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RESEARCH ARTICLE

Big brown bats (*Eptesicus fuscus*) emit intense search calls and fly in stereotyped flight paths as they forage in the wild

Katrine Hulgard^{1,‡}, Cynthia F. Moss², Lasse Jakobsen¹ and Annemarie Surlykke^{1,*}

ABSTRACT

The big brown bat, *Eptesicus fuscus*, uses echolocation for orientation and foraging, and scans its surroundings by aiming its sonar beam at obstacles and prey. All call parameters are highly adaptable and determine the bat's acoustic field of view and hence its perception of the echo scene. The intensity (source level) and directionality of the emitted calls directly contribute to the bat's acoustic field of view; however, the source level and directionality of the big brown bat's sonar signals have not been measured in the field. In addition, for bats, navigation and prey capture require that they process several streams of acoustic information. By using stereotypic flight paths in known areas, bats may be able to reduce the sensory processing load for orientation and therefore allocate echo processing resources to prey. Here we recorded the echolocation calls from foraging *E. fuscus* in the field with a microphone array and estimated call intensity and directionality, based on reconstructed flight trajectories. The source levels were intense with an average maximum source level of 138 dB (root mean square re. 20 µPa at 0.1 m). Furthermore, measurements taken from a subset of calls indicate that the echolocation signals in the field may be more directional than estimated in the laboratory (half-amplitude angle 30 deg at 35 kHz). We also observed that *E. fuscus* appear to follow stereotypic flight paths, and propose that this could be a strategy to optimize foraging efficiency by minimizing the sensory processing load.

KEY WORDS: Bat echolocation, Source level, Directionality, Flight path, Sensory load, Attention

INTRODUCTION

Bats (Chiroptera) are the most ecologically diverse group of mammals. With the exception of most bats in the order Pteropodidae, echolocation is the dominant sensory system for spatial orientation and foraging in these animals (Griffin, 1958). Echolocating bats show flexible call designs and adjust signal structure to suit environmental conditions and behavioural contexts (Neuweiler, 1990; Schnitzler and Kalko, 2001). The big brown bat, *Eptesicus fuscus* (Palisot de Beauvois 1796) (Vespertilionidae), is an aerial insectivorous echolocating bat that typically hunts away from obstacles, but is also quite flexible in its foraging, as demonstrated by occasional prey pursuits close to background clutter (Simmons, 2014). *Eptesicus fuscus* scans its surroundings by aiming its sonar beam at relevant objects, and changes its pulse repetition rate and sonar sound group

production pattern, depending on clutter density and target trajectory (Surlykke et al., 2009a; Kothari et al., 2014). All adjustments of call parameters (frequency, source level, directionality and duration) affect the operational sonar space, resolution and update rate, thereby determining the bat's acoustic field of view and hence its perception of the echo scene. In a foraging context, echolocating bats receive echoes returning at high rates from the surrounding objects, and to reduce the load on the system, bats adapt sonar behaviour to separate echoes returning from targets, including prey, from echoes generated from clutter, such as vegetation or other obstacles.

The sonar operating range is determined by the intensity, directionality and frequency of emitted echolocation calls, the spherical spreading and atmospheric attenuation of these calls, and the sensitivity of the bat's auditory system (Griffin et al., 1960; Neuweiler, 1990; Schnitzler and Kalko, 2001). It has been estimated that *E. fuscus* in free flight produces source levels (emitted intensity 10 cm from the bat's mouth) of 120 dB re. 20 µPa (Roeder, 1966). However, Roeder (1966) was not able to verify that the recorded bats were in fact *E. fuscus*, nor that the bats produced calls on axis with the recording system. More recently, source levels have been estimated for the closely related bats *Eptesicus serotinus* (Jensen and Miller, 1999), *Eptesicus nilssonii* (Holderied and von Helversen, 2003), and *Eptesicus bottae* (Holderied et al., 2005) to be between 121 and 127 dB [peak equivalent root mean square (RMS) re. 20 µPa] when taking only the 10% most intense calls. The most intense call of *E. bottae* was at 133 dB (peak equivalent RMS re. 20 µPa) (Holderied et al., 2005). Apart from Roeder's (1966) ingenious estimates of sonar call intensity based on the sensory response of a moth ear, the emitted sound intensity of *E. fuscus* has only been measured in the laboratory, with estimates of emitted intensity of approximately 110 dB re. 20 µPa at 5–10 cm (Griffin, 1958).

As such, all previous measures of *E. fuscus* call intensity are likely to be underestimates of this commonly studied species' most intense sounds. That is, in general, bats flying in confined spaces emit calls of shorter duration, larger bandwidth and a lower intensity than in the open (Surlykke and Kalko, 2008; Brinkløv et al., 2010). To obtain biologically relevant data and to estimate the bat's sonar range in the natural environment it is important to record signals from freely flying bats in the field. Furthermore, it is important to ensure that intensity measurements are taken along the acoustic axis of the call, since echolocation calls are directional and sound pressure falls off rapidly from the central beam axis. Field recordings using microphone array techniques indicate that maximum bat echolocation source levels are generally +20 dB or more relative to earlier estimates (Jakobsen et al., 2013a). Not only is sonar call intensity greater in the field, but call directionality appears to be higher under field conditions (Surlykke et al., 2009b). However, as with intensity, the directionality of *E. fuscus* calls has only been measured in the laboratory (Hartley and Suthers, 1989; Ghose and Moss, 2003), and not in the field.

