

The acoustic advantage of hunting at low heights above water: behavioural experiments on the European ‘trawling’ bats *Myotis capaccinii*, *M. dasycneme* and *M. daubentonii*

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Summary

We have demonstrated in behavioural experiments that success in capturing prey from surfaces in ‘trawling *Myotis*’ (*Leuconoë*-type) depends on the acoustic properties of the surface on which the prey is presented. Two types of surface structure were ensonified with artificial bat signals to probe their acoustic characteristics. We have shown that perception of prey by echolocation is easier if the prey is presented on a smooth surface (such as calm water) than if it is presented on a structured surface (such as vegetation or the ground). This is because the smooth surface reflects a much lower level of clutter echoes than the structured one if ensonified at an angle typical for bats foraging low over water. The ensonification experiments revealed that the sound pressure level of the echo was even higher for mealworms on a smooth surface than for mealworms suspended in air. This might be because waves travelling *via* the surface also contribute to the echo (e.g. reflection from the surface to the mealworm, back to the surface and then to the

receiver). From the behavioural experiments, we conclude that ‘trawling *Myotis*’ take isolated objects on smooth (water) surfaces for prey. Those objects reflect isolated, stationary acoustic glints back to the echolocating bats. Conversely, ‘trawling *Myotis*’ will not recognise prey if prey echoes are embedded in numerous clutter echoes.

We have demonstrated marked similarities between the three European ‘trawling *Myotis*’ species *M. dasycneme*, *M. daubentonii* and *M. capaccinii* in echolocation behaviour, search image, foraging strategy and prey perception. We propose that a combination of prey abundance and acoustic advantages could have led to repeated and convergent evolution of ‘trawling’ bats in different parts of the world.

Key words: sensory ecology, echolocation, ensonification, prey perception, bat, *Myotis capaccinii*, *Myotis dasycneme*, *Myotis daubentonii*, *Leuconoë*, trawling, convergence.

Introduction

Lakes and rivers are favourable foraging habitats for many bat species (Zahn and Maier, 1997; Warren et al., 2000; Syme et al., 2001). The high productivity of aquatic habitats in terms of insect biomass attracts bats that can be found hunting at different heights over these water bodies. Flying close to water surfaces reduces the flight costs of the bats because of the aerodynamic ‘ground effect’ (Aldridge, 1988; Norberg and Rayner, 1987; Jones and Rayner, 1991). In Europe, three species of bat, all belonging to the genus *Myotis* (Chiroptera: Vespertilionidae), habitually hunt low over water, i.e. between 10 and 50 cm above the water surface (Jones and Rayner, 1988; Kalko and Schnitzler, 1989; Kalko, 1990; Médard and Guibert, 1990; Britton et al., 1997); these three species are Daubenton’s bat *M. daubentonii* (Kuhl), the pond bat *M. dasycneme* (Boie) and the long-fingered bat *M. capaccinii* (Bonaparte).

These bats often glean arthropods from the water surface; a behaviour termed ‘trawling’ in the relevant literature (Jones

and Rayner, 1991; Britton et al., 1997; Boonman et al., 1998; Britton and Jones, 1999; Siemers et al., 2001a). It is important to note, however, that ‘trawling *Myotis*’ do not rake through the water at random, as the literal meaning of ‘trawling’ would suggest. Instead, they gaff prey from the surface with their feet in directed ‘pointed dips’ (Jones and Rayner, 1988; Kalko and Schnitzler, 1989; Siemers et al., 2001a). In the present publication, we use the term ‘trawling bats’ to characterize bats hunting at low heights above water surfaces and (occasionally) gaffing prey from the surface. ‘Trawling *Myotis*’ also catch insects emerging from or swarming over their aquatic habitat in the air. At least for *M. daubentonii*, there is strong telemetric evidence indicating that the bats spend more than 90% of their foraging time over water (M. Dietz, personal communication).

‘Trawling’ bats prefer to forage over calm, open water to foraging over water covered by artificial foam blocks (Mackey and Barclay, 1988), floating plants or debris (Boonman et al.,

1998) or water that is turbulent and covered in ripples (Frenckel and Barclay, 1987; Rydell et al., 1999; Warren et al., 2000). In most cases, this preference cannot be explained by prey abundance (Frenckel and Barclay, 1987; Boonman et al., 1998; Rydell et al., 1999); but see Warren et al. (2000), who demonstrate that insect abundance correlates with the habitat preferences of bats.

As 'trawling *Myotis*' are assumed to find their prey by echolocation, the preference for calm, open water is interpreted in terms of the acoustic conspicuousness of the prey. When foraging for insects sitting on or flying close to duckweed, rippled water, the ground or vegetation, prey perception becomes difficult. In this situation, the bats are faced with the problem of detecting prey echoes in background echoes, the so-called clutter echoes. Clutter echoes may mask the prey echo, thus reducing the chance of prey detection (for a review, see Fenton, 1990) (Neuweiler, 1990; Schnitzler and Kalko, 1998, 2001). The acoustic situation is different for bats foraging for prey flying close to or floating on calm water surfaces. Smooth water surfaces act like acoustic mirrors and, hence, according to Snell's law, reflect the echolocation signal away from the bat when the echo impinges at a small angle relative to the surface; therefore, little or no clutter echo is reflected back to the bat (Mackey and Barclay, 1989; Schnitzler et al., 1994; Boonman et al., 1998; Rydell et al., 1999). In contrast, a target (an insect or, for example, duckweed) floating on a calm water surface will reflect an echo (Boonman et al., 1998; Rydell et al., 1999). Thus, the field studies mentioned above suggest that calm water surfaces are favourable for the perception of prey by echolocation. In contrast, duckweed cover or rippled water reflects clutter echoes that might interfere with prey detection by masking the prey echo.

In the present study, we tested the hypothesis that the perception of prey by echolocation is easier with prey on smooth surfaces than with prey on structured surfaces. To complement previous field studies (Boonman et al., 1998; Rydell et al., 1999), we performed standardised behavioural experiments under controlled conditions. With the exception of Boonman et al. (1998), all previous workers studied bat activity (i.e. foraging effort) but not capture success over calm compared with cluttered water and thus assessed prey perception only indirectly. In our experiments, we used capture success as a measure of prey perception on the basis of the feasible hypothesis that a directed approach to, and capture of, a target must be preceded by the combined task of detection, classification and localisation of prey; i.e. prey perception. We offered prey to bats on artificial surfaces that mimic the echo properties of water (a linoleum screen) and of soil or duckweed cover (a 'clutter screen'). We then measured the capture success of the bats while foraging above the different surfaces. We also presented various prey dummies to test the hypothesis that, for prey detection, 'trawling *Myotis*' species initially use a refinable search image that could be as simple as an echo reflected by a small object on an acoustically smooth surface.

We wanted to focus solely on the acoustic properties of the

surface on which the prey is presented. We therefore varied this parameter only, while all other parameters, including prey abundance, the site where prey was offered and the required manoeuvrability of the bats during prey capture, remained unaltered.

To correlate the bats' performance with the acoustic properties of the different experimental situations, we ensonified our settings and measured their echo properties using an 'artificial bat'. In contrast to previous studies (Boonman et al., 1998; Rydell et al., 1999), we did not use clicks during the experiments, but frequency-modulated signals simulating the search calls used by the bats. Echoes of bat-like signals will be closer to the natural situation than click echoes. We did not expect strong clutter echoes from the smooth linoleum screen and we therefore hypothesised that detection of prey positioned directly on the linoleum screen (and on other smooth surfaces such as water surfaces) must be similar to detection of air-borne prey in open spaces for an echolocating bat. To test this assumption experimentally, we also ensonified a mealworm suspended in the middle of a sound-attenuated chamber.

