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Detection and avoidance of harp traps by echolocating bats

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Researchers often use harp traps and mist nets to capture bats, and need to be aware of factors that affect trap capture efficiency. Ultrasound reflects from small targets in a frequency-dependent manner, so we predicted that higher frequency sound pulses would return stronger echoes from the fine wires and net of bat traps than would lower frequency signals. We also predicted that mist nets would return stronger echoes than harp traps because mist nets are made of a higher density (and often diameter) of material. Ensonification experiments with pulses of 20–110 kHz showed that both harp traps and mist nets reflected higher frequency pulses more strongly. Pocketed areas of mist nets returned stronger echoes than harp traps although at some frequencies differences between trap types were small. Our results provide one verified reason why harp traps are more effective than mist nets at capturing bats, and also predict that bats using high frequency echolocation calls may be more difficult to trap than species emitting low frequency signals. Interspecies differences in how traps are detected are therefore likely sources of bias in field surveys. Observations of bats encountering harp traps in the field showed less than 4% of encounters resulted in capture, and only 8.8% of encounters could be interpreted as a failure to detect the trap. A comparison between two species that differ in echolocation call and flight characteristics (*Rhinolophus hipposideros* and *Myotis nattereri*) showed no difference in trap detection or avoidance. However, differences in behaviour during trap encounters were apparent.

Key words: echolocation, target strength, capture methods, survey bias

INTRODUCTION

Researchers often need to capture echolocating bats to study and survey them. Capture methods are reviewed by Kunz and Kurta (1988), and two of the most frequently employed capture methods are use of harp traps (Kunz and Kurta, 1988; Mills *et al.*, 1996; Duffy *et al*., 2000) and mist nets (e.g., Sedlock, 2001). Tidemann and Woodside (1978) and Francis (1989) found harp traps much more effective than mist nets at catching small rhinolophids and vespertilionids, and the greater acoustic conspicuousness of mist nets may explain this disparity in capture rates. To date, the conspicuousness of bat traps as acoustic targets has not been studied, however.

Constantine (1958) developed the first harp trap, which was later modified to increase effectiveness and portability (Tuttle, 1974; Tidemann and Woodside, 1978; Francis, 1989). The design that is currently most popular for use in temperate regions makes use of two banks of vertically strung, 2.7–3.6 kg monofilament fishing lines with spacings of 2.5 cm (Kunz and Kurta, 1988). The trap is designed so that

bats encountering the first bank of lines will either fall directly into a collecting bag, or pass through the first bank and become trapped in the space between the two banks and fall into the collecting bag.

Kunz and Anthony (1977) made observations at dusk to analyse the proportion of bats that were captured, passed through, bounced off, or flew around harp traps placed at exits to buildings where bats were roosting. Capture rates ranged from 30–80% (Kunz and Anthony, 1977). However, this study did not take account of bats that avoided the trap and flew back the way they came. A more recent study by Dobson *et al*. (2001) used infrared spotlights and low light cameras to observe bats encountering harp traps at forest sites. When all encounters with the trap were considered, only 2.6% resulted in capture (Dobson *et al*., 2001).

To avoid capture in a harp trap a bat must produce an echolocation call that reflects from the trap with sufficient intensity to be audible at a distance that gives the bat the time to take evasive action. Interspecific differences in echolocation call and flight characteristics may therefore affect capture rate. The identification and quantification of bias in capture rate between species would enable harp trap data to be used more accurately.

Call frequency is especially important for a bat's ability to detect objects, as it greatly influences the intensity of returning echoes. As sound travels through air it is attenuated by spherical spreading losses and loss of energy to the atmosphere. Atmospheric attenuation is greater at high frequencies (Bazley, 1976; Lawrence and Simmons, 1982; Pye, 1993), but high frequencies give stronger echoes from very small objects (Pye, 1993; Houston *et al.*, 2004). As sound waves scatter when they reflect from a small object, only a small proportion of the original call is available for the bat to detect as an echo. Reflected echoes are weak if the circumference of the object is smaller than the wavelength of the sound wave (Pye, 1993), as diffraction diminishes the intensity of the reflected wave.

We designed ensonification experiments to test two hypotheses. First, we hypothesized that the reflectivity of sound from bat traps would be frequency-dependent, and predicted that high frequencies would reflect more strongly from traps than would lower frequencies. Second, we predicted that sound would reflect more strongly from mist nets than from harp traps because mist nets typically include a capture surface that consists of a higher density (and often diameter) of material than harp traps. We used ensonification experiments (Siemers *et al*., 2001; Houston *et al*., 2004) to test our hypotheses.

