

ECHOLOCATION CALL STRUCTURE AND INTENSITY IN FIVE SPECIES OF INSECTIVOROUS BATS

DEAN A. WATERS AND GARETH JONES

School of Biological Sciences, University of Bristol, Woodland Road, Bristol BS8 1UG, UK

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Summary

Echolocation call intensity was measured in the laboratory for five species of British insectivorous bats in free flight and in the hand. All species showed similar call intensities of between 80 and 90 dB peSPL (peak equivalent SPL) at 1 m during flight except *Plecotus auritus*, whose call intensity was between 68 and 77 dB peSPL at 1 m. Calls from stationary bats were about 13 dB less intense than calls during flight. A method is proposed to measure the root mean square (rms) amplitude of echolocation calls and, hence, to calculate the energy flux density of the call.

The constant-frequency calls of *Rhinolophus hipposideros* have energy flux densities approximately ten times higher than those of bats using frequency-modulated calls as a result of their longer durations and lower crest factors. It is argued that the low-intensity calls of *P. auritus* allow it to approach tympanate moths more closely before triggering their escape response.

Key words: bat, echolocation, energetics, sensory ecology, foraging.

Introduction

Analysis of the echolocation calls of bats within the time and frequency domains has become commonplace with improvements in transducer design and portable field apparatus (Pye, 1992; Jones, 1993). Measurement of the intensity of echolocation calls has, however, remained a difficult challenge, partly because of the transient nature of the calls (Pye, 1980). The intensity of bat echolocation calls has implications for energetics (Speakman *et al.* 1989; Speakman and Racey, 1991), foraging ecology (Neuweiler, 1983), ranging (Fenton, 1980) and for the interactions between bats and tympanate moths (Surlykke, 1988). Previous studies of call intensity, such as those by Griffin (1958) and Novick (1958), were limited by the technology available at the time, but did provide information on the relative call intensities between species of bats. The most accessible method for measuring the intensity of short-duration pulsed sounds is that of peak pressure, which quantifies the maximum pressure reached during the pulse, even if it is maintained for a fraction of the duration of the pulse. This method provides only limited information on the acoustic power of the call because the average intensity over the duration of the pulse depends on the mean value of the square of the instantaneous pressure with time. Therefore, the total energy of the pulse depends on the time integral of the square of the function defining the pressure waveform. The peak level recorded will depend on the time resolution of the recording device and on the harmonic and phase relationships of the frequency components within the call (Dusenbury, 1992). Calls with similar frequency sweeps

and durations may differ widely in peak pressure–energy relationships depending on the shape of the pressure–amplitude envelope. This issue is of particular importance in the interaction between the echolocation calls of bats and the ears of moths, which appear to be energy detectors (Adams, 1971; Surlykke *et al.* 1988). Studies of dolphin sonar have avoided some of these problems by computing the energy flux density, E , of the signal (Au and Snyder, 1980; Au *et al.* 1985) and by compensating for the density of the transmission medium, which makes it possible to compare directly the source level of cetacean and chiropteran sonar systems (Au, 1993).

Most previous studies of bat echolocation call intensity have concentrated on stationary bats held a known distance from a microphone (Griffin, 1958; Novick, 1958; Schnitzler, 1968; Shimozawa *et al.* 1974). While this standardises the distance of the bat from the microphone, it does not allow for the fact that echolocation and flight appear to be energetically coupled (Speakman *et al.* 1989; Speakman and Racey, 1991) and that flying bats appear to produce stronger calls than stationary ones (Griffin, 1958; Mohres and Neuweiler, 1966). A few studies (Griffin *et al.* 1963; Mohres and Neuweiler, 1966; von Joermann and Schmidt, 1981; Surlykke *et al.* 1993; Miller and Treat, 1993) have measured echolocation call intensity during flight, and they provide the best information about the functional significance of call intensity.