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Even with the ability to adjust call parameters, and thereby the acoustic field of view, the bat still faces the challenge of separating prey echoes from clutter echoes. As for vision-based predators, most hunting scenarios a bat faces require concurrent attention to the environment and to the prey. How do bats accomplish simultaneous monitoring of background while tracking small, sometimes evasive, insect prey? Barchi et al. (2013) reported that *E. fuscus* adopts stereotypic flight patterns when navigating obstacles in the laboratory. In the context of natural behaviour, this finding raises the question of whether bats in the wild adopt stereotypic flight paths as a general strategy to reduce echo-processing load when foraging in a familiar area.

Here we report estimates of emitted echolocation call intensities and signal directionality in foraging *E. fuscus* in the field. Furthermore, we investigate whether stereotypic flight paths occur under natural foraging conditions in the wild. To this end, echolocation calls were recorded from free-flying *E. fuscus*, foraging in a semi-open field, using a microphone array, which allowed us to reconstruct flight trajectories, and estimate call intensity and directionality. These data lay the foundation for understanding how bats sample information from the environment to analyse their surroundings using sonar echoes.

MATERIALS AND METHODS

Study site

The field recordings were conducted at Lake Artemesia, MD, USA, on two consecutive nights in May 2013. The site was a rectangular open space (approximately 50×35 m) flanked by a baseball field and a deserted road at either of the short ends and a thicket of trees and a small creek along the two long sides (Fig. 1).

Visual observations and sound recordings showed that there were at least two *E. fuscus* present at the site while recording on both nights. We did not catch the bats to mark them, and thus have no control over which bat we recorded at a given time.

Sound recordings

On the first night (13 May), the set-up consisted of seven microphones placed in a reversed T-shaped array, with five on a horizontal line and two above the centre microphone. The horizontal microphones were distributed from left to right at 0, 2.58, 3.47, 4.35

and 6.63 m and the vertical microphones were placed 1.80 and 0.60 m above the third microphone at 3.47 m, which was 1.5 m from the ground. The array was facing away from the baseball field towards the asphalt road. On 14 May the set-up was expanded and consisted of nine G.R.A.S. ¼ in microphones placed in a cross-shaped array, six on a horizontal line and two above and one below the centre microphone, hence with four microphones in a vertical line. The horizontal microphones were distributed from left to right at 0, 1.36, 2.70, 3.60, 4.50 and 6.11 m and the vertical microphones were placed 2.85 and 1.15 m above and 0.57 m below the fourth microphone at 3.60 m, which was 1.5 m from the ground. The array was placed within the open green area, facing towards the baseball field with open space and the asphalt road behind the array. Both arrays covered the field between the baseball field and the asphalt road. The ground sloped downwards towards the asphalt road, but sloped upwards again before reaching the road and the array position on 14 May.

The microphones (G.R.A.S. 40 BF ¼ in) were amplified by Avisoft power modules. Sounds were digitized by Avisoft USGH 1216 sampling at 300 kHz and stored on a laptop computer. We recorded 4 s files, 2 s pre-trigger and 2 s post-trigger. The files were triggered manually when calls were observed on the real-time oscilloscope on the PC or heard on a Pettersson D230 Ultrasound Detector. The microphones were calibrated before and after each recording session with a G.R.A.S. 42 AB sound calibrator.

Flight path reconstruction

We localized the bats at each sonar call emission via triangulation, determining the arrival time differences at the microphones in the array using cross-correlation (see Surlykke and Kalko, 2008, for

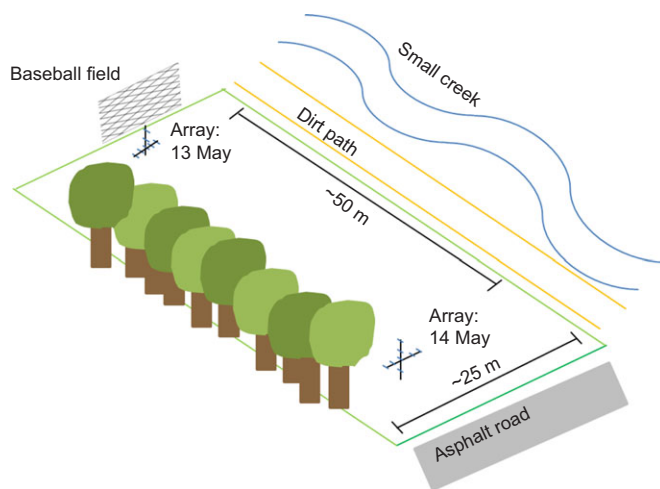


Fig. 1. Schematic of the recording site close to Lake Artemesia, MD.

The recording site was a grass field bordered by trees on one side, a creek and a path on the other side and at one end by a fenced baseball field and at the other end by an old asphalt road.