We also aimed to investigate the responses of bats to harp traps in the field. A study was designed to compare the behaviour during harp trap encounters for two species that clearly differ in the structure of their call, and show some differences in their flight characteristics. A comparison was therefore made between *R. hipposideros* and *M. nattereri.* The frequency with maximum energy in a *M. nattereri* call is 64.6 kHz; in *R. hipposideros* it is 111.0 kHz (Parsons and Jones, 2000). There are close links between the type of echolocation call produced by a bat and its flight morphology and performance (Norberg and Rayner, 1987). *Rhinolophus hipposideros* has a flight speed of around 3.5 ms^{-1} (Jones, 1993), while *M. nattereri* flies at about 4.5 ms^{-1} (Baagøe, 1987). Because of the use of higher frequencies in echolocation, a greater manoeuvrability (the ability to turn in a confined volume of space) and lower flight speed, we predicted that a lower proportion of *R. hipposideros* that encountered the trap would be captured.

Materials and Methods

Ensonification Experiments

The aim of the experiment was to calculate target strengths for harp traps and mist nets when ensonified with ultrasound pulses of different frequencies. As the same speaker and microphone were used to measure the intensity of incident pulses and reflected echoes the difference between these two measurements was used to calculate target strength without the need for calibration of the speaker or microphone.

Pulse Design and Ensonification

Constant frequency ultrasound pulses with frequencies were generated using Avisoft SAS Lab Pro, Version 4.16 (Raimund Specht, Haupstr.52, D-13158 Berlin, Germany), run on a laptop computer with a sound card (National Instruments, Austin TX, U.S.A; DAQCard-6062E, maximum sampling frequency 333 kHz). A sampling frequency of 250 kHz was used to avoid aliasing. Each pulse had a duration of 1 ms and a fade in and fade out time of 0.002 ms. The pulses were passed through an ultrasound amplifier to an ultrasound speaker (Ultra Sound Advice, London, Aberdeen Road, London N5 2UG, U.K.). The volume of the pulses was reduced to a level that did not overload the speaker or the microphone.

For measuring echoes, pulse volume was adjusted to a level that did not overload the speaker, but where possible, gave an echo from the harp trap that could be distinguished from background noise. For measuring the incident sound, the pulses used were designed with a lower volume (using the volume function in Avisoft) to avoid overloading the microphone. The difference in volume between the pulses used to measure reflected and incident sound was taken into account before calculating target strength.

The speaker was positioned 0.5 m from the centre of a 2.4 × 1.85 m harp trap (Faunatech/Austbat, Victoria, Australia) in an anechoic chamber. This distance avoided near field effects and provided clear separation of pulse and echo. A solid dielectric microphone [QMC instruments (now Ultra Sound Advice – address above); PSM-3] was positioned beside the speaker. Great care was taken to align the speaker and microphone so that the pulse reflected from the trap was received by the microphone, i.e. the acoustic axis of speaker and microphone crossed each other at the target. The sound received by the microphone was channelled through an 18 kHz high-pass filter, and recorded on a laptop computer running Avisoft Recorder. A Gould 500 Digital Storage Oscilloscope (200 MHz: Middleton, WI, USA) was used to monitor outgoing pulses and incoming echoes. Before and after making a set of echo recordings the harp trap was removed and the microphone was put in its place, 0.5 m away from the speaker, so recordings of the sound incident on the trap could be made. As the overall echo consists of two echoes reflected from the two banks of the harp trap, 10 cm apart, the echo duration was 1.59 ms (see Fig. 1). For all of the recorded pulses and echoes the root-mean-square (RMS) amplitude was calculated using Avisoft SAS Lab Pro. RMS was used in preference to peak-to-peak voltage to avoid overestimates from spikes in the signal when its intensity was close to background noise.

Measurement of Pulse Intensity

The intensity of the pulses used for echo measurements was recorded 0.5 m from the speaker with a Larson Davis 250-¼ inch air dielectric microphone (1681 West 820 North Provo, UT 84601, USA), calibrated with an acoustical calibrator (Dawe Instruments, England; D-1411E). The microphone was inserted into the calibrator and the peak-to-peak voltage of the reference pulse was recorded from the oscilloscope. The microphone was then placed 0.5 m from the speaker and the peak-to-peak voltage of the pulses used to make the echo measurements was recorded. This value was calculated to give an indication of how the intensities used in the experiment related to those produced by bats, and was not used in target strength calculations.