Our knowledge of foraging habits, echolocation, prey perception and prey capture in *M. daubentonii* is considerable (Jones and Rayner, 1988; Kalko and Schnitzler, 1989; Vaughan et al., 1996; Boonman et al., 1998; Britton and Jones, 1999; Rydell et al., 1999; Warren et al., 2000). However, the foraging behaviour of *M. dasycneme* has been the focus of only one field study (Britton et al., 1997), and there is almost no such information on the Mediterranean *M. capaccinii* except for a note by Kalko (1990). As all three 'trawling' species forage in low searching flight above water surfaces and thus face very similar physical constraints, we hypothesised that all three species will have evolved very similar search images, foraging strategies and sensory abilities. To test this assumption, we performed our study with all three European 'trawling' bat species.

Materials and methods

Animals and experimental enclosures

All the bats used in the experiments were captured with mist nets in transfer flight from a known roost to the foraging area. We captured *Myotis daubentonii* at Klosterreichenbach, Southern Germany, in September 1998, *M. capaccinii* at the Devetaschka cave in Northern Bulgaria in May 1999 and *M. dasycneme* from a colony of males in Binnen, Northern Germany, in June 1999 and in May 2000. All captures were performed under licence of the responsible regulatory authorities (Regierungspräsidium Karlsruhe licence no. 73c1-8852.15, Bulgarian National Environmental Agency no. 4800-708, Bezirksregierung Hannover no. 503.41-22201/3 and 503.62-22202/1). All bats were released at the site of capture after the end of the experiments.

The newly caught bats were released into a transportable flight tent with a ground area of 3.5 m × 7 m and approximately 2.5 m in height. The tent was erected in the field or in a large

room close to the site where the bats were captured and had a natural light regime. For the experiments in the flight tent, we kept those bat that started capturing prey spontaneously on the first or second night in captivity. Depending on the species, 50–70% of the individuals did not capture prey in the flight tent and, hence, were fed by hand and released on the second night.

In contrast to the other bats, the *M. dasycneme* captured in 2000 were taken to Tübingen University, where they were kept under an artificial light regime. There, experiments were performed in a large flight room (6 m × 13 m; 2 m in height).

We present data from two male and one female *M. capaccinii*, two male *M. daubentonii* and six male *M. dasycneme* (three in the flight tent in 1999; three in the flight room in 2000).

Behavioural experiments

Experiments were performed during the activity period of the bats either in complete darkness or with dim light (artificial or moonlight), always with one bat at a time. We observed and video-taped the animals' behaviour under stroboscopic infrared illumination using CCD video cameras (Sanyo, VC 1950; 50 half-frames s⁻¹) and Orion Combi 600 LCD recorders.

Mealworms and dummies on different surfaces

Mealworms (larvae of *Tenebrio molitor*, Coleoptera) were presented to the bats on two background surfaces. One surface was a smooth linoleum screen measuring 1.2 m × 1.4 m. The other surface was a 'clutter screen' of the same size: a Polypropylene carpet with latex/clay half-spheres 5 mm in diameter in a regular pattern with approximately 12 mm spacing between them.

The two screens were placed consecutively into the same experimental area within the enclosure (the flight tent or flight room). Live mealworms (usually five) were placed on the screen and replaced when they had been captured by the bat or crawled away. From the video recording, we counted 'passes' with and without a 'capture attempt'. A 'pass' was defined as a bat flying over the experimental area at a height of less than 1 m. Thus, in every pass, the bats approached the mealworms closer than the 1.28 m average detection distance known for *M. daubentonii* in the field (Kalko and Schnitzler, 1989). We scored a 'capture attempt' when a bat touched a mealworm with its feet or uropatagium, irrespective of whether it managed to retrieve it from the screen. We used the number of 'capture attempts' as a measure of prey perception. As successful and unsuccessful attempts both indicated that the bat had perceived its target, we did not differentiate between the two.

Because the bats rarely captured prey from the clutter screen, we always interspersed a session with prey on the clutter screen between two sessions with the linoleum screen. If the bat captured mealworms in both linoleum screen sessions but not in the clutter screen session, we could exclude a lack of searching effort or of hunger as possible explanations for the

lack of capture success from the clutter screen. In 54 sessions of variable length (approximately 5–20 min, depending on the bat's motivation), 1394 passes and 743 capture attempts were recorded.

To investigate whether the bats would capture prey dummies, we presented metal reflectors (a cylinder 25 mm in diameter and 8 mm in height; a rectangular plate 16 mm high and 3 mm wide) and rubber dummies (electrical shrink-wrap tubing of varying length and diameter) on both surfaces.

Acoustics

Recording and analysis of echolocation calls

Echolocation calls were picked up with an ultrasonic microphone (frequency response ±3 dB between 30 and 120 kHz; at frequencies down to 15 kHz and up to 200 kHz, sensitivity dropped by 0.2 dB kHz⁻¹), digitised (sampling rate 312.5 kHz), stored in a memory array (3.3 s real time) and then read out at one-fifteenth of the original speed, D/A-converted (equipment custom-made; Department of Animal Physiology, University of Tübingen) and recorded with a WM-DC6 Sony Walkman.

For analysis, the time-expanded signals were digitised at a sampling rate of 25.6 kHz, processed through a Fast Fourier Transform (FFT; 256 points, Hanning window, FFTs calculated with 93.75% time overlap; Sona-PC; B. Waldmann, University of Tübingen) and displayed as colour sonagrams. The equipment and analysis are described in detail elsewhere (Siemers and Schnitzler, 2000). Pulse duration and pulse interval were measured from the time signal. For each signal, we computed the averaged power spectrum (calculated at a fixed overlap of 33%) to determine the peak frequency; i.e. the frequency with maximum amplitude. Starting frequency and terminal frequency were determined from the sonagram representation at 25 dB below peak frequency of each signal. We only considered the first harmonic for measurements, because it contained most of the signal energy. For each call, we determined starting frequency, peak frequency, terminal frequency, bandwidth, pulse duration and pulse interval. To cover the individual variability of call parameters, we analysed a total of 970 calls: 16 sequences containing 191 search calls from two individual *M. capaccinii*, 19 sequences containing 261 calls from two individual *M. daubentonii* and 29 sequences containing 518 calls from three individual *M. dasycneme*.

Ensonification

To assess the different acoustic scenes the bats were facing in the behavioural experiments, we ensonified the different settings with an ultrasound signal similar to the bats' search calls (see Fig. 2) and recorded and analysed the echoes. We recorded the echoes from the linoleum screen in the presence and absence of a mealworm, from the clutter screen in the presence or absence of a mealworm and from a mealworm suspended in the air. All ensonification experiments were conducted in a sound-attenuated chamber.

The signal used for ensonification was a linear downward-

frequency-modulated sweep of 2 ms duration from 90 kHz to 25 kHz with a peak frequency (maximum amplitude) of 50 kHz (see Fig. 2D). It was designed using custom-written programs and its amplitude was adjusted to fit the characteristics of the amplifier and speaker. After D/A conversion (Gage CompuGen 1100 1 MB card with 12-bit depth and sampling rate of 10 MHz), the signal was fed into a custom-built amplifier and broadcast by a Polaroid series 600 speaker (protective grid present, d.c. bias 200 V; for technical specification, see <http://www.polaroid-oem.com/pdf/electrans.pdf>). The mean sound pressure level (SPL) of the sweep was 84.3 dB at 1 m from the speaker (99.0 dB peak at 50 kHz).