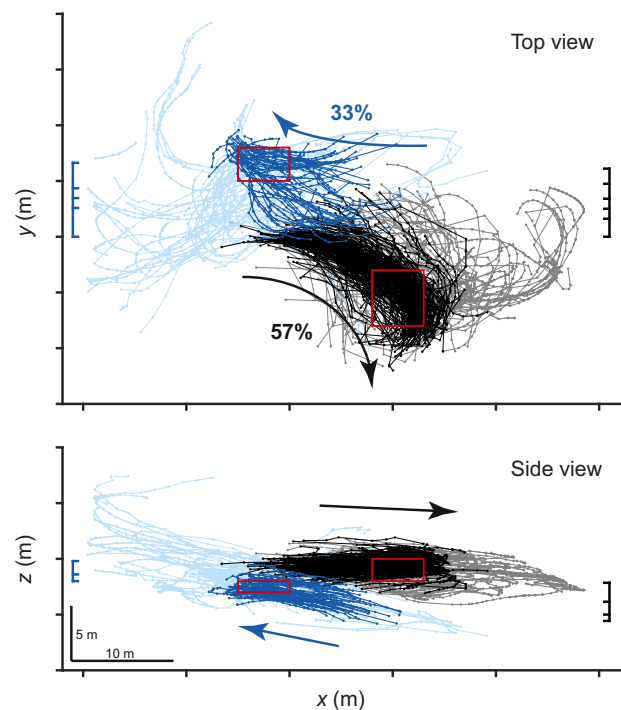


Fig. 2. Flight path reconstruction. Reconstruction of flight paths using the emitted search calls from 13 May (blue: 184 recordings) and 14 May (black: 278 recordings). The highlighted flight paths are the ones where the bat flew in the same direction (indicated by an arrow). On 13 May, 33% of the flight paths were in the same area and direction, whereas that was the case for 57% of the recorded flight paths on 14 May. The red squares indicate the area with most buzzes. The microphone arrays are also shown. The x-axis indicates the ground. The arrays were positioned uphill compared with the middle of the field.

Table 1. Source levels and energy for the search calls of *Eptesicus fuscus*

Date	ASL	AMSL	Median SL	Maximum energy	Average maximum energy	N
13 May	129±5	138±2	128	118	114±2	336
14 May	127±5	133±1	127	116	112±1	150

Data shown are from two recording nights at Lake Artemesia, MD, USA. ASL, average source level (±s.d.); AMSL, average of the 10% highest source levels (±s.d.). All source level (SL) values are in dB RMS re. 20 µPa, and the energy levels are given in dB re. 20 µPa² s. Average maximum energy values are ±s.d.

further details). Subsequently we estimated flight paths based on the timing and positions. The flight paths were trimmed, to remove physically implausible outliers, such as points far outside the bats' trajectory or points that were a result of echoes. The positions relative to the two arrays were recalculated relative to the global field (length 50 m, width 35 m, height 20 m) and displayed in combined figures of top and side view (Fig. 2). Sound files with two clearly separated flight trajectories were classified as a sound file with multiple bats.

Estimating call intensity, duration and energy

Only recordings where the bats were in front of the microphone array and flying directly towards one of the microphones (i.e. the beam aim was directed towards the centre of the array) were included in the intensity estimations, to avoid off-axis calculations. Furthermore, no calls closer than 3 m to the array were used. Array-based positioning is not reliable at great distances, and we therefore excluded all calls further out than 25 m. Only search calls (interpulse interval, IPI >50 ms) were included in the estimates, and no files with more than one bat recorded were included (Griffin et al., 1960).

We compensated the sound pressures measured on all microphones for transmission loss [atmospheric attenuation (ANSI, 1995) and spherical spreading] and microphone directionality (Kjær, 1982) by filtering the recorded call with the impulse response of the transmission loss and microphone directionality, thus obtaining a representation of the call 10 cm from the bat (Jakobsen et al., 2012). We then calculated the RMS sound pressure in a third octave band centred on the peak frequency of each call on each microphone using the 95% energy content of a 17 ms segment containing the call. We calculated the average source levels (ASL) of all estimated call source levels (336 calls from 13 May and 150 calls from 14 May), and average maximum source level (AMSL) as the mean of the 10% loudest calls.

From each recording day a subset of 30 files was randomly chosen and duration and frequency of the search calls were manually measured. By looking at the flight paths the search calls were grouped in three groups: 'flying straight in the open', 'turning' and 'close to obstacles', depending on whether the bat was flying straight in the open, turning or flying close to the vegetation or the array. An ANOVA test was performed to investigate if there were significant differences between durations and between frequencies for the three groups.

We also calculated the energy in each call by integrating the intensity over the duration of the call, $SL + 10 \log_{10}(\text{duration})$. Energy levels are given in dB re. 20 µPa² s.

Directionality estimations

To obtain the directionality of the calls, we first calculated the angle at which each microphone recorded the call from the position of the bat relative to the microphones. We then estimated the beam aim of the bats by fitting a second-order polynomial to the intensity values from the vertical and horizontal microphones for each recorded call. We used the peak of the polynomials as a proxy for beam direction

obtaining a vertical and horizontal beam direction. The flight height of the bats and the distance to the array mean that using standard criteria for directionality estimates yielded too few measurements to obtain the beam pattern (beam aim centred on the array). Instead we chose calls that were centred on the horizontal line of microphones; this was only possible with the set-up from 14 May. We fitted the piston model to each call using the angle at which each microphone recorded the call and the recorded compensated pressure (RMS measured in a third octave band at 35 kHz) on each microphone, normalised to the highest recorded pressure for that call [see Jakobsen and Surlykke (2010) for details]. Because this criterion (calls centred only on the horizontal part of the array) includes calls that potentially aim to the sides of the array we fitted the piston model (using least squares) by varying $k \times a$, a pressure displacement P and an angle displacement τ :

$$R_p(\theta) = \left| \frac{2 \times J_1(k \times a \times \sin(\theta + \tau))}{k \times a \times \sin(\theta + \tau)} \right| + P, \quad (1)$$

where $R_p(\theta)$ is the ratio between the on-axis pressure and the pressure at a given angle θ , J_1 is a first-order Bessel function of the first kind, $k = 2\pi/\lambda$, λ is the wavelength, a is the sound emitter radius, τ is the angular displacement and P is the pressure displacement. Whilst this is not an ideal set-up for beam shape estimation, it gives us a rough approximation of the beam.