Target Strength Calculations

As the incident pulses were recorded at a distance of 0.5 m from the speaker, and reflected echoes travelled 1 m between speaker and microphone, the RMS of the echoes had to be corrected for the difference in atmospheric attenuation between these two distances. Values for atmospheric attenuation at each frequency were obtained from Bazley (1976), using values for temperature and relative humidity measured at the time of the recordings. As the software used to calculate the RMS of the received waves, converted this to a value in dB, the target strength of the trap at 0.5 m was calculated for each frequency using the formula:

$$\text{Target Strength at 0.5 m} = RMS_{reflected} - RMS_{incident}\ [dB]$$

where $RMS_{reflected}$ is the mean RMS of the ten echo pulses, after correcting for atmospheric attenuation and differences in amplitude of the emitted pulse; and $RMS_{incident}$ is the mean RMS of those ten pulses recorded directly opposite the speaker.

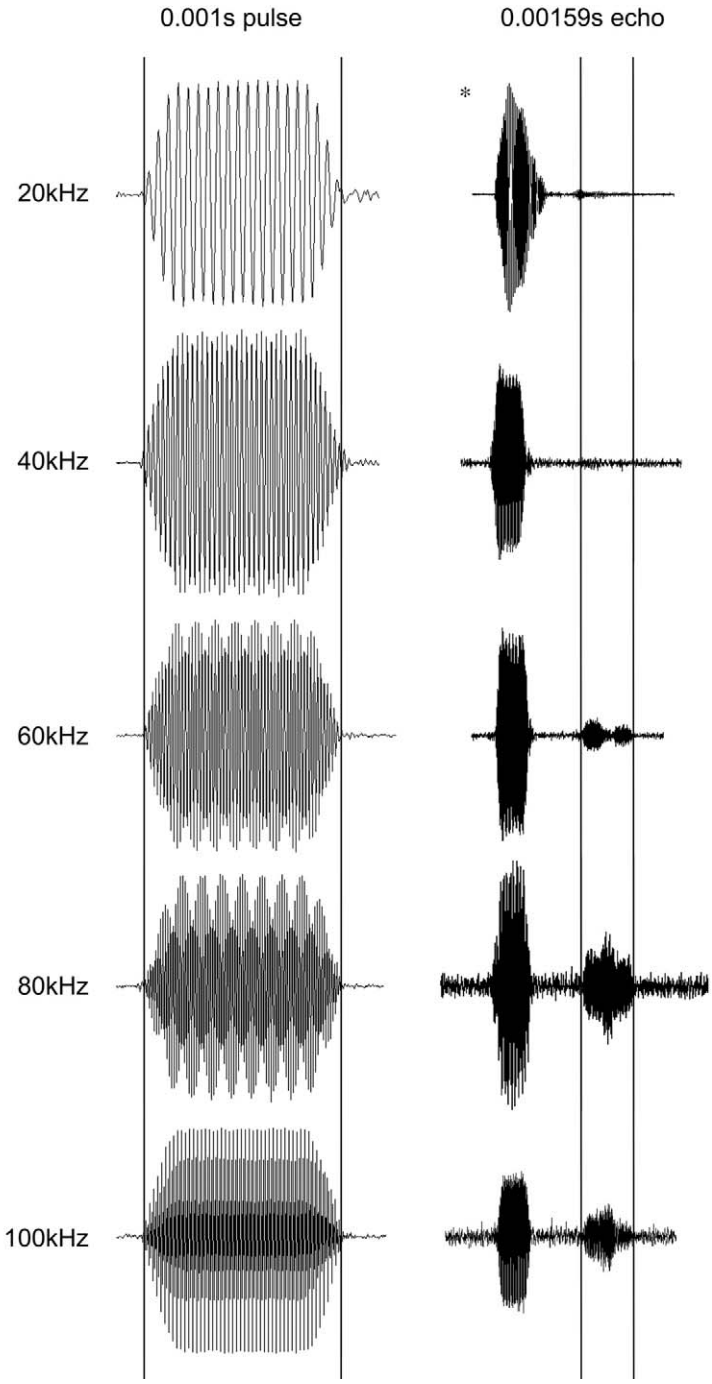

FIG. 1. Incident pulses (1 ms, 20–100 kHz), and echoes reflected from a harp trap 0.5 m from the speaker, as recorded in Avisoft Recorder. The vertical lines enclose the areas that were used to calculate the RMS (root-mean-square) amplitude of the wave. The diagram is not to scale. *The first peak in the echo recordings is the pulse from the speaker; this was not measured as the microphone was off axis with the speaker. Waveforms enclosed by the two lines in the echo plots are echoes from the harp trap: note how these appear as two echoes, one from each bank of strings, at 60 kHz

