent measurements made with microphone arrays have shown that even small aerial feeding species, such as *Pipistrellus pipistrellus*, are calling with intensities as high as 128 dB peak-equivalent sound pressure level (peSPL) at 10 cm (Holderied and von Helversen, 2003). These estimates are considerably higher than previously published estimates of call intensity in aerial feeding bats, and are among the most intense airborne animal vocalisations recorded in nature.

The knowledge of the source level of an echolocation call, allows estimating the echolocation range i.e. the distance range of targets (e.g. flying insect prey) accessible with this call. Yet, the echolocation range is not an exclusively spatial aspect of an echolocation system but also affects temporal aspects: due to the constant speed of sound in air, echolocation range corresponds to a time window of possible echo delays. For low duty-cycle bats (such as *E. bottae*), which remain silent while listening for returning echoes, this affects the decision when to produce the next call. Choosing a pause between two calls

longer than the maximum possible echo delay means waiting for further echoes in vain and wasting time better invested to update echolocation information. Calling more frequently and thus before the last echo from the previous call would have arrived, brings call–echo assignment problems arising from late echoes arriving after the next call. Indeed, Holderied and von Helversen (2003) found that the window of possible echo delays for flying insect prey matches the preferred time interval between calls in eleven European bat species. By this match these bats maximise calling rate, and consequently temporal information flow while searching for flying insect prey, without risking call–echo assignment problems. Surprisingly, this window of possible echo delays also matches the average duration of the wing beat in these species – the so-called ‘wing beat window’ (Holderied and von Helversen, 2003). This second match helps bats to reduce the costs for the production of their intense echolocation signals: by coupling call emission to their wing beat, they can utilize the increased lung pressure generated by the work of the flight muscles for their vocalizations (Heblich, 1986; Speakman and Racey, 1991; Wong and Waters, 2001).

In this study we describe the echolocation and search flight behaviour of the medium-sized (~8–9 g) bat species *Eptesicus bottae* (Vespertilionidae). Specifically, we test the predictions: (1) that the bats will call at intensities within the range of aerial feeding, open space foraging species of similar sizes studied in Europe, i.e. between 120–133 dB peSPL at 10 cm (Holderied and von Helversen, 2003); and (2) that the effective range of echolocation calls of *E. bottae* matches its pulse interval and ‘wing-beat window’. A major aim of this study is to introduce videogrammetry as a valid method for flight path tracking of bats in the field, and to determine whether our estimates of call intensity correspond with measurements from other species studied with well-established acoustic tracking methods.

Materials and methods

The study was conducted around the Ben-Gurion Tomb at the Sede Boqer campus of the Ben-Gurion University of the Negev, Israel between the 2nd and 7th of July 2003. The two video cameras were set up overlooking a gorge in Nachal Zin, where bats hunted for insects in open space. Two digital video cameras (Sony DCR-PC100E) were synchronised with output from a Larson-Davis $\frac{1}{4}$ inch microphone (type 2520, frequency response ± 1 dB from 4–100 kHz). We placed the two cameras at known relative position and orientation to each other on tripods separated by 2.5–3.0 m. The microphone was placed at the edge of the gorge in the field of view of both cameras pointing slightly upwards in the direction of the approaching bats as they flew along the edge of the gorge. No additional lighting was needed, as the whole tomb area is brightly lit at night attracting many insects and hence foraging bats, which were clearly visible. On some nights, we increased the light level using an additional floodlight.

To record bat calls we used a Brüel & Kjær 2670 preamplifier (Nærum, Denmark), 5935L power supply and a

National Instruments (Austin, TX, USA) analog to digital converter card (DAQCard 6062E) in combination with a Toshiba SP6100 Laptop running the Avisoft Triggering Harddisk Recorder (AVISOFT, Berlin, Germany). Calls were sampled with 12-bit precision at 29,4117 Hz. For synchronisation purposes a 31 Hz rectangular sound pulse of 460 ms duration was produced by a custom-built pulse generator, and played after each bat pass simultaneously to the ultrasound input of the DAQCard 6062E and sound channels of both cameras.