RESULTS

We recorded on two nights (13 and 14 May 2013) without precipitation and with a temperature of approximately 12°C. On both nights we observed at least two bats patrolling back and forth in what looked like large figure-of-eights in an open area between a road and a baseball field. Because the bats were wild and recorded in the field without markings, we cannot be sure whether the bats were the same on both nights.

We selected calls emitted when the bat was in 'search phase' (Griffin et al., 1960). *Eptesicus fuscus* emitted very intense search calls with average source levels of 129 dB and 127 dB RMS re. 20 µPa at 0.1 m, and average maximum source levels (average of the

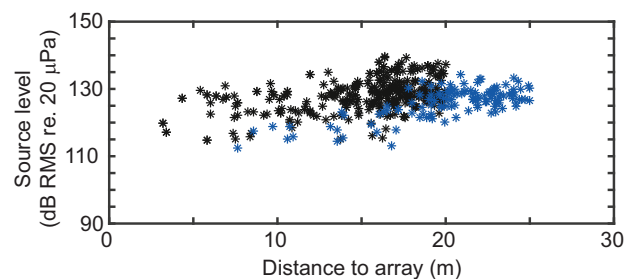


Fig. 3. Source levels in the big brown bat *Eptesicus fuscus*. Estimated echolocation call source levels, i.e. emitted intensities in decibels sound pressure level (SPL) RMS 10 cm from the bat's mouth, as a function of distance between the bat and the microphones, from 13 May (black stars) and 14 May (blue stars). The recordings include estimates from bat distances of up to 20 and 25 m on 13 and 14 May, respectively.

Table 2. Average call duration and average peak frequency

	13 May		14 May			
	Duration (ms)	Peak frequency (kHz)	N (calls)	Duration (ms)	Frequency (kHz)	N (calls)
Straight	7.5±1.5 ^a	30±2.4 ^a	298	10.0±1.5 ^a	26±2.8 ^a	239
Turn	5.8±1.1 ^b	32±1.6 ^b	28	6.8±1.6 ^b	28±1.9 ^b	33
Close to obstacles	4.9±1.3 ^c	33±2.3 ^b	34	5.4±1.3 ^c	31±1.7 ^c	24

The average duration (\pm s.d.) of search calls from 60 randomly selected sound recordings (30 each day). The calls were divided into three groups: 'straight', 'turn' and 'close to obstacles'. There is a statistical significant difference between the average durations and peak frequencies between the three groups for the two recording nights (duration: ANOVA, Tukey's honest significant difference; 13 May: $F_{2,357}=59.3$, $P<0.0001$; 14 May: $F_{2,293}=159.5$, $P<0.0001$) (ANOVA, Dunn's method; 13 May: $F_{2,350}=27.6$, $P<0.05$; 14 May: $F_{2,292}=31.6$, $P<0.05$), marked with a, b and c.

10% highest source levels) of 138 dB (RMS re. 20 μ Pa at 0.1 m) on 13 May and 133 dB (RMS re. 20 μ Pa at 0.1 m) on 14 May (Fig. 3, Table 1).

The average source level (ASL) is the average source levels for all the search calls. These were quite similar for the two recording nights: 129 dB (RMS re. 20 μ Pa at 0.1 m) on 13 May (median 128 dB) and 127 dB (RMS re. 20 μ Pa at 0.1 m) on 14 May (median 127 dB) (Table 1). However, the intensity of some of these calls may be reduced, because the bat was approaching obstacles or the array (Norum et al., 2012; Jakobsen et al., 2013a). We did not estimate source levels from bats close to the array (<3 m) but determined a small decrease in SL of up to -8 dB at the shortest distances (3 m) from the array (Fig. 3). This can cause an underestimation of maximum emitted source levels and therefore Table 1 also includes the average of the 10% highest source levels (AMSL) which were 138 dB (RMS re. 20 μ Pa) and 133 dB (RMS re. 20 μ Pa) on 13 and 14 May, respectively.

The maximum energy was approximately 117 dB (re. 20 μ Pa² s at 0.1 m) on both nights with average values of ca 113 dB (re. 20 μ Pa² s at 0.1 m) (Table 1).

Duration and frequency

When bats flew straight, the duration of the search calls varied significantly between the two recording nights (Table 2), with an average of 7.5 ms (13 May) and 10.0 ms (14 May) (two-sample t -test, $P<0.01$). On both nights, the duration of the search calls decreased significantly when the bat was turning and even more so when flying close to obstacles compared with flying straight in the open [ANOVA, Tukey's honest significant difference (HSD); 13 May: $F_{2,357}=59.3$, $P<0.0001$; 14 May: $F_{2,293}=159.5$, $P<0.0001$ (Table 2)]. These changes were also reflected in the peak frequency of the calls; call frequency increased significantly between straight flight in the open and turning and flying close to obstacles both nights (ANOVA, Dunn's method; 13 May: $F_{2,350}=27.6$, $P<0.05$; 14 May: $F_{2,292}=31.6$, $P<0.05$; Table 2). No significant differences were found between frequencies when turning and flying close to obstacles (ANOVA, Dunn's method; 13 May: $F_{2,350}=27.6$, $P<0.05$; 14 May: $F_{2,292}=31.6$, $P<0.05$; Table 2).