A Polaroid series 600 transducer (protective grid present, d.c. bias 200 V) was also used as a microphone for the recordings. Amplification and power were supplied by a custom-built amplifier. The frequency response of the recording system was non-linear. The sensitivity was $5.0 \pm 1.1 \text{ V Pa}^{-1}$ at 40–60 kHz and decreased gradually to 1.1 V Pa^{-1} at 25 kHz and 1.5 V Pa^{-1} at 90 kHz. The non-linear frequency response was not digitally compensated since this would drastically increase the overall noise level. When calculating mean sound pressure levels, we assumed an overall sensitivity of 5.0 V Pa^{-1} , which is a good approximation in the range 40–60 kHz, where most of the signal energy was broadcast by the speaker. The recorded signals were A/D-converted with a Gage Compuscope 512 PCI 1M Card with 12-bit depth and a sampling rate of 1 MHz. Recording was triggered directly by the CompuGen Card at the start of sound emission. The noise floor of the recording system was 27.0 ± 0.3 dB SPL root mean square (rms). Calibration was performed with a 4138 Bruel&Kjaer 1/8 inch microphone.

For ensonification, the microphone and speaker were mounted on a tripod with a horizontal centre-to-centre distance of 5.6 cm. Both faced the target directly at a distance of 1 m; i.e. their axes intersected at the target. The reflecting surfaces of the apparatus were padded with sound-absorbing material. To ensonify the linoleum screen and the clutter screen, the microphone and speaker were positioned 12 cm above the horizontally placed screens. The axes of the microphone and speaker intersected with the screen surface 1.0 m in front of the 'artificial bat' at an angle of 6.9° . Targets (one mealworm at a time) were placed onto the screens at this point of intersection 1.0 m from the speaker.

The combination of two Polaroid speakers provided strong directionality to the system. The overall intensity of a reflected sweep decreased by 5.5 dB (18.3 dB) for an object 5° (10°) off the system's centre axis.

The echoes of the linoleum screen and of the clutter screen (without mealworm) were recorded 20 times each. The echoes of 25 different mealworms on the linoleum screen were also recorded. Each mealworm was aligned at three angles: 90° (perpendicular), 45° and 0° (parallel) to the impinging sound. Five samples of each setting were recorded and averaged for further statistical analysis. Finally, the echoes of 25 different mealworms on the clutter screen, aligned perpendicular (at 90°) to the impinging sound were

recorded (five samples per mealworm, averaged to obtain one data point per mealworm).

To record the echoes of a mealworm in the air, it was suspended 1.0 m in front of the 'artificial bat' perpendicular to the impinging sound using four nylon threads (diameter 0.1 mm) from the ceiling and one from the floor (25 different mealworms, five samples each). Using the same arrangement, we also ensonified the nylon threads in the absence of a mealworm 20 times.

Data analysis was performed in Matlab 6.0. All signals and echoes were digitally bandpass-filtered from 25 kHz to 90 kHz. Sound pressure levels were calculated from the mean of the squared bandpass-filtered signals over a Hanning window of 100 μs duration. We determined a 2 ms time window when the mealworm echo was to be expected on the basis of the mean peak of the cross-correlation between the sweep and the echoes of the mealworms on the linoleum screen. The window started 5.86 ms after the emission of the sweep. The mean sound pressure levels over this time window were calculated for each recording and compared in the presence and absence of the mealworm on both screens.

We cross-correlated the bandpass-filtered signal (externally recorded 1.0 m in front of the speaker) with the bandpass-filtered echo recordings. Spectrograms were calculated on the basis of a 1024-point FFT over a Hanning window of 256 points extended with zeros to a full size of 1024 points. Overlap was 99.4% (1018 samples), producing a new spectrum every 6 μs .

Statistical analyses

Statistical analyses were performed in Excel 97 for Windows, Systat 10.0 for Windows, JMP 3.2 for Windows and Matlab 6.0. For statistical comparisons among species, call parameters were averaged for each individual; i.e. only one data point per individual was used to avoid pseudoreplication.

Results

Search behaviour and capture success on different surfaces

The three *M. capaccinii* and two *M. daubentonii* started to fly low over the linoleum screen at a height of approximately 5–30 cm ('low searching flight') on the first or second night in the flight tent. Sometimes, they lowered their flight height and brushed their chin over the screen; presumably, they tried to drink from this 'artificial water surface'. The bats never attempted to drink from the clutter screen. All five bats captured mealworms from the linoleum screen. Prey was mostly eaten on the wing, while the bats circled in the flight tent on stereotyped paths higher above the linoleum screen than in low searching flight (usually 50–150 cm). One of the freshly captured *M. capaccinii* males (cap3) gaffed a mealworm from the linoleum screen only 6 min after it was released into the flight tent for the first time. It did not continue to capture prey in the flight tent, however, and thus had to be released to the wild. In the flight tent, the three *M. dasycneme* readily performed aerial catches on tethered

mealworms, but they neither tried to drink from the linoleum screen nor did they capture mealworms from it during five consecutive nights. In the larger flight room at Tübingen University, however, three different *M. dasycneme* readily captured mealworms from the linoleum screen. We assume that *M. dasycneme* did not capture mealworms from the linoleum screen in the flight tent more because of limited manoeuvrability (comparatively high wing loading and a high aspect ratio) (Norberg and Rayner, 1987) than because of sensory limitations. Consequently, quantitative experimental data on prey capture from surfaces and the respective search calls can only be presented for two *M. capaccinii* (cap1, cap2), two *M. daubentonii* (dau1, dau2) and three *M. dasycneme* (dasy1, dasy2, dasy3).

During experimental sessions, all seven bats frequently passed over both the linoleum and the clutter screen (Fig. 1). All bats frequently performed capture attempts at mealworms on the linoleum screen (Fig. 1). The individual bats rarely or never aimed a capture attempt at a mealworm on the clutter screen. Capture attempts by all seven bats of all three species were highly significantly more frequent in passes over the linoleum screen than in passes over the clutter screen (χ^2 -test: $P < 0.0001$ for most bats) (see Fig. 1).

The bats of all three species repeatedly tried to capture the prey dummies (metal and rubber reflectors) on the linoleum screen, but never on the clutter screen.

Echolocation behaviour

Calls recorded during low searching flight from *M. capaccinii*, *M. daubentonii* and *M. dasycneme* were short, downward-frequency-modulated echolocation signals 1.7–3.0 ms in duration (individual means) and 38.9–54.5 kHz in mean bandwidth (=sweep range) (Fig. 2A–C) (Table 1). The species differed slightly but significantly in peak frequency, terminal frequency, bandwidth and pulse duration, but not in starting frequency or pulse interval (Table 1). The largest species, *M. dasycneme*, showed a lower peak and terminal frequency than the two smaller species, *M. capaccinii* and *M. daubentonii*, and bandwidth was highest in *M. daubentonii*. Pulse duration averaged 3.0 ms in *M. dasycneme* and was thus approximately 1 ms longer than in the other two species (Table 1). This was probably an effect of the large flight room, because the three *M. dasycneme* that were kept in the smaller flight tent in 1999 produced search calls that averaged

1.7±0.1 ms in duration (mean ± s.d., $N=172$). Differences between individual bats explained much of the variability in all call parameters (Table 1).

We designed the artificial probe signal that we used to ensimplify our experimental setting to be similar to the signals used by the bats in searching flight during the experiments (Table 1) (Fig. 2). We used a linearly downward-modulated signal sweeping from 90 to 25 kHz, 2.0 ms in duration and with its peak frequency at 50 kHz (Fig. 2D).

