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## Acoustic mirror effect increases prey detection distance in trawling bats

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**Abstract** Many different and phylogenetically distant species of bats forage for insects above water bodies and take insects from and close to the surface; the so-called ‘trawling behaviour’. Detection of surface-based prey by echolocation is facilitated by acoustically smooth backgrounds such as water surfaces that reflect sound impinging at an acute angle away from the bat and thereby render a prey object acoustically conspicuous. Previous measurements had shown that the echo amplitude of a target on a smooth surface is higher than that of the same target in mid-air, due to an acoustic mirror effect. In behavioural experiments with three pond bats (*Myotis dasycneme*), we tested the hypothesis that the maximum distances at which bats can detect prey are larger for prey on smooth surfaces than for the same prey in an airborne situation. We determined the moment of prey detection from a change in echolocation behaviour and measured the detection distance in 3D space from IR-video recordings using stereo-photogrammetry. The bats showed the predicted increase in detection distance for prey on smooth surfaces. The acoustic mirror effect therefore increases search efficiency and contributes to the acoustic advantages encountered by echolocating bats when foraging at low heights above smooth water surfaces. These acoustic advantages may have favoured the repeated evolution of trawling behaviour.

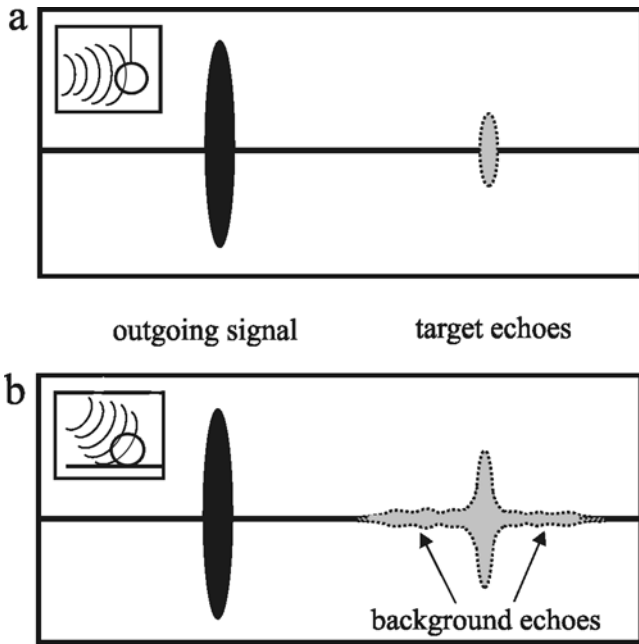
### Introduction

Bats which capture insects or fish from or close above water surfaces are called ‘trawling bats’. This ecotype with its strikingly similar morphological and ecological

characteristics evolved independently in at least three bat families (Vespertilionidae, Noctilionidae, Phyllostomidae; e.g., Kalko et al. 1998; Ruedi and Mayer 2001; Weinbeer et al., in press) and again within one genus (*Myotis*, family Vespertilionidae) it evolved several times convergently through independent adaptive radiations in geographically widely separated areas (Ruedi and Mayer 2001; Fenton and Bogdanowicz 2002). Two factors have been previously reported to have contributed to this convergent evolution. Firstly, aquatic habitats are highly productive in terms of insect biomass and therefore rewarding feeding habitats (Syme et al. 2001). Secondly, the detection of surface-based prey by echolocation is facilitated by acoustically smooth backgrounds such as water surfaces. The echolocation calls of trawling bats typically impinge at acute angles on the water surface and therefore the bats receive no or very low background echo (specular reflection). As a consequence, prey on the surface are acoustically conspicuous for echolocating bats, whereas they cannot find prey positioned on surfaces that produce strong clutter-echoes such as rippled or plant-covered water (Jones and Rayner 1988; Kalko and Schnitzler 1989; Mackey and Barclay 1989; Boonman et al. 1998; Rydell et al. 1999; Siemers et al. 2001; Siemers and Schnitzler 2004).