The peak frequency varied between the recording days (Fig. 4). On 13 May median peak frequency was 32 kHz and mean peak frequency was 31 kHz. On 14 May median peak frequency was 26 kHz and mean peak frequency was 27 kHz. Mean peak frequency was significantly higher on 13 May (two-sample t -test, $P<0.01$).

Directionality

As *E. fuscus* was flying in a large area and mostly at a distance of >10 m from the microphone array, only few recorded calls fulfilled the strict criteria for estimating directionality. Thus the directionality

estimate is based on seven calls from six different recordings and hence should only be taken as an approximate value. Nonetheless, it indicates a narrower beam width [half-amplitude angle (HAM)=30 deg; directionality index (DI)=13 dB; piston fit $R^2=0.76$] than previously reported in the laboratory (Fig. 5), ~45 deg HAM (Hartley and Suthers, 1989; Ghose and Moss, 2003). Mean intensity for the directionality calls was 117 dB (RMS re. 20 μ Pa at 0.1 m) \pm 11 dB (maximum and minimum values were 133 dB and 108 dB RMS re. 20 μ Pa at 0.1 m).

Flight paths

The flight paths based on the acoustic recordings for the two nights showed repeated patterns (see Fig. 2).

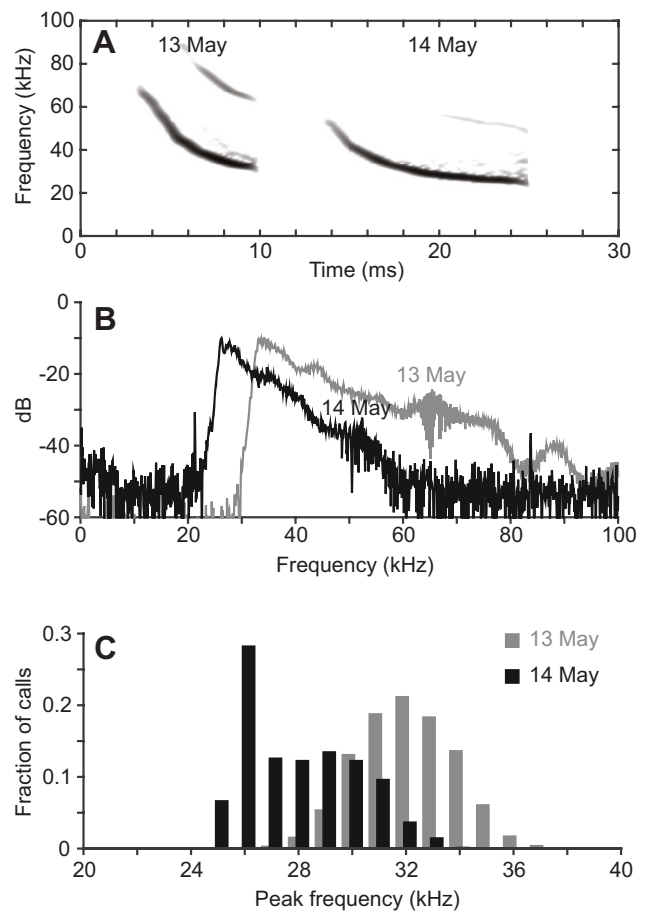


Fig. 4. Spectrogram, spectra and peak frequency distribution. Depicted are typical spectrograms and spectra of search calls (A,B) from 13 May (grey) and 14 May (black) and the peak frequency distribution (C) of the calls from the two recording locations.

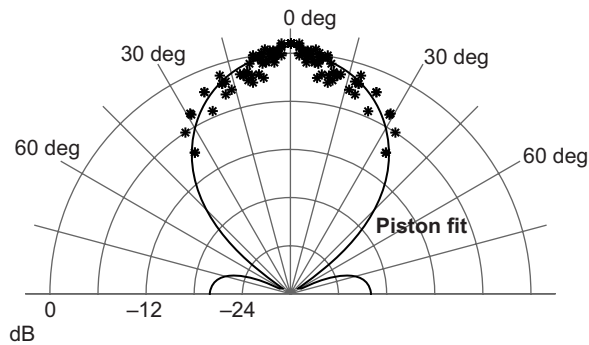


Fig. 5. Directionality. The directionality of calls recorded on 14 May measured in a third octave band centred on 35 kHz. The values are displayed as a mirror image to create a symmetrical plot. The black line is a fitted emission from a piston radiating sound at 35 kHz.

The recorded sound files had both search phases, approach phases and buzz phases. Most of the buzzes occurred around x : 15–20 m, y : 20–23 m and z : 7–8 m on 13 May and at x : 28–33 m, y : 7–12 m and z : 8–10 m on 14 May, indicating that the patches of insects were mostly concentrated in these areas (Fig. 2).

