

DETECTION OF PREY IN A CLUTTERED ENVIRONMENT BY THE NORTHERN BAT *EPTESICUS NILSSONII*

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Summary

We studied the acoustic behaviour of bats (*Eptesicus nilssonii*) hunting for large (wing span 5 cm) non-hearing hepialid moths (*Hepialus humuli*). Groups of silvery-white male *H. humuli* perform a short (30 min) hovering display flight over grassland at dusk. They typically hover at, or below, the tops of grass panicles and are therefore situated in a highly acoustically cluttered habitat. Occasionally, they move to a new position by making short (1–5 s) flights at higher levels. *E. nilssonii* is not a clutter specialist, and yet we found that they attacked *H. humuli* within the ‘clutter overlap zone’. The bats did not change their signal design in any marked manner for this specific task. Measurements of echoes from a moth 10 cm above or below

the grass tops showed that information for detecting the moths was available to the bats. Nevertheless, the bats did not attack moths in stationary hovering display flight, only when they moved above the grass panicles. The duration of the up/down flights (movements) were almost always longer than an entire capture sequence by the bats. Apparently, the bats rely on the movement of the moth in space, monitored over successive echoes, to discriminate moth echoes from overlapping clutter echoes.

Key words: echolocation, clutter–prey echo overlap, predation, detection, bat, *Eptesicus nilssonii*, moth, *Hepialus humuli*.

Introduction

It has been suggested that bats using frequency-modulated (FM) signals cannot detect prey echoes if these are overlapped by the presumably more intense echoes from vegetation or other background (clutter echoes) (Kalko and Schnitzler, 1993). The overlap of prey echo with clutter echo occurs in the so-called ‘clutter overlap zone’, which extends from the clutter-producing objects out towards the bat. The depth of the clutter overlap zone is determined solely by the duration of the echolocation signal of the bat ($0.5 \times \text{speed of sound} \times \text{signal duration}$). This hypothesis has been used in determining the microhabitats that can be exploited by bats using a given signal duration (Schnitzler and Kalko, 1998). Recent studies of *Myotis nattereri* flying in a flight tent and catching prey at different distances from clutter showed that this bat, which uses short broad-band FM signals, is capable of detecting prey in the clutter overlap zone (Siemers and Schnitzler, 2000). However, the angle of attack relative to the clutter is unclear in this study, and the bats may have used directional hearing to separate prey and clutter echoes if they approached the prey parallel to the clutter. Attempts to record capture sequences in the field were unsuccessful (Siemers and Schnitzler, 2000), so whether or not bats using FM signals can exploit the clutter overlap zone remains to be documented under natural circumstances.

In Sweden, the northern bat *Eptesicus nilssonii*

(Vespertilionidae) forages for ghost moths *Hepialus humuli* (Hepialidae) that swarm over uncut hayfields. In contrast to many other nocturnal moths, ghost moths lack tympanic organs and are not therefore capable of hearing bat echolocation calls. They also lack frenulum–retinaculum coupling between the fore- and hindwings, causing their wings to beat independently so that manoeuvrable flight becomes limited (Scoble, 1992). The males of *H. humuli* are silvery white and perform a visually conspicuous display flight for approximately 30 min at dusk (Mallet, 1984; Andersson et al., 1998). The display flight typically takes place over open grassland for 2–3 weeks around the summer solstice. Most of the time, the displaying male moths hover in gaps between grass panicles (tops), but sometimes they emerge above the grass panicles while contesting another male, while displaying for a female or when moving to another display position (Rydell, 1998). The displaying moths are frequently preyed on by *E. nilssonii* (Andersson et al., 1998; Rydell, 1998). This bat normally hunts in the open, along forest edges and in gaps within forest, and is not specialised for hunting close to vegetation (Rydell, 1990). Previous observations have shown that the capture success of the bats was near zero as long as the displaying moths stayed below the grass panicles, which they did most of the time (Rydell, 1998). The capture success of the bats increased slightly when the moths flew 0–0.5 m above the grass

panicles and dramatically when the moths flew higher (see Fig. 1 in Rydell, 1998). It was hypothesised that the grass echoes prevented the bat from detecting the moth. However, *E. nilssonii* occasionally attacked the moths even when these were within 0.5 m of the panicles. The bats must therefore have detected the moths on these occasions. *E. nilssonii* uses search signals with durations of 6–18 ms, depending on flight altitude and habitat (Rydell, 1990). This will result in clutter overlap zones of 1–3 m and, unless the bats had shortened their signals considerably, the detection referred to above occurred in the clutter overlap zone.

The aim of this study was to determine whether and how *E. nilssonii* can detect and recognise displaying *H. humuli* among clutter echoes from the grass. Hence, we recorded the sonar signals used by *E. nilssonii* and the echoes from the grass and displaying *H. humuli*. We also filmed *H. humuli* using infrared video.

Materials and methods

Study sites

Studies were conducted at two sites just outside the town of Ulricehamn in Sweden (57°E4'N, 13°E2'E) in late June 1998 and 1999. Both sites consisted of a large uncut hayfield (around 1 ha; 10 000 m²) surrounded by roads and forest (see Andersson et al., 1998; Rydell, 1998). Visual observations and videotaping of the moths were made at distances of 1–5 m, whereas the bats were visually observed from just above the experimental site to approximately 50 m away. Tape recordings of the bats were good up to at least 15 m from the microphones, having a signal-to-noise level above 14 dB, and the second harmonic was present.