Detection Distance Calculations

The intensity of echoes that would be received by a bat at various distances from the trap was calculated using the formula:

$$\text{Echo Intensity} = SL_{50cm} - A_{sph\ (out)} - A_{atm\ (out)} + TS_{50cm} - A_{sph\ (in)} - A_{atm\ (in)}\ [dB]$$

where SL_{50cm} is the sound level of a bat call 50 cm from the bat [values for *R. hipposideros* and *M. nattereri* were obtained from Waters and Jones (1995)], $A_{sph\ (out)}$ and $A_{sph\ (in)}$ are the spherical spreading losses of the outgoing pulse and returning echo respectively, assuming a 6 dB drop with doubled distance. $A_{atm\ (out)}$ and $A_{atm\ (in)}$ are the losses to atmospheric attenuation of the outgoing pulse and returning echo respectively, and TS_{50cm} is the target strength at 50cm. The echo intensity was used to provide a minimum value for the maximum distance at which a bat would be able to detect the trap, assuming a threshold of hearing of 0 dB SPL although other authors reported a detection threshold of 40 dB. The echo intensity was used to provide a minimum value for the maximum distance at which a bat would be able to detect the trap, assuming the threshold of hearing of 0 dB SPL (Kick, 1982; Neuweiler *et al*., 1984; Coles *et al*., 1989) although other authors reported a detection threshold of 40 dB.

Target strengths at 0.5 m for pulses of 20, 30, 40, 50, 60, 70, 80, 90, 100 and 110 kHz were measured twice on each of two harp traps, and on each of two mist nets. Prominent echoes were only obtained from the mist nets when pulses were directed at a fold in the net where a guideline was used to make a pocket with three layers of netting. The mean target strength values at each frequency of the four readings for the harp traps, and of the two readings for mist nets were analysed.

Behavioural Observations

The behaviour of bats encountering a harp trap was observed at two well-studied sites in Wiltshire, Box limestone mine and Fonthill grottoes (see Parsons *et al.,* 2003). 10.5 hours of observations were made between 19:00 h and 01:00 h on three nights in October 2002, 7.5 hours at Box mine and 3 hours at Fonthill. One of the traps used in ensonification experiments was set up and some of the gaps to the side of the trap were screened with branches.

An infrared light was used to illuminate the area of the trap. Bat approaches were recorded in nightshot mode on a Sony MiniDV Handycam digital video recorder (DCR-TRV9E) fitted with a Kenko digital fisheye 0.43× macro lens. The sound input was connected to a bat detector (Ultra Sound Advice, S-25), with frequency divided (10 times) output. The camera was placed about 4 m from the trap; the bat detector was directed towards the camera about 1 m from the trap and was positioned about 0.75 m from the ground, pointing upwards at an angle of 45°. This set up enabled the echolocation calls of individual bats to be determined as they flew over the camera, and their behaviour to be observed. The videos were later played back on a monitor, with the sound channelled through a sonagraph (Kay Elemetrics, Pine Brook, New Jersey; 5500). This enabled frequency and temporal measurements to be taken from calls that could be attributed to individual bats.

Constant frequency echolocation calls between 100 kHz and 120 kHz were classified as *R. hipposideros* calls. Brief, frequency modulated calls that had a start frequency of 120 kHz or above and an end frequency at or below 32 kHz were classified as *M. nattereri* calls (Parsons and Jones, 2000). This was the most frequently captured bat in the mines during the study period (Parsons *et al*., 2003), and the high start frequency distinguished it from other *Myotis* species present. All other brief, frequency modulated calls that fell outside of the bandwidth specified for *M. nattereri* were categorised as *Myotis* sp. calls. Some of these would have been calls of *M. nattereri* recorded with poor signal: noise ratios.

Each bat that entered the field of view of the camera from the side of the trap where the camera was positioned was considered to encounter the trap. The time between entering and leaving the field of view was considered as a single trap encounter. A bat could make multiple approaches on the trap without leaving the field of view. An 'avoidance' was scored if the bat left the field of view without being captured. Alternatively the bat could 'bounce off' the trap, 'fly through' the lines, 'fly around' the trap or be 'captured'. All bats that avoided the trap on their first approach were assumed to have detected the trap. If the bat did not avoid the trap on its first approach (bounce off, fly through, or capture) we assumed that the trap was not detected. Chi-square tests were used to test the significance of differences in trap detection, capture rates and the outcome of encounters by *M. nattereri* and *R. hipposideros*. Expected values were calculated by predicting a ratio (and consequently number) of outcomes in *R. hipposideros* equal to the observed ratio of outcomes in *M. nattereri.*

RESULTS

Ensonification Experiment

Intensities of the pulses used to measure the echoes from the trap varied between

84–95 dB at 0.5 m between 20–90 kHz, falling to 73 dB at 110 kHz. The calls of *R. hipposideros* and *M. nattereri* are both around 92 dB at 0.5 m when flying in the laboratory. No detectable echoes were recorded above background noise from harp traps for playbacks of 20 kHz, 30 kHz and 40 kHz pulses; the mist nets gave no clear echoes with 20 kHz and 30 kHz pulses; so no target strength could be determined at these frequencies.