DISCUSSION

Our results show that *E. fuscus* emitted intense echolocation calls in the field with an AMSL at 138 dB (RMS re. 20 μ Pa at 0.1 m) on 13 May and 133 dB (RMS re. 20 μ Pa at 0.1 m) on 14 May 2013, and our preliminary estimates indicate that the calls are more directional (HAM=30 deg at 35 kHz) than laboratory estimates. Furthermore, we found that aerial hunting bats also seem to use stereotypic flight paths when hunting in the wild. The recordings we made included search, approach and terminal phase calls (Griffin et al., 1960; Surlykke and Moss, 2000), which confirmed that the bats were foraging and not commuting from one site to another, corroborating a previous report of this area as a hunting field for *E. fuscus* (Surlykke and Moss, 2000). We did not record any calls that could be characterized as *E. fuscus* social calls (Gadziola et al., 2012; Wright et al., 2013, 2014). The AMSL of the echolocation calls recorded was 133–138 dB (RMS re. 20 μ Pa), which is among the most intense ever reported for bats (Roeder, 1966; Jensen and Miller, 1999; Holderied and von Helversen, 2003; Holderied et al., 2005; Surlykke and Kalko, 2008). Previous reported source levels from related species (*E. serotinus*, *E. nilssonii* and *E. bottae*) have all been in peak equivalent RMS (Jensen and Miller, 1999; Holderied and von Helversen, 2003; Holderied et al., 2005). Measuring source levels in peak equivalent RMS always overestimates signal level, which is important to keep in mind when comparing with RMS. The findings are, however, consistent with field estimates of maximum echolocation signal source levels in other bat species (e.g. Surlykke and Kalko, 2008; Jakobsen et al., 2013a). When hunting in an open field with low prey density, emitting calls with very high source levels would be advantageous. The results from our study corroborate reported differences between source levels emitted by bats in the laboratory and the field (Jakobsen et al., 2013a), and confirm that source level estimates based on field recordings are 15–20 dB more intense than that based on laboratory data.

Most of our data points were from bats further than 5 m from the microphone array, so we did not observe strong range-dependent source level reductions. A small reduction was, however, present (up to –8 dB) at the shortest distances (3 m) from the array (Fig. 3). Furthermore, we found significant

differences between maximum durations (Table 1). The echolocation search calls were 10 ms on the second night, but only 7.5 ms on the first night. One possibility for this could be that there were different bats flying on the two recording nights. However, another possibility could be the different position of the array on the two recording nights (Table 1). On 13 May the array was close to a fence around the baseball field at a more cluttered location, which could explain why the echolocation calls were shorter. On both nights the duration of the calls was significantly shorter when the bats were close to obstacles (4.9 ms) compared with when the bats were turning or flying straight in more open space (7.5 and 10.0 ms), as has been seen in other studies (Norum et al., 2012; Jakobsen et al., 2013a). On both nights, bats in the open used longer calls when flying straight than when turning. The differences in surroundings on the two nights also had a large impact on the duration; there was a significant difference between nights when the bats were flying straight in the open. A possible explanation could be that the bats flew higher the second night compared with the first night (Fig. 2), and that there was less clutter in general at one end of the field compared with the other end. The peak frequency of the calls on the two recording nights also differed, with the lowest peak on the second night, which is consistent with previous reports of a negative correlation between call duration and peak frequency in frequency-modulated bats (Surlykke and Moss, 2000; Schnitzler and Kalko, 2001). It is therefore noteworthy that the echolocation data showed no tendency toward higher source levels on the second night. Hence the data suggest that duration and peak frequency are adjusted at greater distances from potential clutter or the ground than is maximum output intensity. The continuous dynamic modulation of duration, frequency and intensity depending on the surroundings emphasises the flexibility of the bat's sound emission. Even in the same general area the calls vary depending on flight pattern and which end of the field the bat was recorded, due to the differences in clutter surrounding the two ends of the field.

Directionality

Previously, directionality has been determined in the wild in trawling bats and in emballonurid bats (Surlykke et al., 2009b; Jakobsen et al., 2015). As trawling bats fly essentially in two dimensions, above water surfaces, it is less difficult to get good on-axis recordings, whereas aerial hunting bats, such as *E. fuscus*, have three degrees of freedom in position. Furthermore, the recording field was very large, and therefore many calls were recorded from a distance of 10–25 m. Thus, the results are more variable, but indicate that directionality of *E. fuscus* calls in the field is narrower than that of vespertilionids in the laboratory (Surlykke et al., 2009b; Jakobsen et al., 2013b).

Flight paths

The acoustic data allowed us to reconstruct flight trajectories from differences in the time of arrival of echolocation calls across the microphone channels, and show that the bats seemed to follow stereotypic flight paths when hunting for prey. The data from the second day of recording, when the array was facing towards the baseball field, especially revealed a clear tendency towards stereotypic flight (see Fig. 2), whilst the flight paths from the first night were not quite as clear. One possible reason for this could be that the more individuals that contribute to the total number of flight paths from a given night, the more muddled the overall image becomes. In fact, approximately 20% of the sound files on 13 May

had simultaneous recorded bats, whereas only about 2% of the sound files on 14 May were recordings of multiple bats. If indeed there was mainly one bat present on 14 May, while there were multiple bats on 13 May, individual differences might explain the difference in flight paths stereotypy. This is in line with laboratory data showing that each individual bat had its own stereotypic ‘signature’ flight path (Barchi et al., 2013). Alternatively, the bats may adapt their flight paths when flying with others. Barchi et al. (2013) did not fly more than one bat at a time; however, Chiu et al. (2010) found that when *E. fuscus* flew in pairs in the laboratory, they used calls of shorter/longer duration and higher/lower peak frequency compared with these same individuals when flying alone. Furthermore, due to the directionality of bat calls, the recorded sound level was below criterion when bats were flying away from the array, and therefore almost all sound files were recorded when the bat was flying in the general direction towards the array. The consequence of this bias in the results is that we can only reconstruct half of the flight path the bats used, and the recordings from the two nights were taken from opposite flight directions.