Sound recordings

We used a 1.5 m long horizontal microphone array, using one Brüel & Kjær (B&K, Nærum, Denmark) 1/4 inch microphone (type 4135) and two Gras (Copenhagen, Denmark) 1/4 inch microphones (type 40BF). The microphones were separated by 0.75 m, and the protective grids were removed while recording. Signals from the three microphones were amplified 40 dB by one of two B&K amplifiers (type 2804 and type WB 1057), high-pass-filtered (–3 dB at 13 kHz, custom-made) and recorded simultaneously on three channels of a Racal 4S high-speed tape recorder at a tape speed of 30 inches s⁻¹ (76.2 cm s⁻¹). The fourth channel was used for comments and bat detector signals. The tape recorder was operated on 24 V lead batteries. The microphones were calibrated every night of recording using a B&K sound level calibrator (type 4230) that gives a 1 kHz tone of 1 Pa (94 dB sound pressure level, SPL, re 20 µPa) root mean square (rms). The 1/4 inch microphones (Gras and B&K) correctly estimate sound pressure arriving perpendicular to the membrane up to 120 kHz (±1 dB), but underestimate sound that arrives parallel to the membrane by 5 dB for 25 kHz and by 8 dB for 50 kHz (Brüel & Kjær, 1982). The entire recording system had a flat frequency response between 13 (–3 dB) and 120 kHz (–1 dB).

The array was placed at the edge of, but within, the hayfield, with the microphones positioned 20 cm above the grass panicles pointing 45° upwards.

Echo measurements

To measure the echoes of *Hepialus humuli* (L.) and the grass, we used a pre-recorded echolocation signal of *Eptesicus nilssonii* (L.) with a duration of 5.2 ms (see Fig. 2). The signal was digitised at 320 000 samples s⁻¹ (Hz) with a DSP (digital signal processing) board (SPB2, Signal Data) in a Toshiba computer using a custom-made program. The signals were then emitted through the DSP card, also at a rate of 320 kHz, via an amplifier and a polarisation voltage unit (custom-made) to an electrostatic loudspeaker (custom-made). The output of the speaker was 99 dB peSPL (peak equivalent sound pressure level) re 20 µPa at 1 m. This system had a flat frequency response between 28 and 122 kHz (±3 dB). The signal was repeated at 70 ms intervals. Outgoing signals and echoes were recorded on a high-speed tape recorder (Racal 4 S) through a 1/4 inch B&K microphone (grid off), a B&K amplifier (WB 1057) and a custom-made high-pass filter (–3 dB at 13 kHz). The microphone and the loudspeaker were placed on one holder next to each other, both pointing in the same direction. This apparatus was mounted on a tripod and pointed towards the grass and the target at an angle of approximately 45° (simulating a reasonable angle for the head of the bat during hunting). The distance from the speaker and microphone to the grass was 1.5 m (in line with the direction in which they pointed).

Echoes were measured from the grass alone, from a dried and spread specimen of *H. humuli* placed either 10 cm below or 10 cm above the grass panicles, and from a live specimen flying 10 cm below the grass panicles. The live specimen was carefully glued to a thin stick and persuaded to fly, in as natural a hovering position as possible, by gently blowing on it. The moth was released after the measurements. The moths (dead or alive) were placed on the acoustic axis of the speaker. Echo measurements were performed just prior to the emergence of the moths and the bats. We therefore avoided interference from other moths and signals from echolocating bats. We determined the target strengths of the dried specimen of *H. humuli*, the grass and the flying *H. humuli*. The target strength is the difference between the level of the target echo 1 m from the target and the incident sound on the target (Møhl, 1988). Transmission loss is calculated from spherical attenuation (–6 dB per double distance) and atmospheric attenuation (0.8 dB m⁻¹ for 30 kHz; Surlykke, 1988). All sound amplitude values are given in dB peSPL (peak equivalent sound pressure level; Stapells et al., 1982) re 20 µPa at a reference distance (specified for each calculation).

Video recordings

It was not possible to film the moths using multi-flash systems for video recording or multi-exposure photographs because the moths flew off when exposed to flashes. We therefore used an infrared-sensitive Philips video camera (type

VCM 6450) and two sources of infrared light, and recorded the *H. humuli* on a portable Sony U-matic videocassette recorder (type VO-6800 PS) operated on 12V batteries. We used a 3 inch Casio LCD colour television connected to the U-matic recorder as an on-line monitor. Comments on the fourth channel of the Racal were recorded simultaneously on channel 1 of the U-matic recorder. Bat detector signals were recorded on channel 2 of the U-matic. The height of the moths relative to the panicles was estimated from two rods marked with reflective tape every 10 cm. One rod was placed 2 m from the camera, the other 3 m away and 1 m to the left of the first rod. Occasionally, the moths moved their display outside the rod area. We then turned the camera to record the display. In such cases, only one rod was present on the video recording. The limitation of this video system was that the bats had to be less than approximately 5 m in front of the video camera to be recorded. Consequently, a bat diving for a *H. humuli* from an altitude of 4 m had to be 3 m from the video camera in a horizontal line if all stages of the detection and capture were to be recorded.

Analysis

The recordings of *E. nilssonii* were played back at 1/16 real time and digitised at a sampling rate of 22 050 Hz, giving a real-time sampling rate of 352 800 Hz, and analysed using BatSound (Pettersson Elektronik AB, Uppsala, Sweden). Signal duration and signal interval were analysed from oscillograms (in BatSound). Peak frequency (the frequency of highest amplitude) and -10 dB bandwidth (measured relative to the peak frequency as the difference between the -10 dB points above and below the peak frequency) were analysed from the amplitude spectrum using a 4096 point Fast Fourier Transform (FFT) with a rectangular window function. An FFT of 4096 points here represents 11.6 ms, which is sufficient to contain even the longest signals recorded. Initial and terminal frequencies were measured from the spectrogram (using definitions from Kalko and Schnitzler, 1993), and the frequency range of the first harmonic was determined as the differences between the two. The spectrogram was constructed from 256-point FFTs using a Hann window function with a 94% overlap between consecutive FFTs, giving a frequency resolution of 1378 Hz. Only signals from bats flying towards the microphones and signals with a good signal-to-noise ratio (indicating that the bat was pointing its sonar towards the microphones) were analysed.