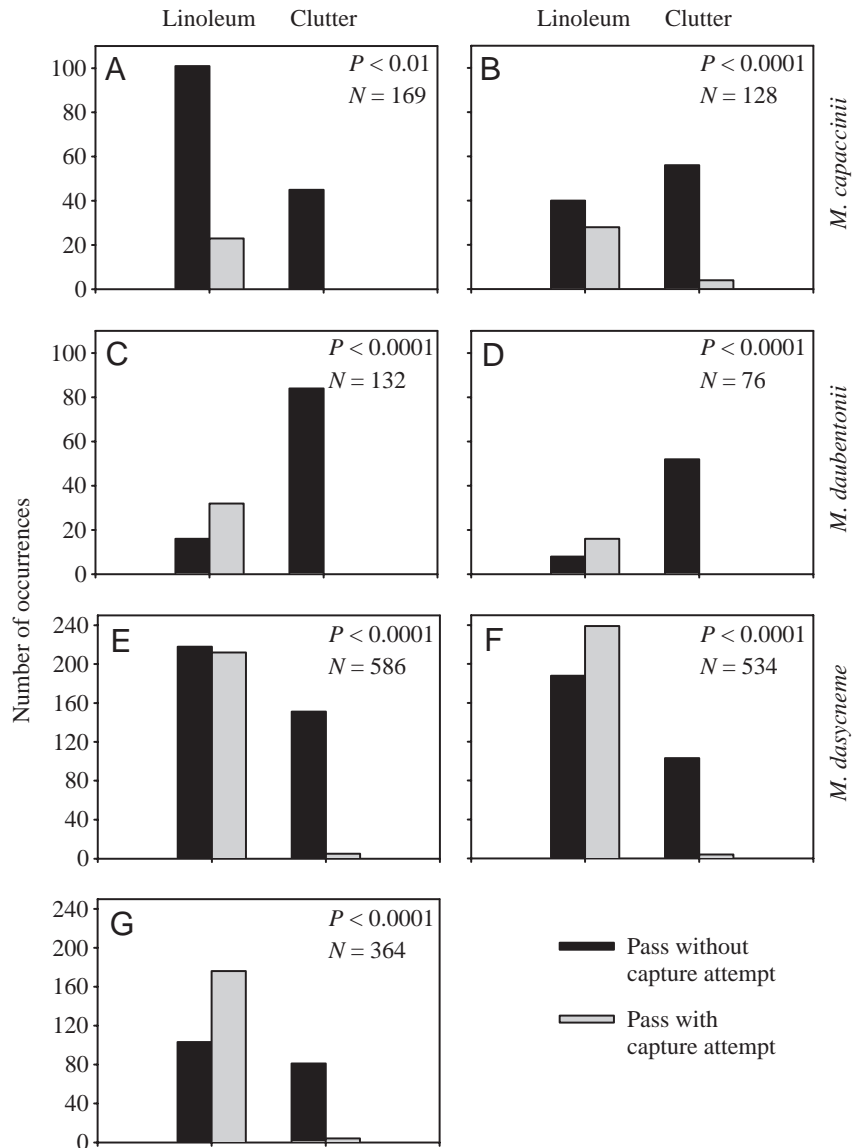


Fig. 1. Mealworms were presented consecutively on a linoleum screen and on a clutter screen with an area of 1.2 m × 1.4 m. During experimental sessions, the two *Myotis capaccinii* (A, cap1; B, cap2), the two *M. daubentonii* (C, dau1; D, dau2) and the three *M. dasycneme* (E, dasy1; F, dasy2; G, dasy3) frequently passed over both the linoleum and the clutter screen without capturing prey (filled columns). All seven bats frequently performed capture attempts (grey columns) on mealworms on the linoleum screen. They rarely or never aimed capture attempts at a mealworm on the clutter screen. All seven bats aimed more capture attempts at mealworms on the linoleum screen than at mealworms on the clutter screen (P -values from Pearson χ^2 -test and sample size are given on the graphs; d.f.=1 in each case).

Ensonification

The 0.1 mm nylon thread in air reflected no conspicuous echo back to our ‘artificial bat’ (Fig. 3A, Fig. 4A). These recordings yielded the same echo SPL as the noise-floor of our apparatus. The linoleum screen reflected a ‘ground echo’ from immediately below the transducer. This off-axis echo followed the outgoing sweep with a delay of 0.73 ms (=12 cm echo travel time, which corresponds to the height of the ‘artificial bat’ above the screen; Fig. 3C, Fig. 4C). In addition, the linoleum screen yielded a weak, smeared, scattered on-axis echo in the frequency range of the outgoing sweep whose SPL was well above the noise-floor of our apparatus (Wilcoxon signed-rank test, $P < 0.0001$) (Table 2). The clutter screen returned a strong, smeared, long echo with decreasing amplitude in the frequency range covered by the outgoing sweep (Fig. 3E), and its SPL was considerably and significantly higher than the echo SPL reflected off the linoleum screen (Wilcoxon signed-rank test, $P < 0.001$) (Fig. 5D) (Table 2).

The echo of a mealworm suspended on fine threads in air perpendicular to the impinging sound was returned as a good copy of the outgoing sweep, as clearly visible in the time signal, the sonogram (Fig. 3B), in the sharp peak of the cross-correlation between sweep and echo ($N=25$ mealworms) (see Fig. 4B) and in the mean SPL (Fig. 5A).

When a mealworm was present on the linoleum screen, a good copy of the outgoing signal could be recorded in the time window when the mealworm echo was expected ($N=75$) (see Fig. 3D, Fig. 4D). Depending on the orientation of the mealworm relative to the impinging sound, the mean averaged echo SPL from the linoleum screen in this time window was 1.8–8.3 dB higher than the background echo reflected by the empty linoleum screen (Fig. 5B) (Table 2). When oriented perpendicular to the impinging sound (90°), the target strength of a mealworm on the linoleum screen was 6.7 dB higher than that of a mealworm suspended in air (Table 2).

When ensonifying a mealworm on the clutter screen, we recorded a strong, smeared, long echo very similar to the clutter screen echo in the absence of a mealworm (Fig. 3E,F). No sharp peak was detectable in the cross-correlation function in the time window when the mealworm echo was expected, either in the presence ($N=25$) (see Fig. 4E) or in the absence ($N=20$) (see Fig. 4F) of a mealworm. The mean averaged echo SPL from the clutter screen in this time

window did not differ in the presence and absence of a mealworm (Fig. 5C) (Table 2).

Discussion

Differences in capture success due to perceptual differences

We tested the hypothesis that prey perception in ‘trawling *Myotis*’ depends on the acoustic properties of the surface on which the prey is presented. We used capture attempts as a measure of prey perception on the basis of the feasible hypothesis that directed approach to and capture of a target must be preceded by the combined task of detection, classification and localisation of the specific prey target; i.e. by prey perception (Schnitzler and Kalko, 1998).