Several studies have shown that *E. fuscus* fly over long distances from their roosts to their foraging sites. Presumably, spatial memory plays an important role in navigating along a familiar route (Holland, 2007). If bats use spatial memory to fly long distances, it is conceivable that they use spatial memory to navigate a field in a foraging situation as well. The development of stable flight paths through an obstacle course over time when *E. fuscus* fly in a confined laboratory (Barchi et al., 2013) and the stereotyped flight paths that our field data demonstrate that for *E. fuscus* building stereotyped flight paths is a strategy that may be commonly used in the wild. Falk et al. (2014) confirmed the development of stereotypy in flight paths in an artificial ‘forest’, but did not find evidence of reduced sonar sampling with experience. Barchi et al. (2013) reported that the established flight paths did not change when the bats were released from different locations in the room. This suggests that the bat mapped out the laboratory in global, not egocentric, coordinates. It is likely that the same is true for a familiar hunting area in the wild, which has many distinctive landmarks (Jensen et al., 2005) to help the bat recognize its position in the space.

It would be advantageous for bats in a foraging situation if they can represent an echo scene, which has been suggested previously (Moss and Surlykke, 2010; Sandig et al., 2014). Creating an internal map of the surroundings with its boundaries and obstacles enables the bat to focus its attention on moving prey targets. Especially on nights with low prey densities, this could be highly advantageous for the bats. Indeed, prey density appeared low on our recording nights, due to cold weather (12°C). Pipistrelle bats also tend to fly in stereotypical (circular) patterns when searching for prey in a familiar space (Fujioka et al., 2014). Flight path stereotypy could be a general strategy for bats hunting insects in a familiar area. The echo scene (sound-scape or echo-scape) returning to the bat during a stereotypical flight round may compare to a well-known ‘melody’ or ‘driving on autopilot’ and only divergence from the normal, e.g. the echo from an insect prey, engages the bat’s attention for target tracking and interception. It has been suggested that bats may have difficulties processing more than one stream of information simultaneously (Barber et al., 2003), just as it is not possible for humans to focus full attention simultaneously on several streams of information through the same modality (Duncan et al., 1997). Bats must navigate the environment and at the same time localize small prey. We suggest that while flying ‘on autopilot’ in a familiar and

stable setting, the bat can focus its attention (echo processing resources) on detecting and tracking prey, and thereby minimize processing demands from concurrent echo streams from clutter, thus increasing the prey capture efficiency.

Anecdotal evidence of big brown bats diving for pebbles thrown in the air indicate that bats do not analyse details of each returning echo in the field, but react to unexpected echoes by adapting both flight and echolocation behaviour in a fast reflex-like manner (Barclay and Brigham, 1994). The big brown bat’s stereotypical flight patterns, combined with high source level and directionality, demonstrate an effective foraging strategy to detect and track prey in a familiar area. Future studies are needed to reveal how general stereotypical search patterns are (across primary modality), to reveal what ‘pop-up’ features of sensory input, e.g. sudden changes in scene or movement of prey and obstacle, attract an animal’s attention.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

K.H., C.F.M. and A.S. conceived and designed the experiment. K.H., C.F.M. and A.S. conducted the field recordings. K.H. and L.J. analysed the data. K.H. wrote the paper with assistance from C.F.M., L.J. and A.S.

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References

- ANSI (1995). *American National Standard. Method for the Calculation of the Absorption of Sound by the Atmosphere*. New York: American Institute of Physics for the Acoustical Society of America.
- Barber, J. R., Razak, K. A. and Fuzessery, Z. M. (2003). Can two streams of auditory information be processed simultaneously? Evidence from the gleaning bat *Antrozous pallidus*. *J. Comp. Physiol. A Sens. Neural Behav. Physiol.* **189**, 843–855.
- Barchi, J. R., Knowles, J. M. and Simmons, J. A. (2013). Spatial memory and stereotypy of flight paths by big brown bats in cluttered surroundings. *J. Exp. Biol.* **216**, 1053–1063.
- Barclay, R. M. R. and Brigham, R. M. (1994). Constraints on optimal foraging: a field test of prey discrimination by echolocating insectivorous bats. *Anim. Behav.* **48**, 1013–1021.
- Brinkløv, S., Kalko, E. K. V. and Surlykke, A. (2010). Dynamic adjustment of biosonar intensity to habitat clutter in the bat *Macrophyllum macrophyllum* (Phyllostomidae). *Behav. Ecol. Sociobiol.* **64**, 1867–1874.
- Chiu, C., Reddy, P. V., Xian, W., Krishnaprasad, P. S. and Moss, C. F. (2010). Effects of competitive prey capture on flight behavior and sonar beam pattern in paired big brown bats, *Eptesicus fuscus*. *J. Exp. Biol.* **213**, 3348–3356.
- Duncan, J., Martens, S. and Ward, R. (1997). Restricted attentional capacity within but not between sensory modalities. *Nature* **387**, 808–810.
- Falk, B., Jakobsen, L., Surlykke, A. and Moss, C. F. (2014). Bats coordinate sonar and flight behavior as they forage in open and cluttered environments. *J. Exp. Biol.* **217**, 4356–4364.
- Fujioka, E., Aihara, I., Watanabe, S., Sumiya, M., Hiryu, S., Simmons, J. A., Riquimaroux, H. and Watanabe, Y. (2014). Rapid shifts of sonar attention by *Pipistrellus abramus* during natural hunting for multiple prey. *J. Acoust. Soc. Am.* **136**, 3389–3400.
- Gadziola, M. A., Grimsley, J. M. S., Faure, P. A. and Wenstrup, J. J. (2012). Social vocalizations of big brown bats vary with behavioral context. *PLoS ONE* **7**, e44550.