Cameras were supported on separate tripods to confer flexibility in their on-site orientation (positioning and pointing direction) to optimise the measurement accuracy and volumetric coverage of the system to the specific recording situation. This flexibility was achieved using multiple images of a 3D calibration frame in combination with photogrammetric bundle adjustment techniques (Granshaw, 1980). These enabled the simultaneous mathematical determination of the relative orientation and internal geometric imaging properties of each camera to be determined (calibration). For the purposes of this work, the calibration frame consisted of a cross with 2 m diameter carrying 48 reflecting point targets at pre-determined locations. To achieve accurate measurements over the complete volume of interest, the target array was imaged in many different places in the field of view of both cameras. Coverage of the whole volume where bats are expected could be achieved with the exception of the limit set by the edge of the gorge. The relative orientation of both cameras were then derived from each pair of corresponding images from the two cameras by evaluating the position of all visible targets in both images. Combining information from a large number of image pairs not only increases the accuracy of the relative orientation of the two cameras, but also ensures that the geometric characteristics (particularly lens distortion) of the video cameras is known at the time that the images are taken. These accurate camera orientations can then be used for triangulating the position of flying bats, or any other objects of interest, visible in both cameras’ field of view by the method of intersection (Shortis et al., 2000). All photogrammetric computations were carried out within Vision Measurement System VMS software (www.geomsoft.com).

The two video recordings of each bat pass were synchronised to the frame level (25 Hz) and grabbed using the software EditDV 2.01 (Digital Origin). To increase contrast between bat and background the pixelwise difference between consecutive frames was calculated. Then the two fields of each frame were separated (deinterlaced) and the missing lines interpolated resulting in an actual frame rate of 50 Hz. Finally the head of the bat was indicated manually in each frame in both videos and the x – y -image coordinates stored. The remaining phase shift between the two videos, which could amount up to $1/25$ s, i.e. 40 ms, was assessed from the synchronisation pulse on the audio tracks with an accuracy of 1 ms. The actual x – y -image coordinates of the bat in the second video at the exact times the corresponding frames in the first video were taken was then interpolated accordingly. These

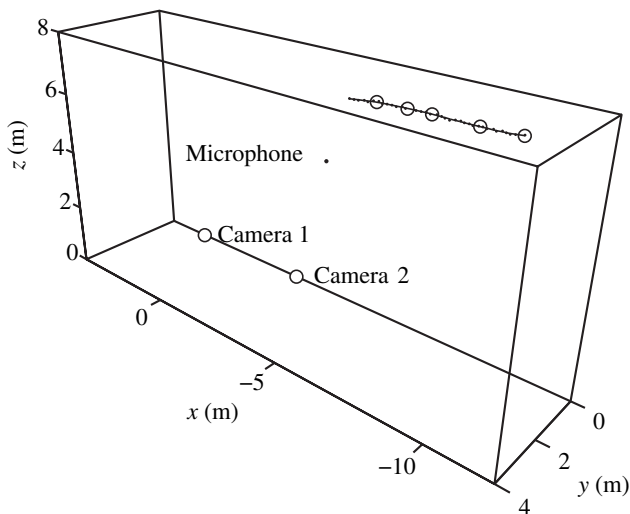


Fig. 1. Typical reconstruction of a flight path of *Eptesicus bottae*. Localisations of the flying bat are represented by small dots, and bat-emitted echolocation calls at positions illustrated by larger open circles. Positions of the cameras and microphone are also illustrated.

steps were all performed with a custom-written program created using the freeware software packages VirtualDub v1.4.10 (by Avery Lee; www.virtualdub.org) and Avisynth v0.3 (by Ben Rudiak-Gould; www.avisynth.org).

Triangulation, based on the list of x - y -image coordinates from both cameras, was performed with VMS software resulting in a series of consecutive 3D localisations for the period of time a bat was visible to both video cameras. The calculated bat localisation precision is of the order of a few mm. A spline was fitted to localisations using MATLAB (The MathWorks Inc., Natick, MA, USA) functions thus creating an interpolated flight path. x -, y - and z -coordinates over time were interpolated separately. Instantaneous flight speed as well as the relative position and flight speed of the bat towards the microphone could then be calculated. In the synchronised sound recordings all bat calls were selected manually with their respective recording time. The actual time and position the bat had produced each individual call was then determined taking the flight speed of the bat and the speed of sound in air into account.