In the present study, we investigate a third possible advantage of foraging above smooth-surfaced water bodies. In previous acoustic measurements, Siemers et al. (2001) showed that the echo sound pressure level (SPL) of a mealworm on a smooth surface (linoleum screen) is on average 6.7 dB above the echo SPL of a mealworm suspended in mid-air (compare Fig. 1). The increase in echo SPL is presumably caused by an acoustic mirror effect which produces echo trains containing not only the direct echo from prey to receiver, but also wavefronts that travel via the smooth surface and add up. From these echo-acoustic properties, we predicted that the detection distance for bats should be larger when foraging for prey on smooth surfaces than when foraging for the same prey in an airborne situation. Due to spherical spreading, sound pressure decreases inversely proportionally over distance.

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**Fig. 1** Schematic illustration of the signal that a bat will receive for the ensonification of a mealworm suspended in mid-air **a** and a mealworm positioned on a smooth surface **b**. Whereas there are no clutter echoes from background for air-borne prey, surface based prey is embedded in weak clutter echoes (unless the surface is an ideally and completely smooth one). The echo SPL for a target on a smooth surface is higher than for the same target in an airborne situation because of an acoustic mirror effect

Accordingly, the sound pressure  $P(D_1)$  at a distance  $D_1$  is related to  $P(D_2)$  at distance  $D_2$  as follows:

$$\frac{P(D_2)}{P(D_1)} = \frac{D_1}{D_2} \quad (1)$$

The sound pressure level (SPL) as a logarithmic measure is defined as  $\text{SPL}(P_x) = 20 \times \log(P_x/P_0)$ ,  $P_x$  being the sound pressure of interest and  $P_0$  the reference sound pressure. It follows from Eq. (1) :

$$\text{SPL}(D_2) - \text{SPL}(D_1) = 20 \times \log\left(\frac{D_1}{D_2}\right) \quad (2)$$

For calculating an echo SPL ( $\text{SPL}_e$ ), we have to assume spherical spreading both from bat to target for the outgoing pulse, and from target to bat for the echo and hence to double the difference in SPL from Eq. (2) :

$$\text{SPL}_e(D_2) - \text{SPL}_e(D_1) = 40 \times \log\left(\frac{D_1}{D_2}\right) \quad (3)$$

From the 6.7 dB difference in echo SPL for a mealworm on a smooth linoleum screen versus a mealworm suspended in air (Siemers et al. 2001) and Eq. (3), we get the factor predicting the increase in detection distance  $D_{\text{linoleum}}/D_{\text{air}}$ :

$$6.7 \text{ dB} = 40 \times \log\left(\frac{D_{\text{linoleum}}}{D_{\text{air}}}\right) \quad (4)$$

and hence:

$$\frac{D_{\text{linoleum}}}{D_{\text{air}}} = 1.5 \quad (5)$$

If detection distance depends on echo SPL and not on noise or clutter in both situations, we would predict that the detection distance for prey on a smooth surface is larger than that for airborne prey by a factor of 1.5 due to the acoustic mirror effect (Eq. (5)). We set up a behavioural experiment using three pond bats (*Myotis dasycneme*) to test this prediction.

## Methods

### Animals and housing

We captured three male, adult pond bats from a colony close to Hannover, Germany under licence (BR Hannover 503.62-22202/1) in May 2000. Pond bats are listed as endangered species in Germany and therefore the number of bats had to be restricted to the small sample of only three individuals. The bats were housed for 8 weeks at Tübingen University with constant access to water and regular supplements of vitamins and minerals and released at the site of capture afterwards.

### Flight room and experimental procedure

The experiments were conducted in a large, sound-attenuated flight room (13 m × 6 m × 2 m) in the dark and with bats flying singly. The bats were trained to capture freshly killed mealworms suspended from 0.1 mm diameter nylon threads 80 cm below the ceiling and to glean mealworms from a 5 m × 3 m smooth linoleum screen (PVC). The mealworms' body axes was aligned perpendicular to the bats flight path (two tethers for airborne prey), to reproduce the setting from the echo measurements by Siemers et al. (2001). One prey item was presented at a time. We recorded echolocation and flight behaviour for (1) control flights with no prey being presented; (2) aerial captures and (3) captures from the linoleum screen.