- Ghose, K. and Moss, C. F.** (2003). The sonar beam pattern of a flying bat as it tracks tethered insects. *J. Acoust. Soc. Am.* **114**, 1120.
- Griffin, D. R.** (1958). *Listening in the Dark*. New York: Yale University Press.
- Griffin, D. R., Webster, F. A. and Michael, C. R.** (1960). The echolocation of flying insects by bats. *Anim. Behav.* **8**, 141-154.
- Hartley, D. J. and Suthers, R. A.** (1989). The sound emission pattern of the echolocating bat, *Eptesicus fuscus*. *J. Acoust. Soc. Am.* **85**, 1348-1351.
- Holderied, M. W. and von Helversen, O.** (2003). Echolocation range and wingbeat period match in aerial-hawking bats. *Proc. R. Soc. B Biol. Sci.* **270**, 2293-2299.
- Holderied, M. W., Korine, C., Fenton, M. B., Parsons, S., Robson, S. and Jones, G.** (2005). Echolocation call intensity in the aerial hawking bat *Eptesicus bottae* (Vespertilionidae) studied using stereo videogrammetry. *J. Exp. Biol.* **208**, 1321-1327.
- Holland, R. A.** (2007). Orientation and navigation in bats: known unknowns or unknown unknowns? *Behav. Ecol. Sociobiol.* **61**, 653-660.
- Jakobsen, L. and Surlykke, A.** (2010). Vespertilionid bats control the width of their biosonar sound beam dynamically during prey pursuit. *Proc. Natl. Acad. Sci. USA* **107**, 13930-13935.
- Jakobsen, L., Kalko, E. K. V. and Surlykke, A.** (2012). Echolocation beam shape in emballonurid bats, *Saccopteryx bilineata* and *Cormura brevirostris*. *Behav. Ecol. Sociobiol.* **66**, 1493-1502.
- Jakobsen, L., Brinkløv, S. and Surlykke, A.** (2013a). Intensity and directionality of bat echolocation signals. *Front. Physiol.* **4**, 89.
- Jakobsen, L., Ratcliffe, J. M. and Surlykke, A.** (2013b). Convergent acoustic field of view in echolocating bats. *Nature* **493**, 93-96.
- Jakobsen, L., Olsen, M. N. and Surlykke, A.** (2015). Dynamics of the echolocation beam during prey pursuit in aerial hawking bats. *Proc. Natl. Acad. Sci. USA* **112**, 8118-8123.
- Jensen, M. E. and Miller, L. A.** (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.
- Jensen, M. E., Moss, C. F. and Surlykke, A.** (2005). Echolocating bats can use acoustic landmarks for spatial orientation. *J. Exp. Biol.* **208**, 4399-4410.
- Kjær, B.** (1982). *Condenser Microphones and Microphone Preamplifiers for Acoustic Measurements*. Nærum, Denmark: Brüel & Kjær.
- Kothari, N. B., Wohlgemuth, M. J., Hulgard, K., Surlykke, A. and Moss, C. F.** (2014). Timing matters: sonar call groups facilitate target localization in bats. *Front. Physiol.* **5**, 179.
- Moss, C. F. and Surlykke, A.** (2010). Probing the natural scene by echolocation in bats. *Front. Behav. Neurosci.* **4**, 33.
- Neuweiler, G.** (1990). Auditory adaptations for prey capture in echolocating bats. *Physiol. Rev.* **70**, 615-641.
- Norum, U., Brinkløv, S. and Surlykke, A.** (2012). New model for gain control of signal intensity to object distance in echolocating bats. *J. Exp. Biol.* **215**, 3045-3054.
- Roeder, K. D.** (1966). Acoustic sensitivity of the noctuid tympanic organ and its range for the cries of bats. *J. Insect Physiol.* **12**, 843-859.
- Sandig, S., Schnitzler, H.-U. and Denzinger, A.** (2014). Echolocation behaviour of the big brown bat (*Eptesicus fuscus*) in an obstacle avoidance task of increasing difficulty. *J. Exp. Biol.* **217**, 2876-2884.
- Schnitzler, H. U. and Kalko, E. K. V.** (2001). Echolocation by insect-eating bats. *Bioscience* **51**, 557-569.
- Simmons, J. A.** (2014). Temporal binding of neural responses for focused attention in biosonar. *J. Exp. Biol.* **217**, 2834-2843.
- Surlykke, A. and Kalko, E. K. V.** (2008). Echolocating bats cry out loud to detect their prey. *PLoS ONE* **3**, e2036.
- Surlykke, A. and Moss, C. F.** (2000). Echolocation behavior of big brown bats, *Eptesicus fuscus*, in the field and the laboratory. *J. Acoust. Soc. Am.* **108**, 2419.
- Surlykke, A., Ghose, K. and Moss, C. F.** (2009a). Acoustic scanning of natural scenes by echolocation in the big brown bat, *Eptesicus fuscus*. *J. Exp. Biol.* **212**, 1011-1020.
- Surlykke, A., Pedersen, S. B. and Jakobsen, L.** (2009b). Echolocating bats emit a highly directional sonar sound beam in the field. *Proc. R. Soc. B Biol. Sci.* **276**, 853-860.
- Wright, G. S., Chiu, C., Xian, W., Wilkinson, G. S. and Moss, C. F.** (2013). Social calls of flying big brown bats (*Eptesicus fuscus*). *Front. Physiol.* **4**, 9.
- Wright, G. S., Chiu, C., Xian, W., Wilkinson, G. S. and Moss, C. F.** (2014). Social calls predict foraging success in big brown bats. *Curr. Biol.* **24**, 885-889.