For harp traps the mean target strength at 0.5 m ranged from -57.8 dB SPL with pulses of 50 kHz, to -44.5 dB SPL with pulses of 110 kHz. Using pulses of higher frequency clearly gave greater target strengths (Fig. 2). At the highest frequencies used this effect was less pronounced, and the increase from 100 kHz to 110 kHz did not see a great increase in target strength.

The mean target strength at 0.5 m of the mist nets was generally slightly higher than the target strength of the harp traps. It ranged from -51.4 dB SPL at 70 kHz to -38.7 dB SPL at 110 kHz. While the highest frequencies used did produce the greatest target strengths, the relationship between pulse frequency and target strength was more complex than that seen with harp traps, and there was greater variation between nets. An analysis of covariance showed that both trap type ($F_{1, 12} = 8.14$, $P = 0.015$) and frequency ($F_{1, 12} = 16.59$; $P = 0.002$) affected target strength. Therefore mist nets possessed significantly higher target strengths than harp traps, and target strength increased significantly with increasing frequency. However, at some frequencies, differences between the target strengths of the two trap types were small (Fig. 2).

Predicted maximum detection distances were calculated using the harp trap target strengths. Maximum detection distances were greater at higher frequencies ranging from 2.48 m at 50 kHz to 3.01 m at 100 kHz. Therefore, increases in trap conspicuousness caused by the frequency-dependent effects of target strength had a stronger effect on detection distance than did atmos-

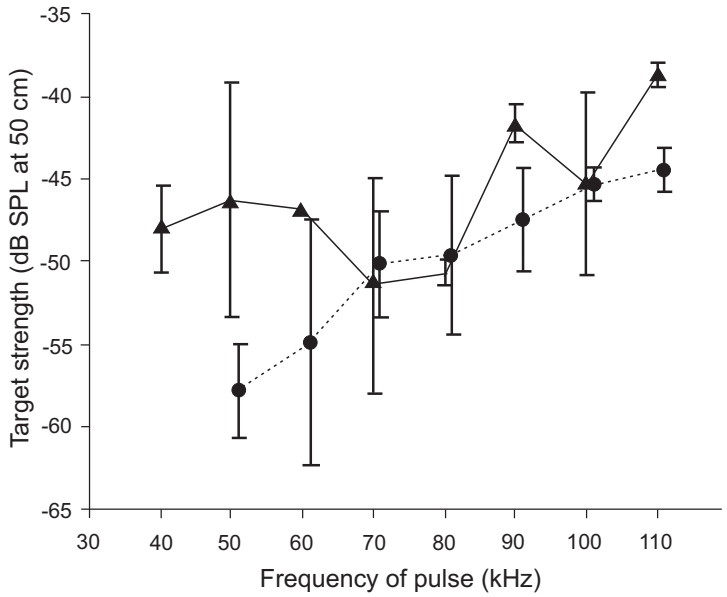

FIG. 2. Mean target strengths at 0.5 m for single frequency pulses reflected from harp traps (circles, dashed line: $n = 2$) and mist nets (triangles, solid line: $n = 2$); error bars show SE of the mean

pheric attenuation, which reduced detection distance with increasing frequency. At frequencies above 70 kHz maximum detection distance leveled off, however, because target strength increased more slowly and the effects of atmospheric attenuation were strong (Fig. 3). Maximum detection distances for mist nets ranged between 2.83 m at 80 kHz and 3.92 kHz at 40 kHz. The lack of a general trend over frequency and the rather changeable detection distances reflected the large differences in target strengths between frequencies with measurements from mist nets.