The temporal and frequency variables of the echolocation calls of flying bats are limited in resolution by a number of

factors. Solid dielectric capacitance microphones often show a non-linear frequency response and unpredictable reactions to differing conditions of temperature, humidity and the tension applied to the membrane (Kuhl *et al.* 1954; Fenton, 1988). The directionality of the call as emitted by the bat with respect to its angle to the microphone will influence the sound spectrum recorded. Frequency-dependent 'nulls' in the acceptance angle of the microphone contribute to this problem, but it is largely caused by the geometry of the source influencing the emission pattern of the sound from the bat. The geometry results in greater directionality at higher frequencies (Hartley and Suthers, 1987, 1989; Shimozawa *et al.* 1974) and an altered sound spectrum as the bat's angle with the microphone's surface deviates from normal. Finally, the attenuation of ultrasound by the atmosphere is more pronounced at higher frequencies (Griffin, 1971), resulting in a predicted alteration of sound spectrum with increasing distance from the bat (Pye, 1992). All these factors interact to make it difficult to define the 'true' structure of the echolocation call (Pye, 1993). The most important implication of these limitations is that the higher-frequency components of calls may go unrecorded, and these frequencies limit the spatial resolution of the call (Møhl, 1988).

This study provides absolute peak sound pressure measurements of the echolocation calls of five species of bats during flight in the laboratory and whilst stationary. Calculations are made of the energy flux density of the calls based on the rms (root mean square) measurements of a subsample of calls. The call structures are described from recordings made in a frequency-linear manner. The findings are discussed with reference to the foraging ecology of the species investigated.

Materials and methods

Animals and husbandry

All bats were obtained under licence from English Nature, either from hibernation sites within Avon, UK, or by hand-netting at summer day-roosts. Two individuals each of *Pipistrellus pipistrellus* (Schreber), *Myotis brandtii* (Eversmann), *M. nattereri* (Kuhl) and *Plecotus auritus* (Linnaeus) were obtained. One *Rhinolophus hipposideros* (Bechstein) was obtained from the wild. We also studied another *R. hipposideros* which was being rehabilitated after being found injured. This individual was not used for the flight experiments. Bats were maintained either in 20 cm × 25 cm × 30 cm boxes and exercised daily, or were allowed to fly freely in a 3 m × 3 m × 2 m room with hessian roosting sites attached to the walls. Bats were maintained under a 14 h:10 h light:dark regime at 20 °C and had free access to fresh drinking water. Mealworms (larvae of the beetle *Tenebrio molitor*) were available *ad libitum* as food. *Rhinolophus hipposideros* was provided with *Drosophila* for food.

General experimental methods

All experiments were performed in a 4 m × 4 m × 2.6 m room

lined with 1 cm thick sound-attenuating foam. Environmental conditions were maintained at 12 °C and 85% relative humidity, similar to those experienced by bats in the field in the summer. Bats were released from the hand at a height of 1.4 m and flew 3 m towards a frequency-linear recording system. A multiframe stereophotogrammetry system was positioned 3 m to the side and was used to record the position of the bat along its flightpath. The timing of the flashes, and hence the position of the bat, could be correlated with each echolocation call to establish the three-dimensional distance of the bat from the microphone when the call was emitted.

Recording system

The recording system consisted of a Brüel and Kjær 6.35 mm microphone, type 4135 (without protective grid), attached to a type 2204 sound pressure meter. A 2 cm diameter plastic ring was placed around the microphone to prevent collision of the bat with the delicate microphone membrane. The addition of this ring did not noticeably affect either the directionality or the frequency response of the system. The signal from the meter was passed through a custom-made high-pass filter to attenuate signals below 4 kHz and recorded onto one channel of a Racal Store 4DS instrumentation recorder at 76 cm s⁻¹. Overall system response from 4 to 120 kHz was ±3 dB. A second microphone (PSM-3, QMC Instruments) was positioned close to the flashgun array to record the faint ultrasound pulses produced when the flashguns fired. This was recorded onto a second channel of the instrumentation recorder and allowed each image of the flying bat to be correlated with the corresponding echolocation call.