Call source levels were determined as described by Holderied and von Helversen (2003). The microphone was amplitude calibrated at the beginning and the end of each recording session with an acoustical calibrator (D-1411E;

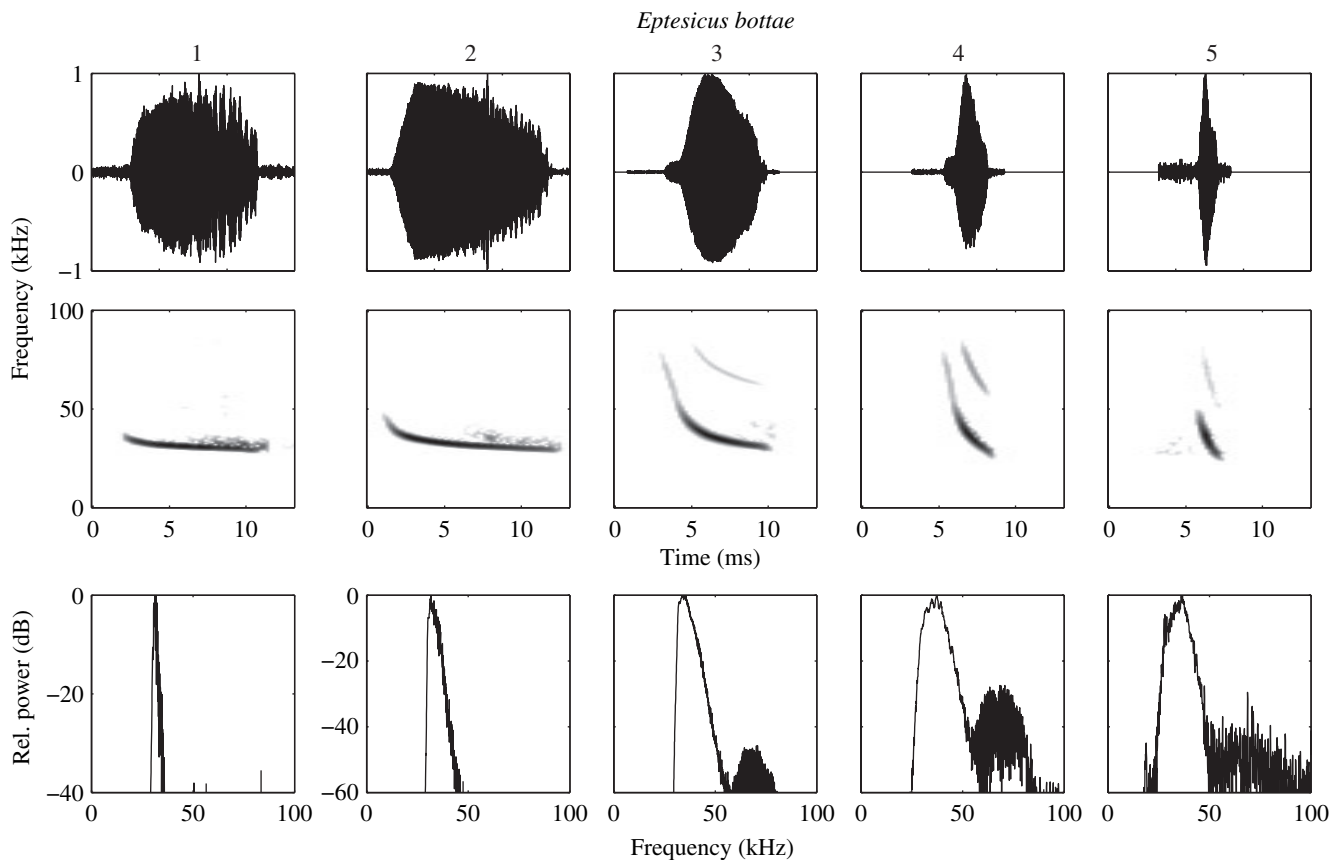


Fig. 2. Echolocation calls emitted by *Eptesicus bottae* in a range of different situations. (1) Search phase call, (2) another search phase call emitted prior to a capture sequence, (3) an approach phase call, (4) a call from the middle of a terminal buzz and (5) a call from the end of a terminal buzz. For each call oscillograms (upper panels), spectrograms (middle panels –1024 Hanning window, 97% overlap) and power spectra (lower panels) are illustrated.