Mealworms on the linoleum screen were readily attacked by

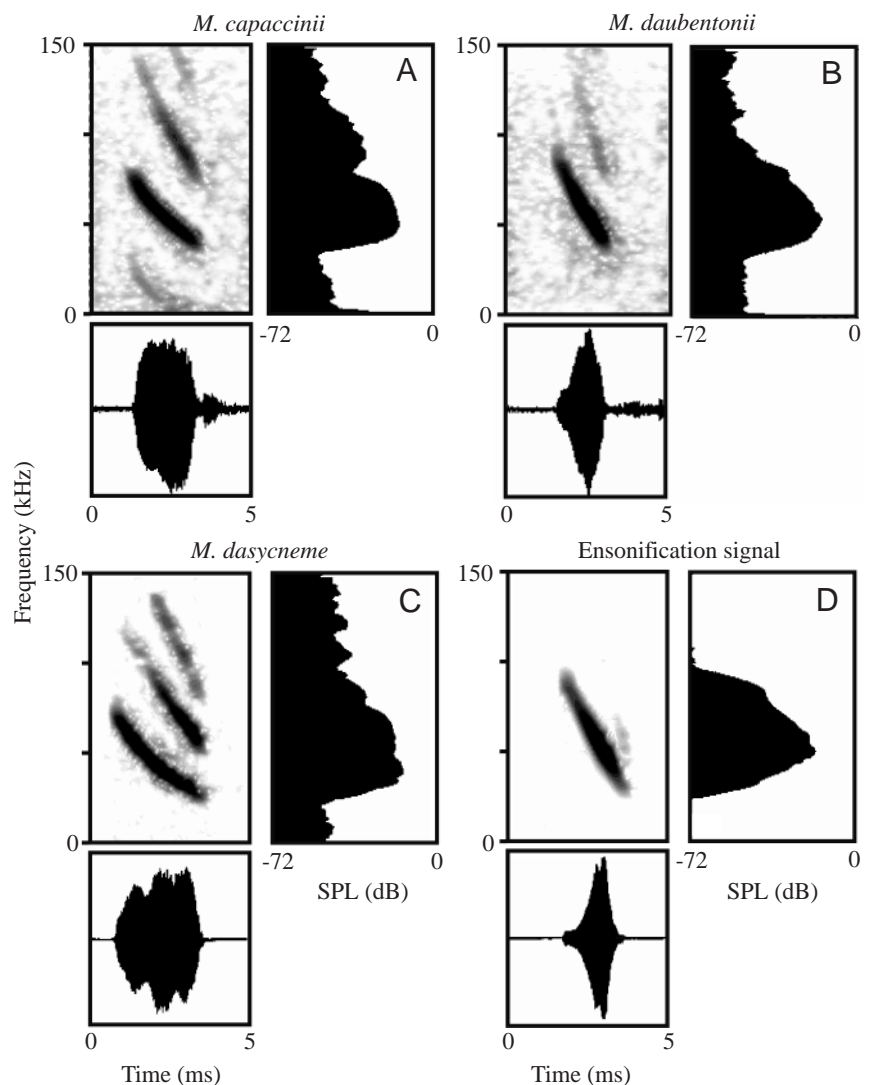


Fig. 2. In low searching flight over the experimental area, all bats emitted short, downward-modulated echolocation signals. Representative calls for *Myotis capaccinii* (A), *M. daubentonii* (B) and *M. dasycneme* (C) are presented as sonograms with the averaged power spectrum on the right and the oscillogram below. The artificial probe signal that we used for ensonification (D, measured 1 m from the speaker) was designed to be similar to the signals used by the bats.

Table 1. Calls recorded during low searching flight from two *Myotis capaccinii* and two *M. daubentonii* in the flight tent and from three *M. dasycneme* in a larger flight room

	Individual	Starting frequency (kHz)	Peak frequency (kHz)	Terminal frequency (kHz)	Bandwidth (kHz)	Pulse duration (ms)	Pulse interval (ms)
<i>M. capaccinii</i>	Cap1 <i>N</i> =73 calls	79.5±8.8* 63.4; 100.1	50.3±4.7 43.5; 64.1	36.6±1.6 33.7; 41.2	42.9±9.0 24.4; 62.6	2.2±0.4 1.4; 3.3	60.2±23.2 18.7; 139.0
	Cap2 <i>N</i> =118	74.6±4.1 66.0; 84.4	50.1±7.1 41.6; 69.0	35.7±1.5 31.5; 35.7	38.9±4.6 27.8; 49.5	2.2±0.3 1.6; 3.1	56.9±18.8 19.8; 118.2
	<i>M. daubentonii</i>	Dau1 <i>N</i> =121	89.8±4.7 65.6; 99.0	53.3±6.2 42.0; 75.0	35.2±2.3 30.4; 42.0	54.5±5.0 33.8; 63.8	1.7±0.24 1.2; 2.5
Dau2 <i>N</i> =140		81.2±5.0 62.2; 91.9	50.2±6.7 39.7; 67.9	31.6±2.7 26.6; 41.2	49.6±6.3 28.9; 60.0	1.8±0.3 1.0; 2.5	47.5±16.9 18.1; 110.6
<i>M. dasycneme</i>		Dasy1 <i>N</i> =152	79.6±5.6 64.9; 93.7	41.8±2.7 33.7; 47.6	28.1±1.2 24.4; 30.7	52.6±5.7 36.4; 66.4	3.0±0.4 2.2; 4.3
	Dasy2 <i>N</i> =167	77.5±4.3 63.0; 88.9	41.8±3.3 34.9; 52.2	27.8±0.9 25.1; 30.0	49.7±4.3 36.8; 61.1	3.0±0.3 2.2; 3.8	69.8±28.6 21.7; 185.5
	Dasy3 <i>N</i> =199	76.1±3.7 60.4; 86.2	41.7±3.7 31.5; 48.7	27.5±1.1 24.0; 30.7	48.5±3.9 33.4; 58.9	3.0±0.4 1.8; 4.4	65.0±20.9 17.5; 162.4

ANOVA

Species
d.f.=2*F*-ratio
*P*3.36
0.1388 (NS)61.16
0.001025.75
0.005110.31
0.0263801.42
<0.00016.27
0.0584 (NS)

Nested ANOVA

Species
d.f.=2*F*-ratio
*P*3.91
0.1142 (NS)73.67
0.000529.12
0.004110.76
0.0240270.18
<0.00017.58
0.0400Individuals nested in
species (random
effect) d.f.=4*F*-ratio
*P*69.04
<0.00016.29
<0.000180.36
<0.000127.11
<0.00014.61
0.00115.66
0.0002

To cover the individual variability of call parameters in this standardised behavioural situation, we analysed 73–199 calls from 8–10 sequences per bat (a total of 970 calls).

When performing an ANOVA on the mean values (i.e. one data point per individual, to avoid pseudoreplication), species differ slightly but significantly in peak frequency, terminal frequency and bandwidth but not in starting frequency and pulse interval. *M. dasycneme* search calls were longer than those of the other two species, probably because they flew in a larger enclosure during the recordings.

Using the raw data for a nested ANOVA (individuals nested in species and assigned a random effect) yields similar results for the differences among species and shows that differences among individuals explain much of the variability of all call parameters.

Values are given as means ± S.D.; and minimum and maximum values are also given.

NS, not significant.

all seven individuals of all three species of European ‘trawling *Myotis*’ bat. Mealworms on the clutter screen in the same experimental area were almost never attacked. Conditions with respect to flight performance and manoeuvrability were the same for the two surfaces. We conclude, therefore, that the differences in capture performance between the two surfaces must be explained by perceptual differences between the two tasks. We conclude that the bats could not (or hardly) perceive mealworms on the clutter screen, whereas on the linoleum screen, the worms were easy to perceive.