To test whether the bats used a special search signal design for detecting moths in and near the clutter, we analysed search signals recorded from bats in four different situations: (i) flying above the hayfield searching for *H. humuli*; (ii) just prior to a dive towards a *H. humuli* (capture attempt); (iii) just prior to a capture of a *H. humuli*; and (iv) as in 1, except that the bats hunted above a road adjacent to the field and were not searching for *H. humuli* (searching for prey in a non-cluttered habitat).

In sequences containing a capture or an unsuccessful attack, we defined the first approach signal to be the one after which

signal duration and interval decreased continuously. Signals prior to that were assumed to be search signals. The terminal phase (buzz) was marked by an abrupt decrease in signal duration and interval.

The duration of the up/down flights of the moth, i.e. from the moment the moth emerged above the panicles until it had descended to this level again, was measured by counting frames (each represents 40 ms) on the video recording. We measured the duration of 96 up/down flights.

Statistical analyses

Means were calculated for each variable analysed in a sequence, and mean values of variables for a given situation were calculated from the mean value over several sequences. We used a Kruskal-Wallis test and a Tukey-like non-parametric multiple-comparison to test for differences between situations i-iv. Significant rejection levels were 0.05 throughout.

Values are presented as means \pm s.d. unless stated otherwise.

Results

Behaviour of the bats and moths

The behaviour of the bats and the moths was the same as described previously (Rydell, 1998). Approximately 20 *E. nilssonii* flew above each of the two hayfields hunting for *H. humuli* every night. The bats were spread over the entire hayfield and flew in circles approximately 3-4 m above the grass (estimated by comparison with lampposts and a house at the edge of the field).

The *H. humuli* spent most of their time hovering below or at the level of the panicle tops. Occasionally, the males made short excursions above the panicles. Such flight excursions consisted either of up/down flights in the same location or of flight up in one location and down in another. We observed the bats attacking moths only during such flight excursions and not while the moths were hovering. Our video recordings show only one incident of a moth flying more than 50 cm above the panicles in an up/down flight; the moths usually flew only 30 cm above the panicles. This is consistent with the data presented previously (Rydell, 1998).

Overall, the bats produced very few feeding buzzes considering the many insects other than ghost moths that were present. However, all attacks on insects, *H. humuli* or other species, contained feeding buzzes. In general, we rarely observed the bats attacking any of the other insects present, but we frequently saw the bats diving for *H. humuli*, and we have one capture attempt recorded on the video. The bat aborted this attack, however, presumably to avoid collision with our equipment.

Since the bats constantly flew 3-4 m above the grass, all attacks (successful or not) on *H. humuli* began from this altitude. Attacks consisted of almost vertical dives towards the grass, occasionally after a 180° turn as if the bat had detected something immediately below it and therefore had to turn to get back and down to the prey. The bats must, therefore, have

pointed their sound beam towards the grass at an angle of between 45 and 90°. Also, the ear position of bats passing above us, observed against the sky, indicated that they typically listened for echoes coming from below (see also Rydell, 1998).

Characteristics of search signals

Search signals were analysed for bats in four situations: (i) searching for *H. humuli* above a hayfield, (ii) just before an unsuccessful attack on a *H. humuli*, (iii) just before a capture of *H. humuli*, and (iv) as in situation i only the signals were recorded from bats flying above a road where *H. humuli* were not present. The search signal durations used in the four different situations are shown in Fig. 1A together with the corresponding extent of the clutter overlap zone (right-hand y-axis). The signal durations used above the road (situation iv) were significantly longer (9.2 ± 0.3 ms, $N=7$ sequences, 107 signals) than durations used above the hay field (situation i, 7.1 ± 0.8 ms, $N=35$ sequences, 439 signals; situation ii, 7.7 ± 0.6 ms, eight sequences, 74 signals; $P < 0.001$). Statistics for situation iii were omitted because of small sample size ($N=2$ sequences, 26 signals). The bats hunting for *H. humuli* above the hayfield experienced a clutter overlap zone of between 0.95 and 1.5 m (Fig. 1A).

The bats hunting above the road (situation iv) used significantly longer signal intervals (155 ± 30.7 ms, $N=7$ sequences) than those hunting above the hayfield (situation i, 95 ± 13.0 ms; situation ii, 96 ± 12.5 ms; $N=35$ and eight sequences, $P < 0.005$, Fig. 1B).

The duty cycle (the percentage of time that the bat cries) for bats hunting above the road was significantly lower ($6.3 \pm 1.2\%$, $N=7$ sequences) than for those hunting above the hayfield (situation i, $7.5 \pm 1.1\%$; situation ii, $8.7 \pm 1.3\%$; $N=35$ and eight sequences, $P < 0.005$, Fig. 1C).

The terminal frequency and the peak frequency were the same for all four situations (29.7–30.4 kHz and 32–32.7 kHz, respectively; Table 1). Bats hunting above the road (situation iv) used significantly ($P \ll 0.001$) narrower bandwidths (–10 dB and frequency range of first harmonic) than those hunting above the hayfield (situations i and ii; Table 1).

Clutter and target echoes

A dried and spread *H. humuli* was placed 10 cm above and 10 cm below the top of the grass panicles and ensonified with a search signal of *E. nilssonii*. In both positions, a distinct echo from the moth was seen in the spectrogram (Fig. 2), but it was difficult to differentiate between the moth and the clutter echoes in the oscillogram. The echo from the grass appears like a noise band containing the frequencies present in the outgoing signal (Fig. 2). The noise band occurs because the grass consists of several layers that reflect the signal from different depths. In addition, the grass echo comes predominantly from the lower layers, i.e. 25–35 cm below the panicles. The clutter overlap zone therefore protrudes from the lower layers rather than from the panicles.