Dawe Instruments, England). Geometric and atmospheric attenuation of the sound on its way from the bat to the microphone were calculated for the peak frequency of the call (Bazley, 1976) using temperature and relative humidity as measured at the study site at the time of the recording. The directionality of the recording microphone at the relevant frequencies (~30 kHz) is very broad (e.g. Pye, 1993) and thus results in a maximum potential underestimation of 2 dB in the measured source levels. Even though we selected for bats approaching the microphone (11 out of 17 flight paths), it remains uncertain whether they also directed the acoustic axis of their sonar beam towards the microphone. Due to this effect, some of the measured call source levels will be slight underestimates. Unless we know the exact shape and orientation of the sonar beam for every single call it is not possible to control for this error. Yet, the maximum source level will, if at all, only be moderately affected: first because call beam patterns in this genus are rather broad (Ghose and Moss 2003) and second because it is very likely that bats approaching the microphone occasionally have pointed their acoustic beam axis in this direction by chance. All source levels are given in dB peSPL (peak equivalent sound pressure level) re 20 μ Pa, i.e. the sound pressure level of a continuous pure tone of the same amplitude, and were related to a reference distance of 10 cm in front of the sound source.

We calculated detection distances for two types of targets that differ in their echo spreading: point sources, which generate a spherically spreading echo (e.g. flying insects or conspecifics) and large plane background objects, which mirror the sound back to the source (e.g. a water surface from above or a wall from the front). In both cases, we assumed a target strength of 0 dB in 10 cm, i.e. the target sends all the impinging acoustic energy back into the direction of sound incidence, which serves as an approximation to the largest possible targets of each type (e.g. conspecifics or flying predators). Maximum detection distances for calls were calculated using the sonar equation (Møhl, 1988) for the loudest call encountered in each species as described in Holderied and von Helversen (2003). Spreading losses of call and echo were determined according to Bazley (1976). The detection threshold of the bats was assumed to be 0 dB SPL (Coles et al., 1989; Kick, 1982; Neuweiler et al., 1984).

Call duration was determined from the spectrogram using Avisoft SASLab Pro v4.2 (window length 512 Hanning; 100% frame; 93.75% overlap). Pulse interval was measured from the start of one pulse to the start of the next. Peak frequency and bandwidth 15 dB below the peak frequency were measured from the mean spectrum of the entire call (window length 512, Hanning). Aerial hawking bats frequently couple call emission to their wing beat to reduce the energetic costs for echolocation (Heblich, 1986; Speakman and Racey, 1991; Wong and Waters, 2001). As they also skip calls, the distribution of pulse interval has several peaks reflecting integer multiples of the wing beat period (Holderied and von Helversen, 2003). The lowest peak was taken as a measure of the mean wing beat period. Approach phase signals were distinguished from search

Table 1. Search phase echolocation call parameters measured from *Eptesicus bottae*

	<i>Eptesicus bottae</i>		
	N	Mean	S.D.
Duration (ms)	143	6.9	1.32
Peak frequency (kHz)	143	32.5	0.87
Bandwidth (kHz)	134	8.7	1.75
Pulse interval (ms)	134	155.6	61
1st peak in intervals	90 (67%)	118.7	

N, number of calls; S.D., standard deviation; 1st peak in intervals = the total number and percentage of all calls in the first peak of the frequency histogram of pulse intervals, i.e. calls that are emitted with one call per wing beat.

phase ones qualitatively from a prolonged increase in pulse repetition rate (usually leading to a 'terminal buzz'), an associated decrease in call duration, and a change in call shape to more broadband signals.

Wing morphology was measured for *E. bottae* from bats captured in the study area (data from Korine and Pinshow, 2004). Wing shape parameters follow definitions by Norberg and Rayner (1987). Theoretical optimum flight speeds (minimum power speed and maximum range speed) were calculated based on these measurements using the software Flight for windows v1.12 (Pennycuick, 1975; Pennycuick, 1989). This program does not aim to calculate the full airflow around the wing or to model the aerodynamic forces directly but to provide a simplified model based on flight mechanics 'to represent those features and processes that mostly determine the work and power.' One advantage of this model is that most of the necessary morphological parameters are easily obtained from live animals (i.e. mass, wing span and wing area).