Prey perception by echolocation

How did the bats perceive the prey? Visual information was not used (and hence not necessary) for prey perception because the bats were able to capture prey in the dark. Passive acoustic information, such as insect sounds, was not necessary either because the bats also captured dead mealworms and silent prey dummies. We therefore exclude prey perception by passive cues (passive mode). We conclude that *M. capaccinii*, *M. daubentonii* and *M. dasycneme* perceived prey by using echolocation (active mode). This is in agreement with previous

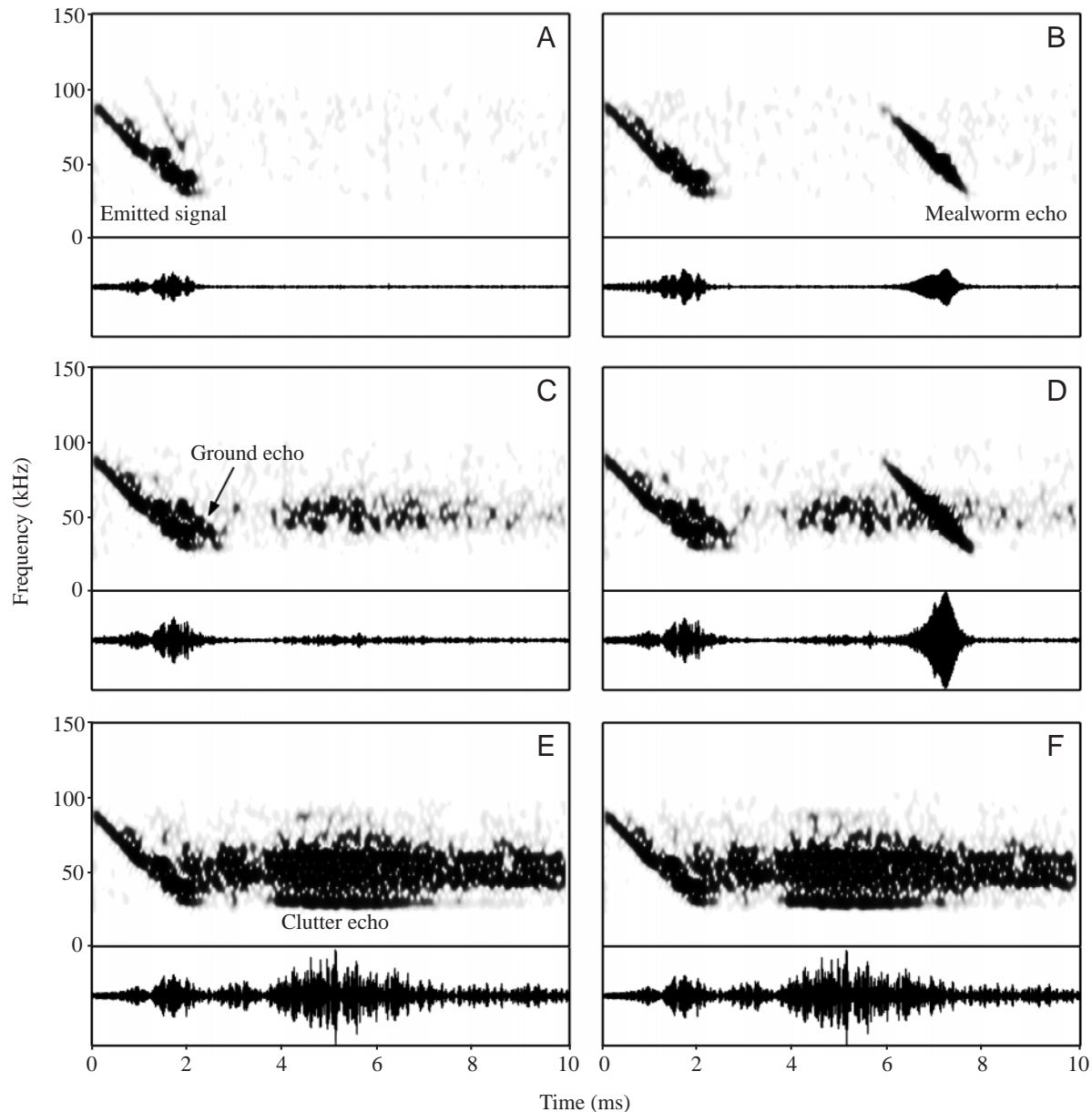


Fig. 3. Six different experimental settings were ensounded with a probe signal, and the echoes were recorded. Representative recordings are plotted as oscillogram (above) and spectrogram (below) representations. In all recordings, the outgoing signal and its second harmonic can be seen as recorded by the microphone positioned 5.6 cm laterally to the speaker. These are distorted because of the frequency-specific directionality and lateral position of the speaker and microphone. A good recording of the outgoing signal is shown in Fig. 2D. We ensounded the nylon threads in the air in the absence of a mealworm (A) and in the presence of a mealworm (B), of the linoleum screen in the absence of a mealworm (C) and in the presence of a mealworm (D) and of the clutter screen in the absence of a mealworm (E) and in the presence of a mealworm (F). In all the recordings depicted here, the mealworm was positioned at approximately 90° to the impinging sound. In air and on the clutter screen, the mealworm reflected back a good copy of the ensounding signal (B,D), whereas the echo from the clutter screen did not differ when a mealworm was absent (E) or present (F). Threads in air did not reflect any conspicuous echo (A), and the recording was identical to a recording of the noise floor of our apparatus. The level of clutter echoes reflected off the linoleum screen (C) was low in comparison with that reflected off the clutter screen (E). The latter yielded a smeared echo that extended over a wide time period. The linoleum screen reflected a strong 'ground echo' only from immediately below the 'artificial bat'.

studies on *M. daubentonii* (Jones and Rayner, 1988; Kalko and Schnitzler, 1989; Britton and Jones, 1999). The *Myotis* bats did not forage randomly by raking at previously successful sites of capture for some time; a behaviour known from, for example, fishing *Noctilio leporinus* (Schnitzler et al., 1994).

Different acoustic properties of the linoleum screen and clutter screen can explain the bats' performance

The 'artificial bat' in our ensounding experiments mimicked the situation of a bat foraging low over a surface. In agreement with our expectation, the linoleum screen proved to

Table 2. The mean sound pressure levels of the echoes in the 2 ms time window when the mealworm echo was expected

	Mean sound pressure level (dB SPL rms)		Comparison of echo SPL in the presence and absence of a mealworm
	Without mealworm	With mealworm*	<i>P</i> -value (Wilcoxon signed-rank test)
Air	27.11±0.33 (20)	90 ° : 38.00±2.54 (25)	0.001
Linoleum screen	36.47±0.16 (20)	90 ° : 44.75±2.07 (25)	0.001
		45 ° : 41.37±2.21 (25)	0.001
		0 ° : 38.29±1.22 (25)	0.001
Clutter screen	49.01±0.15 (20)	90 ° : 49.06±0.34 (25)	0.522 (NS)

Values are given as means ± s.d. (*N*).

NS, not significant.

*Orientation relative to impinging sound is given in bold type.