The echo level of the moth recorded at the microphone was –4 dB relative to the echo level of the grass, irrespective of the

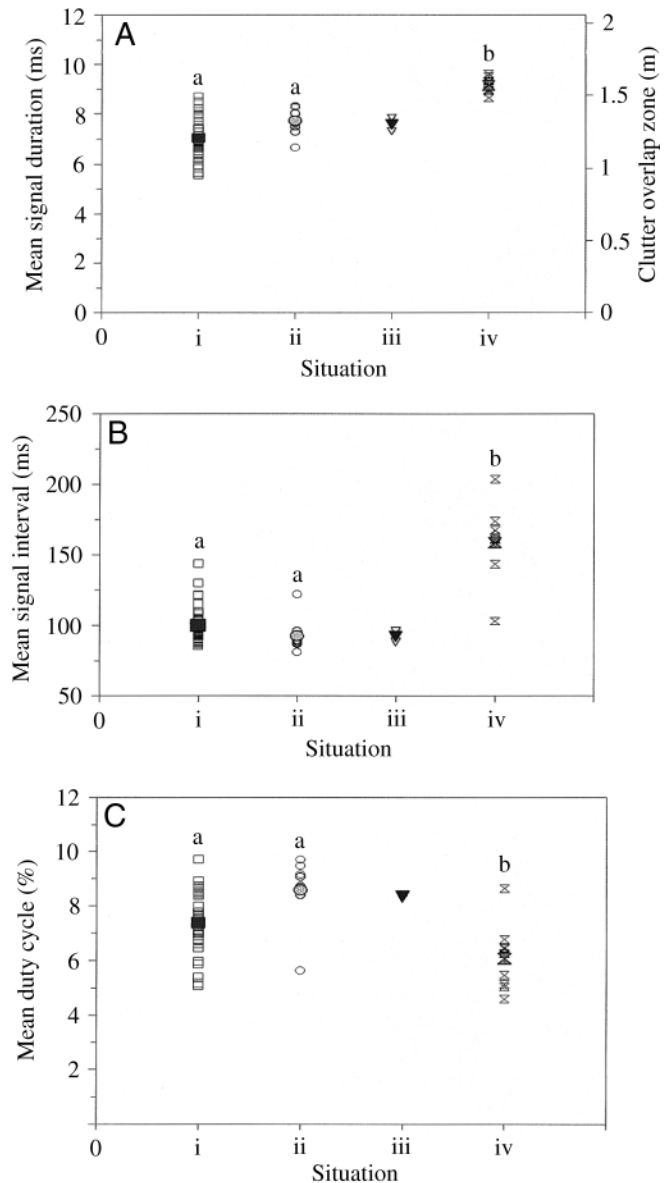


Fig. 1. Mean signal duration (A), signal interval (B) and duty cycle (C) for searching signals recorded from bats in four situations: (i) flying above the hay field searching for *Hepialus humuli*, (ii) prior to an attack on a *H. humuli*, (iii) just prior to capture of *H. humuli*, and (iv) as in i, except that the bat was searching for other insects above a road. Open symbols are means of sequences, and filled symbols are the overall mean for each situation. Different letters indicate a significant difference ($P < 0.005$) between situations. No letters are given for situation iii because of the low value of N (see text for explanation).

position of the dried and spread moth. The target strength of the dried and spread moth (wing span 5.5 cm) positioned just above the grass was –34 dB at 1 m, whereas that of the grass was –25 dB at 1 m (measured from the lower layers). The target strength of the flying *H. humuli* varied between –43 and –35 dB at 1 m.

Fig. 3 shows 12 consecutive echoes of a *H. humuli* flying 10 cm above the grass tops. The intensity of the moth echoes