### Sound recording and analysis

We picked up echolocation calls with 1/4 in. Brüel & Kjaer condenser microphones (Type 4135), amplified and high-pass filtered the signal at 22.4 Hz with Brüel & Kjaer amplifiers (Type 2608) and recorded them on tape at 30 in./s using a Racal Store 4DS high speed recorder (speed 8-times; 1/4 in. tape). The signal was played back at 1/8 of the recording speed and digitized with 51.2 kHz sampling rate (corresponding to 409.6 kHz effective sampling rate relative to tape speed during recording). Digital sound analysis was performed using the colour spectrograph Sona-PC (B. Waldmann, Universität Tübingen; details in Siemers and Schnitzler 2000). We chose a 256 FFT (Hann window,

93.75% overlap), resulting in a frequency resolution of 1.6 kHz. We measured starting and terminal frequency on the first harmonic of each signal at 25 dB below peak frequency from the spectrogram. Pulse duration and pulse interval were measurements on the time signal with a resolution 0.039 ms. Pulse interval was measured from the onset of one pulse to the onset of the preceding pulse.

### Video recording and 3D reconstruction

The flight behaviour of the bats was video taped with two cameras for subsequent three-dimensional (3D) reconstruction of the bat's position. Sound and video recordings were synchronised using a VITC controller. We used Sanyo VC 1950 CCD video cameras, 4.8 mm objectives, Orion Combi 600 LCD recorders and custom-made infra-red stroboscopes. The cameras were mounted in fixed position relative to each other, 2 m apart. The maximum overlap of the camera images was at a distance of 6 m and the resulting surveyed area approx. 6 m wide. The camera setup had previously been calibrated for 3D reconstruction (backward calculation of camera positions using defined pass points; Langeheinecke 2000). Photogrammetry permits reconstruction of the 3D position of an object from images taken with two well-separated cameras with known relative positions (forward reconstruction; see Finsterwalder and Hofmann 1968; Schwedefsky and Ackermann 1976). Errors for reconstruction of a 1 m calibration rod in 3D space at about the bats distance from the setup averaged  $1.4 \pm 1.1$  cm (mean  $\pm$  sd, max. = 3.6 cm,  $n=10$ ); i.e., generally below 3%.

The videos were digitized (Fledermaus 1.5, HaSoTec), 2D-positions of the bat (most anterior point; if visible the nose) and the mealworm extracted and their 3D positions calculated using custom written software (Ftrans, D3D, Plot; D. Menne & P. Pilz, Animal Physiology, Universität Tübingen).

### The criterion for prey detection

We determined the first reaction of the bats to the prey from a change in their echolocation behaviour relative to the control flights (no prey present). The first call in capture situations that markedly deviated from the call patterns typically observed in control sequences was used to indicate a prey-related reaction (reaction call). The echo of the preceding call must therefore have conveyed prey information to the bat. We assumed that this preceding call marked the moment of prey detection (detection call). Accordingly the 3D distance between the bat at the moment of prey detection and the mealworm is the 'detection distance'.

We chose call duration as the criterion parameter because it was less variable during control flights than pulse interval and showed a prey-related change earlier during an approach sequence than starting or terminal frequency. From the control flight sequences (five for two bats, four for the other one), we calculated an individual threshold for

each bat at that individual's mean call duration (2nd order means) minus one standard deviation (mean of the standard deviations for all sequences per individual). The first call of an approach sequence whose call duration dropped below this threshold, followed by decreasing pulse duration until the terminal group or 'buzz', was considered to be the 'reaction call'. The preceding signal was accordingly considered to be the 'detection call'.

*Statistical tests* were calculated using Systat 10 (SPSS).

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## Results

Search calls from the control flights had average pulse durations of about 3 ms and the first harmonic swept from about 75 kHz down to 27 kHz. When the bats passed the area in the flight room where prey was usually presented, they shortened pulse interval from around 3 ms to around 2.5 ms even in control flights, but never broadcast an approach sequence or a buzz. When prey was presented, the bats switched from search calls to approach calls after prey detection. During the approach, the bats shortened pulse interval and pulse duration continuously until reaching the shortest and nearly invariant values in the 'buzz II' (Table 1; series of short calls at about 6 ms pulse interval, accompanied by sudden drop in terminal frequency, Griffin 1958; Kalko and Schnitzler 1989). Differences in call parameters between approaches on airborne mealworms versus mealworms on the linoleum screen were small, albeit significant in some cases (Table 1).