Eptesicus bottae (Peters 1869) is a small/medium-sized vespertilionid bat (body mass 7–9 g, average forearm length 41.4 mm, $N=21$, Korine and Pinshow, 2004) found throughout Egypt, Middle East, Iraq, Turkestan and Afghanistan (Qumsiyeh, 1985). Recently it has been recorded in Rhodes, Greece (von Helversen, 1998) and Turkey (Spitzenberger, 1994). In the study area, *E. bottae* typically foraged within 2–5 m of the gorge edge, and also around streetlights and above water. It is found in the study area all year round (Korine and Pinshow, 2004).

Results

Reconstructions of flight paths

A representative reconstruction of a flight path of *E. bottae* (Fig. 1) shows the positions of the bat relative to the cameras and recording microphone. We restricted our analysis to flight paths measured within 10 m of the cameras to minimise potential distance-dependent triangulation errors. In total, we reconstructed 17 flight paths from *E. bottae* individuals flying towards the recording microphone. We estimated that at least five bats were present in the study area. Jensen and Miller

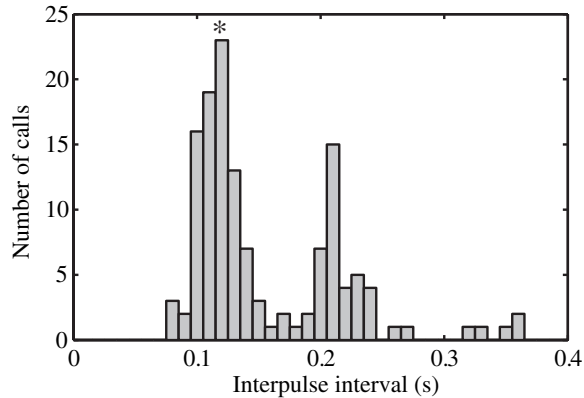


Fig. 3. Frequency histogram of pulse intervals of echolocation calls of *E. bottae*. The asterisk indicates the calculated maximum echo delay this bat can expect to achieve with the loudest observed call (details see text).

(1999) commented on the dangers of recording echolocation calls of open space bats by using microphones on the ground. Because our recordings were made on the edge of a gorge and were made from bats several meters away from the gorge edge, we can be confident that our measurements are reliably in 'open-space' situations.

Echolocation behaviour

Representative calls in different situations (search phase, approach phase and feeding buzz) are illustrated in Fig. 2, with summary data from search phase calls in Table 1. In search flight *E. bottae* emitted calls of ~7 ms duration and a peak frequency of 32.5 kHz, a bandwidth of 8.7 kHz, and a mean pulse interval of 155.6 ms, giving an average call repetition rate of 8.42 Hz and a duty cycle of 7.6%. The distribution of pulse intervals was multimodal (Fig. 3): 67% of calls were followed with a pulse interval at the lowest peak; the remainder of calls had double (29%) or sometimes triple (4%) this interval showing that the bats skipped emitting calls relatively frequently. We did not observe multiple calls per wing beat during search phase. Feeding buzzes were emitted during pursuit of aerial prey (Fig. 4). Calls decreased in peak frequency towards the end of the buzz, though there was no evidence in any of five buzzes with high signal:noise ratios of a clearly defined 'buzz II' (Kalko and Schnitzler, 1993). Calls became shorter and more broadband during the approach and terminal phases, with shortest calls recorded at the end of terminal buzzes (Fig. 2).

Flight morphology and behaviour

Eptesicus bottae had a mean mass of 8.1 ± 1.2 g, wingspan of 28.16 ± 0.7 cm and wing area of 112.6 ± 6.7 cm² ($N=6$). This species flew at an average speed of 5.70 m s⁻¹ (17 flight paths) (Fig. 5).

This is close to the minimum power speed (5.3 m s⁻¹), and well below the maximum range speed (mechanical power: 8.7 m s⁻¹) predicted according to Pennycuik (1975, 1989).

Call intensities

All calls from 11 individual flight paths recorded on several days were analysed. During the recordings always more than one bat was present at the recording site. Thus, we are confident that source levels originate from several individuals. For *E. bottae*, calls recorded close to the microphone showed relatively low source levels (typically 105–115 dB peSPL in 10 cm with the bat 2–3 m from the microphone; Fig. 6). These lower intensities were recorded from approach and early terminal phase calls as the bat unsuccessfully pursued an insect flying near the microphone. Beyond 3 m from the microphone, source levels were independent of the distance between bat and microphone (*E. bottae*: distance to microphone 3.1–8.7 m; regression coefficient 0.198 dB m⁻¹; $R^2=0.002$; $F_{1,44}=0.0889$; $P=0.77$), giving confidence that there were no distance-related errors in our intensity estimates. Source levels during search phase frequently exceeded 120 dB, with maximum levels of 133 dB peSPL (121 ± 7.8 dB mean \pm s.d.). Intensity showed a significant relationship with call duration: approach phase calls of short duration, emitted close to targets, had lowest intensities (Fig. 6; $R^2=0.50$; $F_{1,64}=64$, $P<0.0001$).