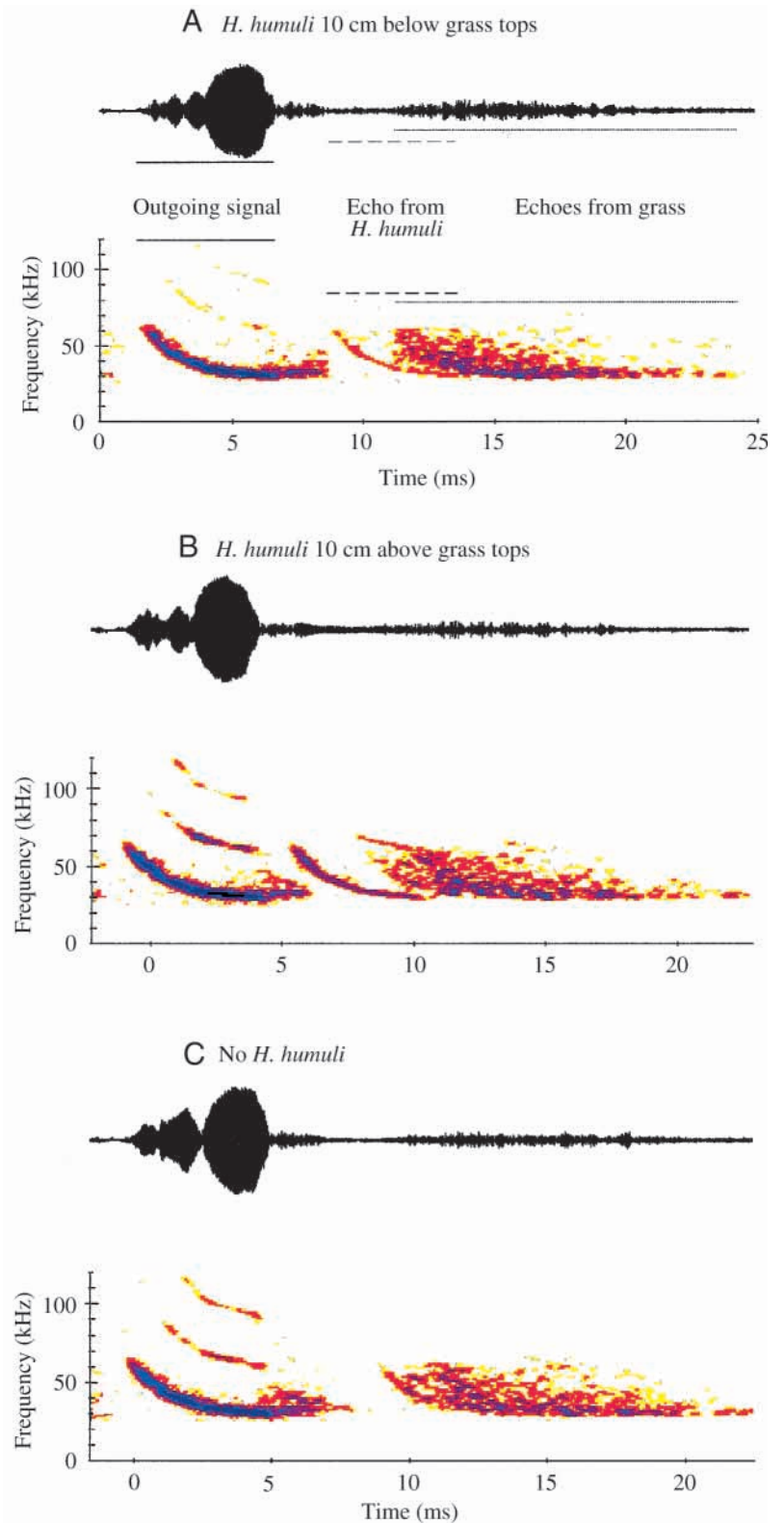


Fig. 2. Oscillograms and spectrograms of the outgoing signal and the incoming echo from a dried specimen of *Hepialus humuli* with outspread wings and of an echo from the grass. Since the loudspeaker is highly directional (a directionality that differs with frequencies) and the outgoing signal is recorded immediately next to the speaker, the signal will appear distorted in the spectrogram. (A) The *H. humuli* is placed 10 cm below the grass panicles. (B) The *H. humuli* is placed 10 cm above the grass panicles. (C) No *H. humuli* is present, and only echoes from the grass are seen. Spectrograms are constructed from consecutive 256-point FFTs using a Hann window function.

changes from echo to echo, as do the frequencies of highest energy (compare the first and last echoes in the upper panel in Fig. 3). The changes in moth echo intensity were almost rhythmical; relatively strong over approximately 4–5 consecutive echoes and weak or absent in the following

approximately 4–5 echoes. When an echo from the flying moth is missing in the spectrogram, it is probably due to the limitations of our equipment and not because it is missing in reality. The fluttering of the moth wings changes the echo intensity. Echoes will be stronger when the sound hits the wing

Table 1. Characteristics of the search signals from the four situations described in Fig. 1

Situation	Peak frequency (kHz)	-10 dB bandwidth (kHz)	Terminal frequency (kHz)	Frequency range, first harmonic (kHz)	Duration (ms)	Interval (ms)	Duty cycle (%)
Search (i)	32.4±0.3 (35)	14.9±1.1 (35)	30.4±0.1 (35)	37.8±0.6 (35)	7.0±0.1 (35)	100.0±2.3 (35)	7.4±0.2 (35)
Attempt (ii)	32.7±0.2 (8)	16.0±1.1 (8)	29.9±0.2 (8)	41.5±0.9 (8)	7.7±0.2 (8)	92.7±4.4 (8)	8.6±0.4 (8)
Capture (iii)	32.0±0.4 (2)	13.2±0.7 (2)	29.7±0.5 (2)	36.8±0.6 (2)	7.6±0.3 (2)	92.3±3.8 (2)	8.4±0.1 (2)
'Road' (iv)	32.2±0.3 (7)	9.8±0.9 (7)	30.1±0.3 (7)	26.9±1.6 (7)	9.2±0.1 (7)	158.8±11.2 (7)	6.1±0.4 (7)

Values are means ± S.E.M. (N).

i-iv refer to the four different situations examined (see Materials and methods).

perpendicular to the surface and weaker when the sound arrives more parallel to the surface. It was not possible to determine the exact wingbeat frequency because the wings beat almost independently. Echoes from the grass were constant in strength and peak frequencies.

Duration of *H. humuli* up/down flights and bat attacks

Male moths occasionally made short flights above the panicles as described above. These flights rarely extended higher than 50 cm above the panicles and were typically approximately 30 cm above them (estimated from the video recordings; see also Rydell, 1998). The time the moths spent above the panicles, the 'up/down time', was divided into

intervals of 0.5 s, and the number of up/down flights within these intervals was counted. The results are shown in Fig. 4. A majority (86%) of the up/down flights lasted between 0.5 and 2.0 s. For comparison, a full acoustic capture sequence lasted 0.7 s measured from the start of the last search signal until the start of the last feeding buzz just before capture of the *H. humuli* (Fig. 5). The diving time of a bat, if only gravity is taken into account, is approximately 0.8–0.9 s for bats flying at an altitude of 3–4 m. We recorded only two captures of *H. humuli* on the tape recorder but observed several other captures, all of which contained feeding buzzes (determined from the bat detector). In both recordings, the moths were less than 50 cm above the grass tops. In the filmed attack, the moth