Behavioural Observations

In the 10.5 hours of observations 2574 trap encounters were recorded; 1901 at Box mine, and 673 at Fonthill. 731 encounters were from *M. nattereri*, 188 from *R. hipposideros*. At Box mine 3.95%, and at Fonthill 2.82%, of trap encounters resulted in capture. The outcomes of encounters with the harp trap from the two sites are shown in Fig. 4. When the data from both sites were combined, there was a significant

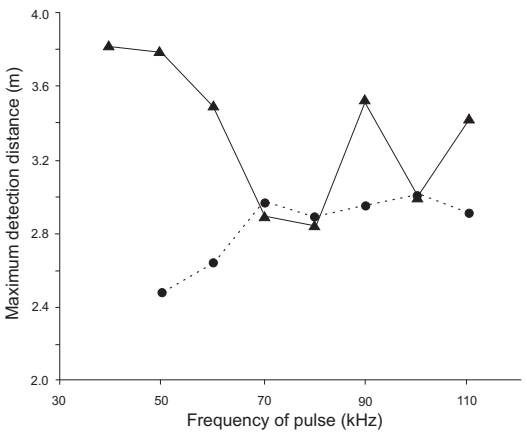

FIG. 3. Predicted maximum detection distances of harp traps (circles, dashed line: $n = 2$) and mist nets (triangles, solid line: $n = 2$) for bats emitting constant frequency pulses of 92 dB SPL. Calculated using mean target strengths and assuming a threshold of hearing of 0 dB

difference between *M. nattereri* and *R. hipposideros* in the outcome of encounters ($\chi^2_4 = 129.2$, $P < 0.001$). There was no significant difference, between the two species, in the proportion of encounters that ended in capture ($\chi^2_1 = 0.89$, $P = 0.345$). A significantly greater proportion of *R. hipposideros* bounced off the trap ($\chi^2_1 = 22.74$, $P < 0.001$), or avoided the trap and made more than one approach ($\chi^2_1 = 83.14$, $P < 0.001$). A greater proportion of *M. nattereri* avoided hitting the trap and left immediately ($\chi^2_1 = 18.09$, $P < 0.001$). The difference in the proportion of bats of each species that flew through the trap was not significant ($\chi^2_1 = 3.53$, $P > 0.05$), and the difference in numbers flying around the trap could not be analysed, as the data were insufficient.

In only 8.8% of the harp trap encounters observed could the bats' behaviour be interpreted as failure to detect the trap (i.e. they hit the trap on their first approach). The number of encounters where *R. hipposideros* and *M. nattereri* were presumed to detect the trap was compared. At neither site was there a significant difference in the proportion of *R. hipposideros* and *M. nattereri* that were presumed to detect the harp trap (Box, $\chi^2_1 = 1.84$, $P = 0.17$; Fonthill, $\chi^2_1 = 3.80$, $P = 0.051$).

Significantly more *R. hipposideros* encounters involved more than one approach on the trap, compared to *M. nattereri* encounters at Box mine ($\chi^2_1 = 36.5$, $P < 0.001$) and Fonthill ($\chi^2_1 = 95.3$, $P < 0.001$). Almost a third (29.1%) of all *Myotis* spp. (including *M. nattereri*) observed flew in close pairs or triplets; while all *R. hipposideros* were alone.

DISCUSSION

Echoes from Harp Traps

As predicted from diffraction and Rayleigh scattering, target strength increased as

signal wavelength decreased. The wavelength of the pulse was greater than the circumference of single lines in the trap (wavelength at 100 kHz = 3.4 mm, circumference of harp trap string = 0.79 mm) so diffraction probably decreased the amount of reflected energy. The increase in target strength when increasing pulse frequency from 50 kHz to 110 kHz, and the linear relationship between pulse wavelength and target strength, were also expected due to frequency-dependent Rayleigh scattering.

The values calculated for maximum detection distances showed a difference of about 50 cm between calls of 50 kHz and 110 kHz, indicating the stronger reflectivity of high frequencies was sufficient to overcome the effects of increased atmospheric attenuation. The calculated maximum detection distances are minimum estimates as, for spherical spreading calculations, the echoes were considered to originate from a point source. In reality, it is likely that positive interference from the multiple lines of