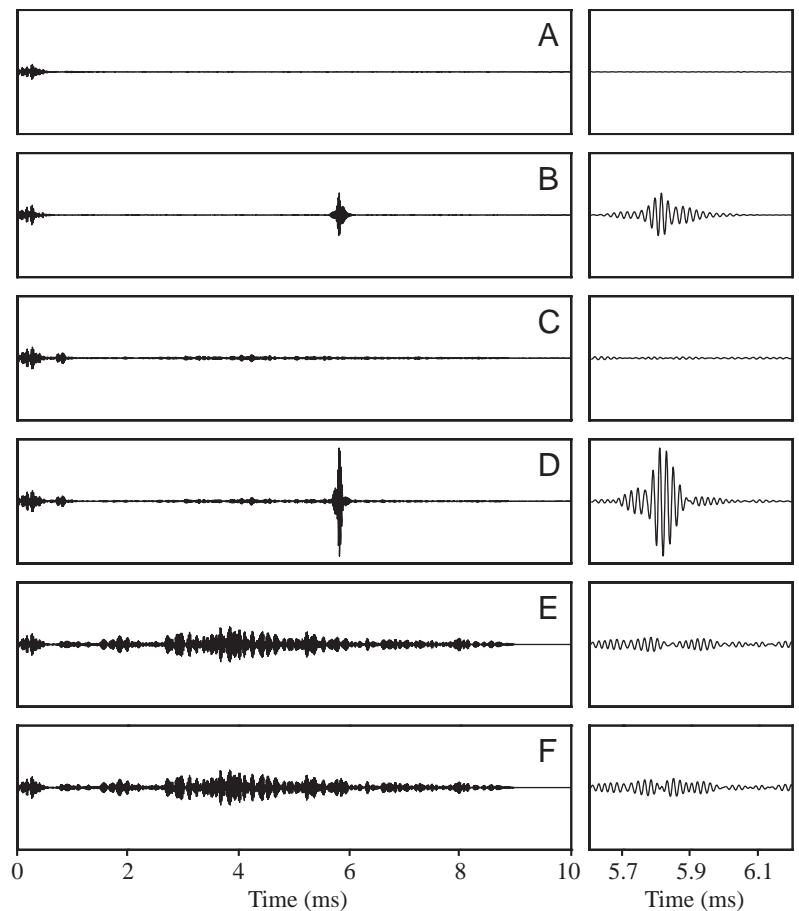
Mean sound pressure levels (SPLs) differed in the absence and presence of a mealworm in air and on the linoleum screen, but not on the clutter screen. The noise threshold of the recording apparatus, measured without an outgoing signal, was 27.0±0.3 dB SPL root mean square (rms).

Echo SPL for mealworms on the linoleum screen depended on the orientation of the mealworm relative to the impinging sound (Wilcoxon signed-rank test, 90 °:45 ° *P*<0.0001, 90 °:0 ° *P*<0.0001, 45 °:0 ° *P*<0.0001).

The SPL of a mealworm in air perpendicular to the impinging sound was lower than the echo SPL of mealworm aligned perpendicular to the linoleum screen (Wilcoxon signed-rank test, *P*<0.0001 for 90 °).

The target strength of an object is defined as the SPL of the reflected signal at a distance of 1 m from the object (i.e. the recorded echo SPL in our experiments) minus the SPL of the sound at the object (i.e. 84.3 dB as recorded for the outgoing sweep at a distance of 1 m from the speaker). Target strength, therefore, can easily be calculated from our data.

Fig. 4. Cross-correlation of the artificial sweep with the echoes (the right-hand column shows the time window of expected correspondence on an enlarged scale). (A) The echo of the nylon threads in air yielded no conspicuous correspondence with the sweep. (B) The echo of a mealworm suspended in air had a distinct correspondence peak with the sweep at the expected time. (C) The echo of the empty linoleum screen yielded a conspicuous correspondence with the sweep only from immediately below the ‘artificial bat’. No distinct peak was present in the time window where the mealworm echo would be expected. (D) The echo of the mealworm on the linoleum screen had a distinct correspondence peak with the sweep at the expected time. (E) The cross-correlation of the artificial sweep with the echo of the empty clutter screen was rippled because of the many overlapping echoes. (F) The cross-correlation with the echo of the mealworm on the clutter screen showed no obvious match.



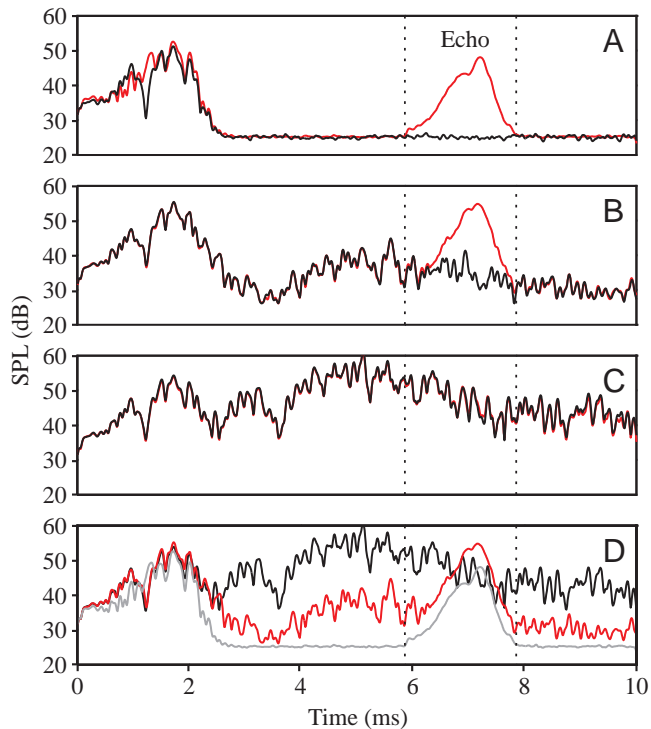


Fig. 5. Mean sound pressure levels of the echoes (significance levels are given in Table 2). (A) In the air, the sound pressure level (SPL) in the 2 ms time window of the expected echo (enclosed by vertical dotted lines) was significantly higher in the presence of a mealworm (red) than in its absence (black). (B) On the linoleum screen, the SPL in the same 2 ms time window was significantly higher in the presence (red) than in the absence (black) of the mealworm. (C) On the clutter screen, the SPL in the presence of the mealworm (red) did not differ significantly from that in the absence of the mealworm (black). (D) A, B and C (with mealworm) plotted on one graph for comparison. The SPL reflected by the mealworm on the linoleum screen (red) is higher than that reflected by the mealworm in air (grey). Clutter screen: black.

be an acoustically smooth surface. In accordance with Snell's law, the level of clutter echoes reflected back to the artificial bat by the linoleum screen was considerably lower (12.5 dB) (Table 2) than that of the clutter screen. A mealworm on the linoleum screen yielded a clear echo above the clutter echoes. We suggest that the bats heard an echo very similar to the one we recorded and that they were therefore able easily to perceive and capture mealworms on the linoleum screen.

The echo of a mealworm on the clutter screen completely overlapped and interfered with the many echoes reflected by the half-spheres of the screen itself. Even a powerful tool such as cross-correlation analysis failed to detect an echo within the clutter screen echoes that could be attributed to the mealworm. We therefore suggest that the foraging bats could not (separately) detect the mealworm echo in the background echoes. Hence, they almost always failed to capture the mealworms from the clutter screen. The results of the ensonification experiments match our findings from the behavioural experiments well. They corroborate the hypothesis

that for 'trawling *Myotis*' perception of prey on smooth surfaces is easier than on rough, textured surfaces; i.e. that prey perception depends on the acoustic properties of the surface on which the prey is presented.

Acoustic properties of foraging over smooth surfaces

The linoleum screen reflected a low (but easily detectable) on-axis clutter echo back to the artificial bat. However, we recorded an off-axis echo of higher SPL from immediately below the artificial bat. Smooth surfaces reflect such a 'ground echo', because the sound wave in this case impinges (and is reflected back) almost perpendicular to the surface. When the aiming direction is kept constant, the intensity of this echo depends greatly on the directionality of the transmitter and receiver, which are not the same for our artificial bat and a real bat. For a real bat, the 'ground echo' will have some surplus attenuation at short echo delays because of the contraction of the middle ear muscles (for a review, see Grinnell, 1995). Still, it is probable that 'trawling' bats also perceive such an echo from the water surface immediately below them. Depending on flight height, this echo will overlap and interfere with the emitted signal to a greater or lesser extent. By evaluating this reflection of off-axis energy from below (or its interference patterns with the outgoing signal), the bats might control and maintain their flight height over the water surface.