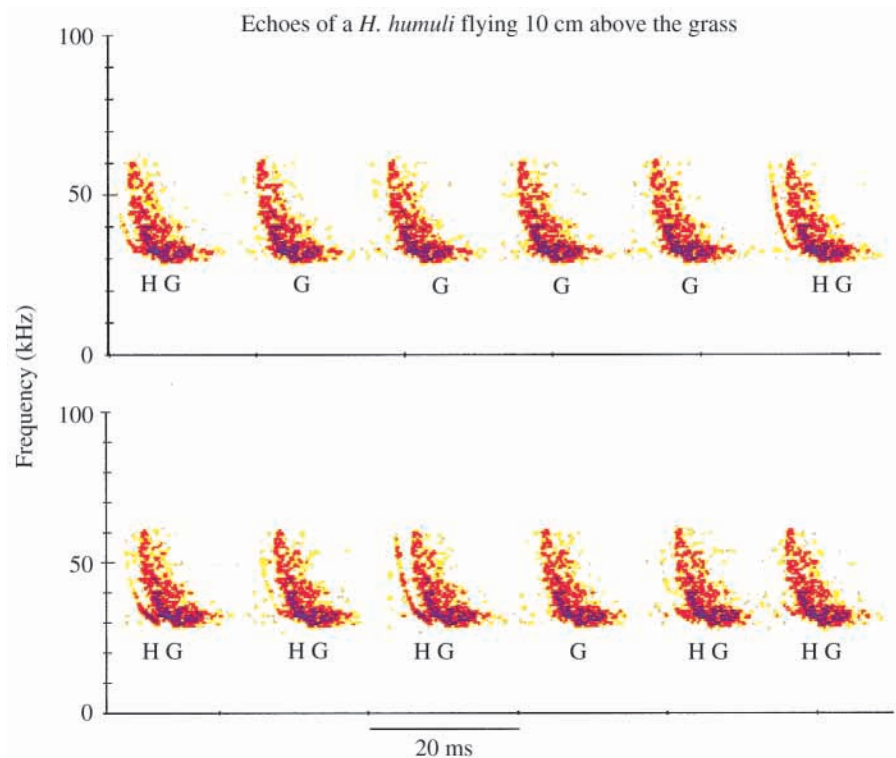


Fig. 3. A sequence of 12 echoes from a *Hepialus humuli* flying tethered to a stick 10 cm above the grass panicles. The sequence is edited so that the outgoing signals have been cut out. In real time, there was 70 ms between each echo. Note how the intensity of the moth echo changes from pulse to pulse because of the fluttering of the moth's wings. Spectrograms are constructed from consecutive 256-point FFTs using a Hann window function. H denotes an echo from the *H. humuli*. G denotes an echo from the grass.

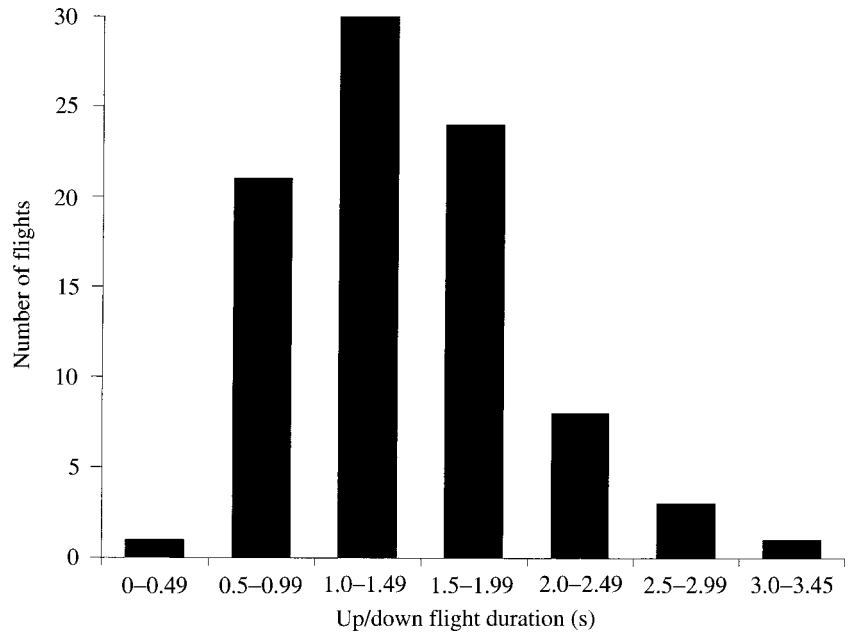


Fig. 4. The number of up/down flights by *Hepialus humuli* lasting for different times. The flight duration was estimated by counting frames from the video recordings ($N=92$).