Maximum detection distances and echo delays

The calculated maximum detection distance of *E. bottae* for very large flying targets (0 dB target strength) is 20.8 m, which corresponds to a maximum echo delay of 120 ms (temperature and relative humidity at the time of recording at the recording microphone: 25.2°C, 54%). This is in almost perfect agreement with the lowest peak in the frequency distribution of pulse intervals (119 ms, Table 1), which in aerial hawking bats corresponds to the mean wing beat period (Jones, 1994). The maximum detection distance for background targets is 38.8 m (maximum echo delay = 224 ms).

Discussion

Stereo videogrammetry is a viable alternative method to

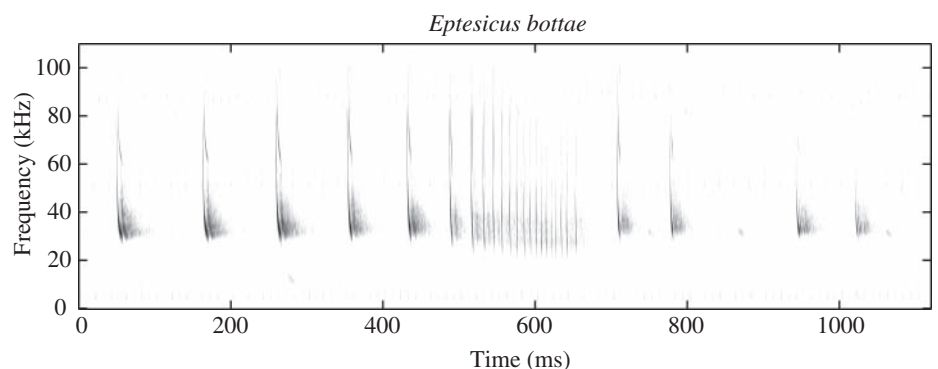


Fig. 4. Spectrogram of a representative feeding buzz from *Eptesicus bottae* (FFT: 1024, Hanning window, 75% overlap).

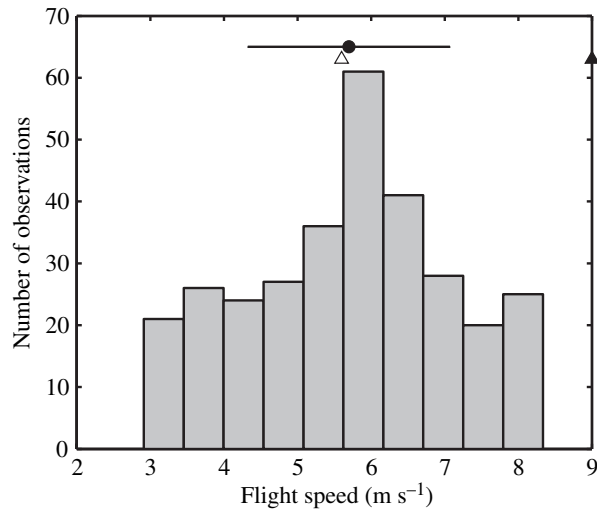


Fig. 5. Frequency distribution of flight speeds of *Eptesicus bottae*. Mean flight speed is illustrated by a filled circle. Predicted minimum power speed (see Materials and methods) is depicted by an open triangle, and predicted maximum range speed by a filled triangle.

acoustic localisation for reconstructing flight paths of bats in three dimensions in the field. The methods outlined here are also applicable for quantifying the escape responses of insects approached by echolocating bats and to study bat species inaccessible to acoustic localisation due to the limited bandwidth of their sonar signals (e.g. rhinolophids, hipposiderids). We are confident in the accuracy of our measurements because the call intensities reported are almost identical to those measured for bats of similar size using acoustic localisation (Holderied and von Helversen, 2003). Moreover, like Holderied (Holderied, 2001) we found bats typically flying close to the predicted minimum power speed. This suggests that foraging bats in search flight are flying close to the speed that minimises the power required to be flying.