We hypothesised that the detection of prey on the linoleum screen (and on other smooth surfaces such as water surfaces) must be similar to the detection of air-borne prey in open spaces for an echolocating bat. In our ensonification experiments, we found that the echo SPL was approximately 6.7 dB higher for mealworms on the linoleum screen than for mealworms suspended in air. The SPL of the target echo may be higher on a smooth surface than in air because, in addition to the echo reflected directly by the mealworm, waves reflected *via* the surface also contribute to the echo because of summation of their pressure amplitudes. Sound reaches the target as a reflection from an area of the surface very close to the target. In addition, target echoes may be reflected down to the surface and, from there, travel back to the receiver.

Differences in echo travelling time between direct and indirect echoes will depend on the elevation of the target above the surface. For a mealworm approximately 3 mm in diameter lying directly on the surface, the maximum difference in travelling distance is 0.07 mm or 2 μ s in travelling time. Thus, the multiple wave fronts are likely to be perceived as a single echo by the bats (Mogdans et al., 1993). Depending on target size and wavelength, interference between the multiple wave fronts may produce characteristic notches. At a time delay of 2 μ s, the first notch will appear at 250 kHz. This frequency was not contained in our ensonification signal or in the bats' signals, so no notches are to be expected. Pressure amplitudes will at least partly sum and can serve to explain the increase in echo SPL of mealworms on a smooth surface compared with that of air-borne mealworms in our ensonification experiments. A floating moth or a chironomid sitting on the water surface will protrude sufficiently above it to reflect an echo of higher intensity than the echo of

the same insect in air. Thus, the target echo will be louder for prey on water surfaces than for the same prey in air. However, bats foraging for air-borne prey in open spaces will face a very favourable signal-to-noise ratio (Table 2).

In our experiments, the prey echo was embedded in a detectable clutter echo from the linoleum screen at an ensonification angle of 6.9° . Real water reflected detectable echoes to the apparatus of Rydell et al. (1999) only at angles of 24° and greater and to that of Boonman et al. (1998) at angles of 65° and greater. We therefore suggest that the ratio of target echo to clutter will be more favourable for real water surfaces than for our linoleum screen. Nevertheless, bats in a natural situation might be faced with a task of prey detection in clutter when foraging above water surfaces. The increase in target echo SPL for prey on a smooth surface in comparison with prey in air, however, will be the same for our linoleum screen and real water. It is possible, therefore, that the prey detection distance of 'trawling *Myotis*' is greater when they forage for a certain prey type on or close above the water surface than when they forage for the same prey in open space. Future research might test this hypothesis.

From an echolocation viewpoint, prey perception over water surfaces is far easier than over grass or soil, as outlined above. Our ensonification experiments also suggest that detection of prey low over smooth water surfaces may even be easier than in open spaces. The combination of prey abundance (Warren et al., 2000), reduced flight costs because of the ground effect (Aldridge, 1988; Jones and Rayner, 1991) and acoustic advantages could have led to repeated and convergent evolution of 'trawling' bats in different parts of the world.

A hypothetical search image

In the field, 'trawling *Myotis*' sometimes capture and, hence, mistake floating seeds, duckweed, pebbles, moving leaves or other prey-sized inedible objects for prey (Kalko and Schnitzler, 1989; Barclay and Brigham, 1994; Boonman et al., 1998). The latter two studies found the floating motion of the duckweed patches to be a key factor responsible for the false catches by the bats. The bats in our experiments, however, also captured non-moving prey and prey dummies from the linoleum screen. Motion will give the bats additional information but it cannot be considered a necessary cue indicating the presence of prey. On the clutter screen, the bats could not detect crawling mealworms, which indicates that motion is not sufficient for prey detection either. We thus conclude that 'trawling *Myotis*' might have a simple search image: small and isolated echo-reflecting objects on or above an acoustically smooth surface are considered as prey. Conspicuous echoes reflected from such stationary targets are called stationary glints. We propose that it is crucial for prey detection in 'trawling *Myotis*' that these glints are isolated spatially. In agreement with the proposed search image, a *Myotis daubentonii* took small fish for prey when the fish's head protruded from the water, and the bat was able to lift the fish out of the water in a laboratory experiment (Siemers et al., 2001a).

The glints from the mealworms on the clutter screen were not spatially isolated but embedded in many overlapping glints from the clutter screen. The inability of the bats to detect mealworms on the clutter screen indicates that they could not discriminate the mealworm echoes from the clutter echoes. In agreement with our results, the *M. daubentonii* in the study of Boonman et al. (1998) had difficulty in finding floating mealworms among dense duckweed cover. In the wild, foraging *M. daubentonii* do not forage above water surfaces that are covered by many small non-prey objects (Kalko and Schnitzler, 1989; Boonman et al., 1998). This evidence, taken together, indicates that 'trawling *Myotis*' will not recognise prey if prey echoes are embedded in many clutter echoes. We suggest that a surface reflecting many glints back to the foraging bat does not match its search image. Consequently, we propose that an experimentally naive bat would not attack mealworms on linoleum or water if the whole surface was densely covered with mealworms.

In behavioural experiments, *Myotis* bats can be trained to discriminate mealworms from dummies (Griffin et al., 1965; Boonman et al., 1998). However, the learning processes involved in such sophisticated discrimination performance will perhaps only pay off energetically for the bats if they encounter a very stereotyped prey-specific situation over a longer period (such as that offered by behavioural scientists in discrimination experiments).

The 'trawling' neotropical *Noctilio* seem to have a more specific search image. Capture attempts by *N. leporinus* are selectively triggered by the temporary glints produced by jumping fish. Capture attempts by *N. albiventris* are elicited by temporary glints modulated onto the echoes by fluttering insects in air or on the water surface (Schnitzler et al., 1994; Kalko et al., 1998). European 'trawling *Myotis*', however, also react to stationary glints reflected by non-fluttering prey and prey dummies, as shown in the field (Kalko and Schnitzler, 1989; Britton et al., 1997; Boonman et al., 1998) and in our behavioural experiments and those of others (Britton and Jones, 1999). As mentioned above, we propose that it is crucial that these glints are spatially isolated. A less specific search image will cause a certain amount of false captures, but it will include rewarding prey such as motionless floating insects and chironomids that rest on the water surface.

The capture performance and search image of all three species of bat were very similar. We therefore propose that interspecific competition may contribute to the almost non-overlapping distribution of the similar-sized and similarly manoeuvrable *M. daubentonii* and *M. capaccinii*.

Subgenus Leuconoë: monophylum or ecomorph?

Because of their morphological similarities, the 'trawling' species of *Myotis* have been systematically grouped together into the subgenus *Leuconoë* (Findley, 1972). A recent study of molecular systematics within *Myotis* suggests that the morphological similarities within subgenera often reflect similar adaptations to similar niches rather than close phylogenetic affiliation (Ruedi and Mayer, 2001). Ruedi and

Mayer group *M. daubentonii* into a monophyletic clade with the foliage-gleaning, forest-dwelling *M. bechsteini*, whereas they group *M. dasycneme* in a separate clade including the gleaner *M. emarginatus*. The phylogenetic position of *M. capaccinii* remains uncertain. Their results indicate that the 'trawling *Myotis*' ecomorph evolved at least twice convergently in the Palaearctic region and probably several more times worldwide. Different species of 'trawling' bat show remarkable similarity in flight morphology and performance (Jones and Rayner, 1991). Convergent (or at least parallel) evolution has resulted in an equal degree of similarity in the echolocation behaviour, search image, foraging strategy and prey-capture behaviour of the 'trawling' species *M. dasycneme*, *M. daubentonii* and *M. capaccinii*, as demonstrated here. This and other comparative studies (Surlykke et al., 1993; Siemers et al., 2001b) suggest that rigid physical constraints canalise the evolution of foraging and echolocation behaviour, leading to convergent solutions in different phylogenetic clades of bat.

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