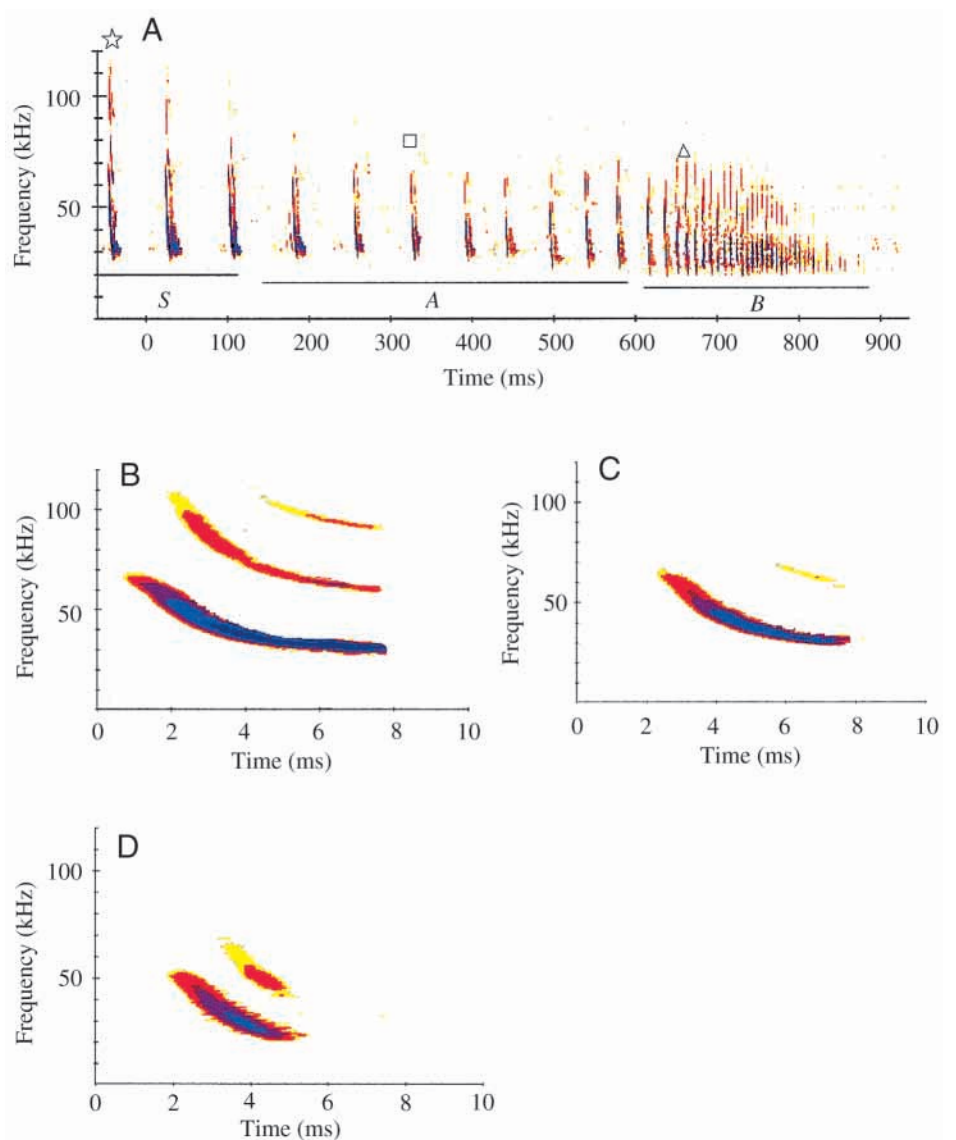


Fig. 5. A spectrogram of a capture sequence in which an *Eptesicus nilssonii* catches a *Hepialus humuli*. (A) The entire sequence. *S* denotes search-phase signals. *A* denotes the approach phase. *B* denotes the terminal phase (buzz). The first approach signal is defined as the first signal after which the signal duration and interval decrease continuously. The terminal phase (buzz) starts with an abrupt decrease in signal duration and interval. (B) The search signal below the star in A. (C) The approach signal below the square in A. (D) Terminal signals below the triangle in A. The spectrograms are constructed from 256-point FFTs using a Hann window function.

was never more than 30 cm above the panicles, and the bat used search signal durations of 7.3 ms just before the approach phase, giving a clutter overlap zone of 124 cm.

Discussion

In this study, we document that the northern bat *E. nilssonii* can detect ghost moths *H. humuli* in acoustic clutter without dramatically changing its echolocation signals. Other factors, such as flight height (Jensen and Miller, 1999), can account for the signal changes recorded from bats foraging over grassy fields. The signal duration and intervals recorded from bats above the road were somewhat shorter than previously published field recordings of *E. nilssonii* (Rydell, 1990). This too can be explained by the lower flight altitude used by the bats in the present study.

Temporal variables, such as signal duration, signal interval and duty cycle, recorded above the hayfield differed significantly from those recorded above the road. This variation between the two habitats is probably adaptive in the sense that it reflects a difference in flight altitude (bats above the road were hunting at an altitude of approximately 5 m, whereas those above the hayfield were at an altitude of 3–4 m). Short search signal durations and intervals are typically associated with low flight altitude in this and related species (Rydell, 1990; Jensen and Miller, 1999). However, the short signals used above the hayfield could have been an adaptation to the specific task of detecting ghost moths in clutter, since the clutter overlap zone would be reduced. However, in the present case, the bats experienced an overlap before an attack, even with the reduction in signal duration (see below).

An increased duty cycle would probably be advantageous for detecting a fluttering target such as *H. humuli*. However, the bats maintained a low duty cycle of between 5 and 9% (Fig. 1) while hunting for *H. humuli*. This corresponds to duty cycles obtained for other bats using FM signals that forage in the open (Schnitzler et al., 1987; Surlykke et al., 1993; Jensen and Miller, 1999). In any case, the fact that the bats never attacked hovering moths (see below and Rydell, 1998) strongly suggests that the bats did not use echoes from the fluttering wings (i.e. glints) as a cue for detection (Sum and Menne, 1988; Moss and Zagaeski, 1994).

The increased bandwidth of searching signals used by bats flying above the hayfield could increase the resolution of the echo received and thereby enhance detection of the moths. This may not necessarily be a specific acoustic adaptation for hunting ghost moths, but could simply be attributed to flight at lower altitudes (Jensen and Miller, 1999). Another explanation could be that the bats above the road were flying alone, whereas approximately 10–20 bats were hunting simultaneously for *H. humuli* above the field. The closely related *E. serotinus* changes its signal variables significantly when hunting close to conspecifics (M. E. Jensen, unpublished data). Our present data do not permit examination of this possibility.

Bats using FM signals that are specialists in hunting close to vegetation use short signals of broad bandwidth (Siemers

and Schnitzler, 2000). This is reasonable considering that the microhabitat sets constraints for signal design (for a review, see Schnitzler and Kalko, 1998; see also Neuweiler, 1984). It is therefore no surprise that *E. nilssonii* change their signal design when flying close to vegetation or to the ground (Rydell, 1990). Therefore, using the arguments above, we believe that *E. nilssonii* did not design their search signals for the specific task of detecting ghost moths. Instead, they used the signal design they would normally use at this flight altitude in an open habitat, and this design was apparently sufficient for the detection of ghost moths in the clutter overlap zone.

Clutter overlap and target echoes

The signal duration used by *E. nilssonii* while searching for *H. humuli* gave clutter overlap zones between 0.95 and 1.5 m. The most intense clutter echoes originated from the lower layers of grass, 25–35 cm below the top of the panicles, so the interfering clutter overlap zone protruded from the lower layers of the grass. Hence, the clutter overlap zone above the panicles was approximately 0.60–1.25 m. The bats occasionally attacked the moths when they were within 0.5 m of the panicles (see Fig. 1 in Rydell, 1998), which means that *E. nilssonii* must have been able to detect echoes from the moth even when these were overlapped by clutter echoes. This must also be the case for bats pointing their sound beams at an angle of approximately 45° towards the ground. This angle will increase the distance between the prey and the clutter in line with the acoustic axis by approximately 25 cm. We cannot assume that masking clutter occurs only on the acoustic axis. Grass consists of an irregular surface, reflecting echoes in many directions. Thus, it is also difficult to determine the amount of masking experienced by the bat and hence to calculate the exact amount of prey–clutter overlap the bat experiences.