The bats entered the camera-surveyed area at flight heights of around 90 cm when hunting airborne prey, and at around 50 cm when foraging for mealworms on the linoleum. As predicted, the 3D detection distance was larger for prey on linoleum ( $1.55$  cm  $\pm$  0.1 m; mean  $\pm$  SEM;  $n=3$  bats) than for airborne prey ( $1.15$  m  $\pm$  0.1 m; individual data and statistics in Fig. 2). The individual mean detection distances for prey on linoleum were on average  $1.4 \pm 0.1$  times (mean  $\pm$  SEM,  $n=3$  bats) larger than the individual mean detection distances for airborne prey.

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## Discussion

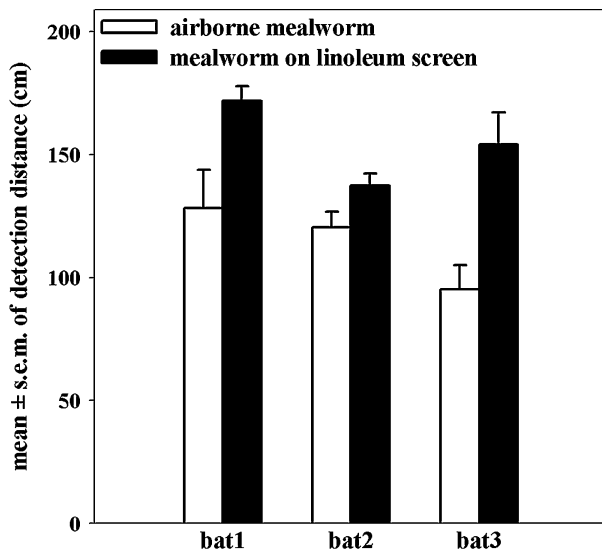
Despite the small sample, restricted to only three bats for conservation reasons, we found the detection distance for prey on the smooth surface to be significantly larger than that for the same prey in mid-air. Furthermore, the increase in detection distance recorded (factor 1.4) was close to the one we had predicted (factor 1.5) building on the acoustic measurements by Siemers et al. (2001). This close match suggests that detection depends on echo SPL rather than on noise or clutter. The weak clutter echoes present for mealworms on the linoleum screen, but not for the prey in mid-air (Fig. 1; Siemers et al. 2001), do not seem to influence the prey detection performance of the bats to a large extent. Otherwise one would have expected shorter detection distances for surface-based as compared to airborne prey. As the background echoes for natural calm water

**Table 1** Comparison of call parameters from prey capture sequences

	Search phase	Initial approach	buzz I	buzz II
Starting frequency (kHz)	air: 76.7±4.0	74.5±6.4	53.1±4.3	30.2±1.9
	lino: 76.0±3.6	69.8±4.8	57.0±4.6	29.7±1.6
	$F_{1,28}=1.50$ $p=0.2301$	$F_{1,26}=7.22$ $p=0.0124$	$F_{1,28}=6.90$ $p=0.0138$	$F_{1,28}=0.74$ $p=0.3954$
Terminal frequency (kHz)	air: 27.1±0.7	24.5±0.8	18.9±1.1	10.9±0.7
	lino: 27.1±0.7	24.9±0.5	21.8±1.5	11.3±1.3
	$F_{1,28}<0.01$ $p=0.9982$	$F_{1,26}=2.26$ $p=0.1451$	$F_{1,28}=39.88$ $p<0.0001$	$F_{1,28}=1.24$ $p=0.2741$
Pulse duration (ms)	air: 3.0±0.3	1.9±0.2	1.1±0.2	0.7±0.1
	lino: 3.2±0.1	2.0±0.1	1.2±0.1	0.6±0.1
	$F_{1,28}=9.21$ $p=0.0051$	$F_{1,26}=1.84$ $p=0.1871$	$F_{1,28}=2.29$ $p=0.1413$	$F_{1,28}=4.55$ $p=0.0417$
Pulse interval (ms)	air: 58.7±9.2	21.7±4.6	8.1±1.0	5.0±0.1
	lino: 62.5±7.3	28.5±3.9	9.0±0.9	5.0±0.1
	$F_{1,28}=2.10$ $p=0.1587$	$F_{1,26}=25.18$ $p<0.0001$	$F_{1,28}=9.13$ $p=0.0053$	$F_{1,28}=1.90$ $p=0.1791$
Number of calls per phase		air: 6.5±4.1		38.1±4.0
		lino: 5.2±2.6		30.6±2.8
		$F_{1,28}=1.46$ $p=0.2363$		$F_{1,28}=40.22$ $p<0.0001$
Sample size (sequences, calls)	bat1 air: 5,108	5,27		5,193
	lino: 6,113	6,16		6,195
	bat2 air: 5,141	5,41		5,187
	lino: 6,117	6,24		6,114
	bat3 air: 5,116	5,30		5,192
	lino: 5,109	5,31		5,153