Eptesicus bottae shows echolocation behaviour similar to that of other aerial-feeding vespertilionid bats. In open space, calls are relatively narrowband and adapted for detection (Parsons et al., 1997; Schnitzler and Kalko, 2001). The call design resembles that of its larger (~23 g) congener *E. serotinus* (e.g. Jensen and Miller, 1999), except call frequencies are higher, and pulse duration and intervals are shorter; trends expected for a bat of smaller size (Jones, 1999). The mean call peak frequency of 32.5 kHz is considerably higher than in the individuals from Rhodes (28 kHz; von Helversen, 1998) perhaps because in Israel this species is smaller than in Turkey (Spitzenberger, 1994). As insect prey is approached during foraging, call repetition rate increases and calls become shorter (so pulse-echo overlap is avoided), as well as more broadband, favouring localisation rather than detection (Parsons et al., 1997; Schnitzler and Kalko, 2001).

Our main aim was to determine call intensities for bats foraging in open spaces. The values measured for *E. bottae* (up to 133 dB; 121 ± 7.8 dB mean \pm S.D.) are similar to those reported by Holderied and von Helversen (2003) for other

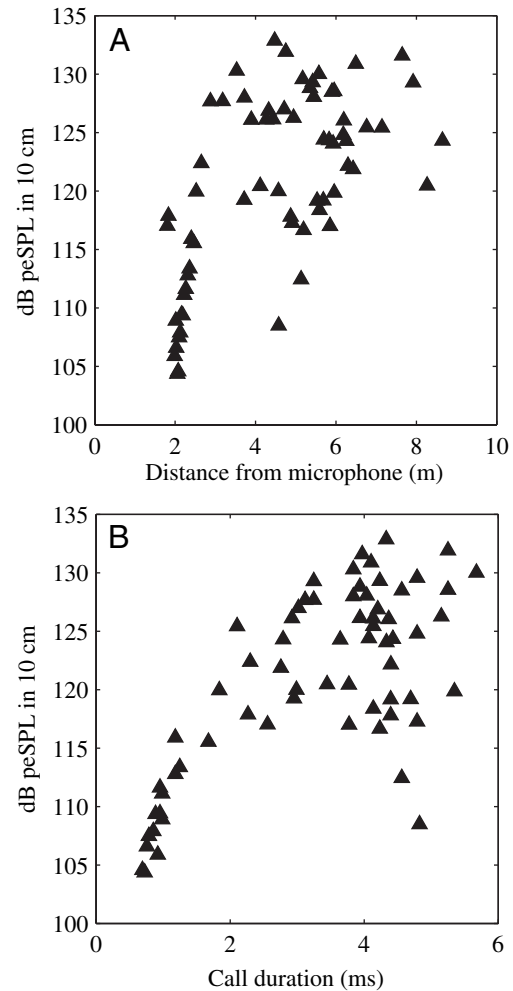


Fig. 6. Relationships between source level and distance from microphone (A) and call duration (B) for *Eptesicus bottae*.

aerial hawking species: these values are among the highest source levels recorded for vocalising animals. Source levels are similar to and sometimes higher than those reported by Jensen and Miller (1999) for *E. serotinus*.

The interval between consecutive echolocation pulses gives insight into understanding echolocation ranges, as it makes no sense for a bat to delay the production of a call if the echo from the outer limit of its echolocation range has already arrived. In *E. bottae*, we found a very good agreement between the calculated maximum detection distance for flying targets and the mean wing beat period (assuming the bat produces one call per wing beat in search phase). This corroborates the finding of Holderied and von Helversen (2003; their fig. 3c) that aerial-hawking vespertilionids generally match wing beat period and detection range for flying targets. The tendency of *E. bottae* to skip one call in 29% of cases, can be interpreted as an adjustment to more distant planar background targets: twice the wing beat period is 238 ms, which corresponds well to the maximum echo delay for background targets of 224 ms. This species cannot expect echoes to arrive later than that, therefore it makes sense that it very rarely skips more than one call (4%

of calls, $N=5$). *E. bottae* fits well with other vespertilionids studied in this respect (Holderied and von Helversen, 2003). The full corroboration of findings from other species obtained with different tracking methods gives further evidence that stereo videogrammetry is a functional method for the study of free-ranging bats in field.

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