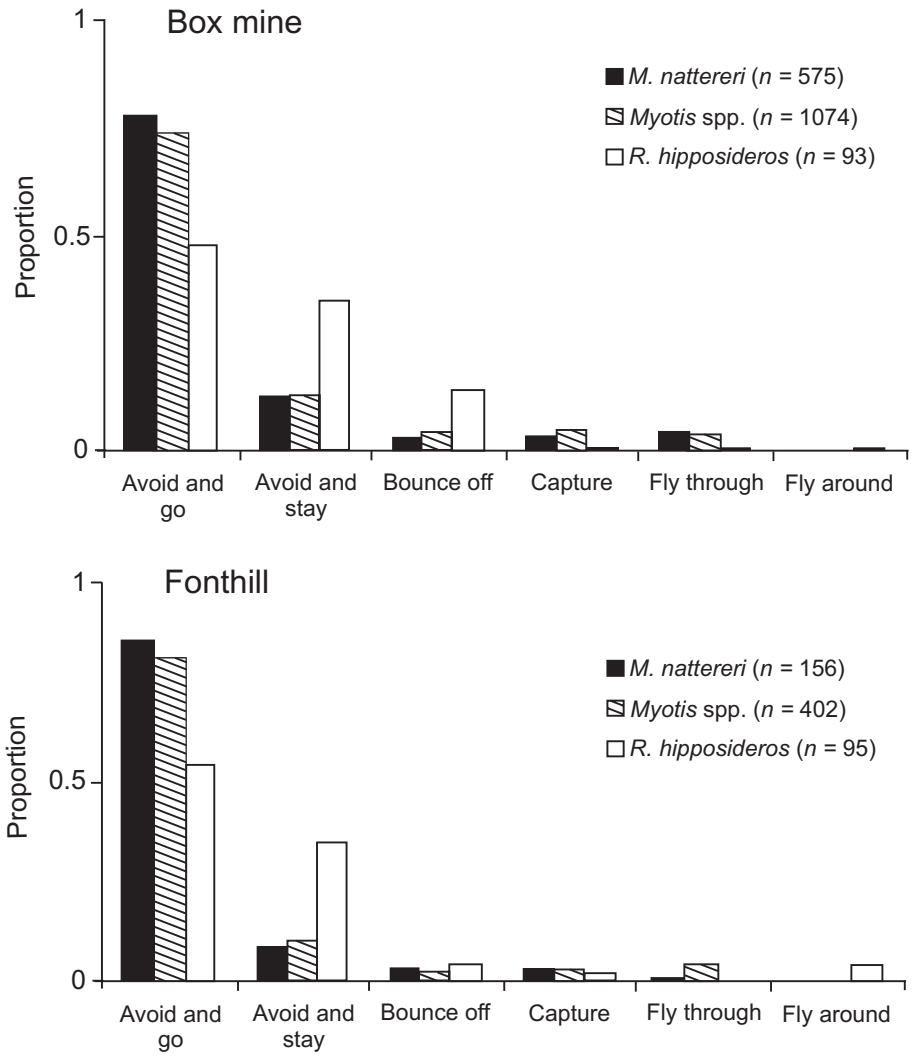

FIG 4. Comparison of outcome of encounters with a harp trap by *M. nattereri*, *R. hipposideros*, and *Myotis* spp. at Box mine and Fonthill

the trap means it acts more like a flat reflective surface than a point source. A single, fully ensonified line would result in cylindrical spreading, resulting in a -3dB per doubling distance spreading law. Therefore the target strengths of harp traps with incident bat calls would be stronger than the target strengths seen in this study, as the beam width produced by a bat is likely to be greater than that produced by the speaker used here (Holderied, 2001). This would enable the bat to ensonify a far larger area of the trap, giving it a chance to receive echoes from more of the lines and from a larger proportion of each line. This may have a disproportionate effect, as positive interference from the echoes of adjacent lines is likely to produce a strong reflected wavefront and the echoes carry further due to 'more cylindrical' spreading of each line's echo.

The calculated maximum detection distances ranged between 2.5 m to 3 m. If actual detection distances were much greater than this, bats that avoided the trap may not have been observed in this study as the camera was positioned about 4 m from the trap. Call intensities used in detection distance calculations were measured in the laboratory by Waters and Jones (1995), which may be similar to those emitted by bats flying in confined spaces such as the mine tunnels studied here, whereas many bat species can produce much higher call intensities in free, unobstructed flight (Holderied and von Helversen, 2003).

The ensonification experiments indicated that all the species at the study sites produce calls that should enable them to detect the trap. This was supported by behavioural observations, which showed that most bats reacted to the trap. Only 8.8% of trap encounters resulted in behaviour that could be interpreted as a failure to detect the trap. This is comparable to the study by Dobson *et al*. (2001) where there was no trap detection in 8.3% of encounters. The measured target strengths and detection distances for the harp traps suggest that *R. hipposideros* should be better at detecting harp traps than *M. nattereri* as their call frequency with maximum energy is higher; but no between species differences in trap detection were seen in this study.