For every echolocation phase, all calls were averaged per sequence. The sequence means (1st order means) were subjected to repeated measures ANOVAs (several sequences per individual bat) testing for differences between approaches to airborne targets (air) and targets on the linoleum screen (lino). The resulting  $F$  and  $p$  values are tabulated here together with 2nd order means±standard deviation for the respective phases and experimental conditions. We analyzed a total of 32 sequences containing 1907 calls; the breakdown of the sample size into individual bats and phases are tabulated in the last row

The approach sequence is subdivided into the initial approach and a terminal group or 'buzz', which can be further subdivided into 'buzz I' and 'buzz II' (Griffin 1958; Kalko and Schnitzler 1989; Siemers and Schnitzler 2000)



**Fig. 2** Prey detection distances for the three pond bats. The detection distance for prey on the smooth linoleum surface was significantly larger than the detection distance for airborne prey (repeated measures ANOVA:  $F_{1,26}=20.56$ ,  $p=0.0001$ ). Sample sizes per bat were (airborne/linoleum): bat1 (5/4), bat2 (5/6), bat3 (5/5)

bodies are still lower than for linoleum (compare Siemers et al. 2001 and Stilz 2004), our experiments were conservative estimates of the natural situation a bat will encounter when foraging above a pond. Field detection distances for

trawling bats are within the range we measured (1.28 m for *M. daubentonii*, Kalko and Schnitzler 1989; about 2 m for *M. dasycneme* Britton et al. 1997).

In contrast to tethered mealworms, airborne prey in the field will be flying insects in most cases. Due to acoustical glints produced by their moving wings (Kober and Schnitzler 1990), flying insects might be echo-acoustically more conspicuous to bats than resting insects. If at all the echoes of the frequency modulated (FM) calls convey conspicuous glints, their echo SPL will likewise be increased by the acoustic mirror effect, provided the insects are flying very close to the water surface.

The acoustic mirror effect will only be effective if a prey object protrudes sufficiently above the water surface to generate wave fronts that travel back to the bat via the surface. Apart from insects flying close to the water surface, this could well be imagined for emerging chironomids that often sit on the water surface or for floating large arthropods, e.g., moths. In such a situation, the acoustic mirror effect will increase the detection distance for a foraging bat, and thereby enlarge its search volume and hence search efficiency. Presumably an enlargement of the search volume right in front of the bat will not be very important, because the foraging bat will already sample sufficiently straight ahead as it flies at 2–6 m/s and emits 7–15 calls/s (Jones and Rayner 1988; Kalko and Schnitzler 1989; Britton et al. 1997). The enlargement of the surveyed area to the left and the right of its flight trajectory will directly translate

into increased foraging efficiency. Obviously, the search volume of a bat foraging at low heights above water is truncated at its lower end by the water surface, whereas in open space bats can survey larger volumes. Foraging efficiency is further influenced by prey abundance that often will be higher above water as compared to the open sky. Data on the directionality of the bats' echolocation systems under field conditions and on prey abundance will be necessary to work out quantitative predictions that are testable in the field. Our data show that the acoustic mirror effect increases prey detection distance and it appears very likely that bats benefit from it when foraging over calm, open water bodies. Along with the high insect biomass and very low background echo level of water bodies, this acoustic mirror effect renders aquatic habitats very favourable for echolocating bats and might, in part, explain the repeated convergent evolution of trawling bat species.

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