The target strengths of a flying *H. humuli* varied from –43 to –35 dB at 1 m, and a bat using a source level of 120 dB peSPL at 10 cm (Jensen and Miller, 1999) flying at an altitude of 3 m would receive an echo level of 34–42 dB SPL. Comparing this with the laboratory performance of *E. fuscus* and other bats in detection experiments (for a review, see Moss and Schnitzler, 1995), an echo of 30–40 dB SPL should be easily detected. Information for detecting the moth echo was, therefore, present in terms of echo intensity and frequency/time separation from the grass (Fig. 2). However, the bats attacked moths flying at the level of the panicles or lower in only 3% of all attempts, although the moths spend 93% of their time at this level (Rydell, 1998). This fact suggests that the identification of moth echoes as prey among clutter echoes is not trivial. Furthermore, the bats may have been capable of dealing with a limited percentage of overlap between prey and clutter echoes, and an increased overlap may interfere with the detection capabilities. Experiments in the laboratory with the related *Eptesicus fuscus* showed that the detection performance deteriorates if a noise pulse arrives at the bats less than 2 ms after the arrival of the target echo (Møhl and Surlykke, 1989). The two bats in this experiment used, on average, signal

durations of 1.7 and 2.5 ms and, with a delay of the noise pulse by 1 ms, the detection threshold increased by 5 dB. Although the performance deteriorated when the target echo was overlapped by noise, the target was still detected.

Possible cues for detection

A foraging bat not only must detect the echoes of prey but must also perceive them as prey. In the present study, the grass panicles also produce echoes, which will appear as acoustically 'dots' here and there. Moth and panicle echoes will be overlapped by clutter echoes from the underlying grass, which may make it difficult for a rapidly moving bat to discriminate between panicles and moths. Several laboratory experiments have revealed the high resolution and good discrimination capabilities of several species of bat (for a review, see Moss and Schnitzler, 1995). However, in such experiments, the bat is usually sitting on a platform and is required to discriminate between two echoes, whereas bats foraging near vegetation in the field have to relate to multiple echoes returning from different directions every time they emit a pulse. The performance of bats in natural situations may, therefore, be different from that in laboratory experiments. In fact, a field study in which bats were simultaneously presented with edible and inedible targets showed that these bats would attack inedible targets as often as edible ones if the targets were of the right size (Barclay and Brigham, 1994).

The bats attacked moths that moved in space, but not those hovering between the grass panicles (Rydell, 1998). Successive echoes from a moth moving in front of vegetation will differ as the position of the moth changes relative to the background. Since *E. nilssonii* normally hunts flying prey in the open (Rydell, 1990), it is probably more sensitive to moving than to stationary targets. For example, aerial hawking bats readily attack pebbles thrown up in the air, and it is easier to train free-flying bats to catch moving prey than stationary prey (M. E. Jensen, unpublished observations). It seems likely that these bats initially classify moving objects as prey and stationary objects as non-prey. A perceptual mechanism for this task could be auditory scene analysis in which the bat uses the three-dimensional information from successive echoes to isolate the echo or object moving in space (Bregman, 1990).

Even when moths were attacked, the capture success was low (approximately 40%; Rydell, 1998). It seems possible that the up/down flights of the moths were so brief that the moth disappeared back into the grass before the attacking bat could catch it. However, the flight excursions of the moths were usually much longer than the duration of an attack and were long enough to permit the bat to obtain several consecutive echoes. For this comparison, we make the assumption that the bat detects the moth the instant it emerges above the grass panicles, which is unlikely to be the most frequent case. Furthermore, if the bat needs several successive echoes to perceive them as echoes from a moth while using signal intervals of approximately 100 ms, it may not start the attack until several hundred milliseconds after the moth has left the grass. The echo patterns of a flying moth (Fig. 3) reveal that

some echoes are weak, which may further increase the number of echoes the bat needs for recognising the prey. Hence, the time actually available to attack and capture a ghost moth before it disappears back into a hovering display among panicles may be very short indeed.

Eptesicus nilssonii does not possess the wing morphology necessary for prolonged slow flight or hovering (Norberg and Rayner, 1987), so these bats may have to abort attacks on ghost moths that have moved back into the grass to avoid crashing, even if they know exactly where the moth was located. The low capture success reported (Rydell, 1998) could have been related to restrictions on manoeuvrability rather than to acoustic restrictions.

Pipistrelle bats have been observed attacking insects positioned only outside the clutter overlap zone and, hence, it was assumed that they could not exploit that zone (Kalko and Schnitzler, 1993). However, the prey available when these bats were observed may not have been profitable enough in terms of energy content. Although, *E. nilssonii* has a low capture success when hunting *H. humuli* close to clutter, these moths are very favourable energetically as food (Rydell, 1998). Non-clutter-specialist bats may, therefore, only choose to hunt prey situated close to clutter if the prey has a high energetic value.

As mentioned above, the observation that bats did not usually attack ghost moths in stationary, hovering display suggests that they were unable to use the wingbeat-generated Doppler shifts as cues or 'glints'. The moths were large and shining white and, therefore, visually conspicuous against the dark grass (Andersson et al., 1998), which raises the possibility that the bats made use of vision while searching for the moths. This possibility was tested explicitly during the summer of 2000 (M. E. Svensson, J. Eklöf, T. Tranefors and J. Rydell, unpublished observations). A preliminary analysis of the data suggests, however, that they do not use vision and, hence, corroborates our assumptions. The bats only attacked moths moving in space, and such movements reduce the masking effect of clutter overlap on detection.

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