Because *M. nattereri* can produce calls with a start frequency as high, or higher than, the frequency with maximum energy in a *R. hipposideros* call (Siemers and Schnitzler, 2000) it may make use of the high frequency components for detecting traps. Although the capacity of *M. nattereri* to hear the highest frequencies of its call has yet to be demonstrated; their ability to detect complex substrates, such as spider's webs (Attenborough, 2003), may suggest that they can use the high frequency component of their calls to resolve targets with lower, and more frequency-dependent, reflectivity than harp traps. It is also possible that the harp traps reflected echoes from calls of both species that were strong enough to enable detection over a sufficient range for them to react to the trap, so no difference in capture rates would be apparent.

Echoes from Mist Nets

The higher target strengths of mist nets suggest that they are easier for bats to detect than harp traps. However, in this study echoes were only apparent when the pulses were aimed directly at a triple layer of netting with a guideline running through that formed the pocket. A mist net is a far more complex target than a harp trap, and echoes will be affected by a range of positive and negative interference effects from various parts of the mesh. Francis (1989) found that harp traps were 60 times as effective at capturing small- to medium-sized rhinolophoid and vespertilionid bats when compared with mist nets. Francis' (1989)

hypothesis that the difference in capture rates was attributable to the greater ease with which mist nets are detected by echolocation is supported by our study, although Francis (1989) used harp traps with four banks of strings in his studies. Mist nets include horizontal strings, whereas harp trap strings are vertical, and this could have some influence on the higher detectability and avoidance of mist nets if bats are better able to detect horizontal targets than vertical ones. Francis (1989) showed that the ratio of captures in mist nets compared with harp traps was higher for bats calling at lower frequencies compared with bats emitting higher frequency calls. This observation is consistent with our finding that mist nets return stronger echoes than harp traps at low frequencies, whereas at high frequencies the difference in echo strengths in relation to trap type is much smaller. Mist nets may also be more apparent visually to bats than harp traps, and differences in visual conspicuousness may affect capture rates especially at dusk and dawn.

Capture Rates

The capture rates (per approach) from the two sites of 3.95% and 2.82% are similar to those reported by Dobson *et al.* (2001) for different species. Of course many approaches came from repeated flights of the same bat, but there was no way of avoiding this in our analysis. If the encounters where bats avoided the trap by flying back the way they came from are not included — as with the study by Kunz and Anthony (1977) where capture rates were between 30% and 80% — 31% of encounters resulted in capture. The methods of species identification used here allowed 36.1% of bats encountering the trap to be identified to species level, but there was no significant difference in the proportion of trap encounters that resulted in captures of *R. hipposideros* and *M. nattereri*. This supports the finding that there was no difference in trap detection between the two species, and suggests that any differences in flight characteristics are not sufficient to affect the proportion of bats that are captured.

Bat Behaviour

While there was no difference in the proportions of *R. hipposideros* and *M. nattereri* that were captured, there were notable differences in their behaviour during an encounter with the trap, and in the outcome of that encounter. The typical behaviour of *R. hipposideros* was to avoid the trap initially, but stay in the vicinity and fly left to right across the front of the trap. This is demonstrated by the number of individuals that avoided the trap initially and stayed to make more approaches, and that had encounters that involved more than one approach; both of which were significantly greater in *R. hipposideros* than in *M. nattereri*. It may also explain why more *R. hipposideros* bounced off the trap. The typical behaviour of *M. nattereri* involved circling immediately to fly back in the direction of the approach. These clearly different behaviours may suggest differences in the way the traps are perceived, perhaps indicating *R. hipposideros* can discriminate individual lines while *M. nattereri* perceives the trap as a single surface. Behavioural differences could also be due to differences in flight characteristics, as *R. hipposideros* may be more adept at hovering and changing direction.

Support was found for the observation that bats at swarming sites often follow conspecifics (Parsons *et al*., 2003), with 29.1% of all *Myotis* spp. observed involved in following behaviour. As *R. hipposideros* were not swarming, differences in motivation between the two species could have affected

their behaviour when encountering the trap; perhaps discouraging *M. nattereri* from remaining in the vicinity once the trap had been detected.

In conclusion, we have shown that harp traps are conspicuous acoustic targets to bats, and many bats avoid being captured in them and showed behaviours consistent with detection of the traps. Target strengths from traps are frequency-dependent, with higher frequencies reflecting more strongly. Mist nets return stronger echoes than harp traps. Although we detected no differences in capture rates of two species with different echolocation call designs, differences in motivation may have overridden any differences in the ability of the bats to detect the traps. Differences in the acoustic conspicuousness of harp traps and mist nets, and frequency-dependent reflectivity of echoes from traps should be considered when planning capture surveys of echolocating bats.

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