Multiframe stereophotogrammetry

The multiframe stereophotogrammetry apparatus consisted of two motor-driven Nikon SLR cameras (FE and FM2 models) equipped with 55 mm lenses mounted in parallel 250 mm apart on a machined plate. Eight Sunpak 622 flashguns with a Guide number of 50 (ISO 100/meters) were connected to a sequential relay box and could be fired in volleys of eight at frequencies of 20 or 30 Hz. The flashguns were placed on the floor under the flightpath of the bat and were triggered by the cameras' shutters. In order to prevent sound from the cameras and flash system altering the bat's echolocation call structure, the flashguns were placed in a sound-proofed glass aquarium tank, and the cameras and motordrives were covered in sound-attenuating foam. Flash power was switched to 1/32 of full power, producing an approximate pulse duration of 10⁻⁴ s. Exposures were typically f8 at 0.5 s on Ilford XP2 400 ASA film. The cameras were triggered simultaneously *via* an electrical switch, and the 0.5 s shutter speed allowed eight images to be recorded on each frame. Films were developed and enlarged to A4. A representative photograph from a stereo pair of an individual of *P. auritus* in free flight towards the microphone is given in Fig. 1.

Reconstruction of the flight paths

Photographic data were digitised on a BBC Master Series

Fig. 1. Left-hand stereo photograph of *Plecotus auritus* individual 2 in free flight towards the microphone (on the right of the picture). Flash frequency was 20 Hz.



microcomputer through a Summagraphics One digitising tablet. Data were transferred to an IBM computer and recalculated in three dimensions following methods given by Wolf (1983). The accuracy of this technique and the algorithms used are discussed in detail by Spedding *et al.* (1984) and Rayner and Aldridge (1985), and some applications of this technique are given in Jones and Rayner (1988, 1989a, 1991) and Rayner *et al.* (1989).

Analysis

Sequences where the bat was flying in an apparently straight line towards the microphone were printed as projected onto the x,y and y,z planes. The -3 dB angular acceptance of the microphone (up to 100 kHz) was 60° , and images were only accepted if the incident angle of the bat's trajectory was less than this. An angle of 30° was chosen for the -3 dB limit of the echolocation call of the bat because of its directionality, based on Schnitzler and Grinnell (1977), Shimozawa *et al.* (1974) and Hartley and Suthers (1987, 1989). Again, sequences were not used if the microphone was outside this angular range. Echolocation calls and the timing sequences from the flashguns were analysed simultaneously on the two channels of a Kay DSP Sonagraph model 5500. Since each pulse from the flashgun corresponded to an image of the bat, the timing of an echolocation call could be correlated with an image or with a fixed point between images. The distance of the bat at the time of the echolocation call could then be calculated using simple three-dimensional geometry. The time taken for the call to reach the microphone caused a small error in calculating the position of the bat at the time of the call. This was estimated to be less than 30 mm at 2 m from the microphone, the error reducing as the bat approached the microphone. The peak amplitude of the call was measured on the Sonagraph as the logarithmic amplitude of the envelope of the call averaged every 0.1 ms. This averaging constant was chosen since further expansion of the time-base produced no additional increase in the peak amplitude. The recorded amplitude was compared with calibrating signals of constant-frequency sine waves of known sound pressure levels. The difference (in dB) between the measured signal and the calibrating signal was then used to calculate the rms sound pressure level of a constant-frequency sine wave of equivalent peak-to-peak amplitude, providing the measure of dB peSPL (Stapells *et al.* 1982; Møhl, 1988). All other call analysis was performed on the Sonagraph by using a waveform display for call duration, a 512-point FFT transform sonagram with Hamming window for visual inspection of the signal and a

1024-point FFT power spectrum with Hamming window for peak frequency and frequency range measurement (frequency resolution 928 Hz, real-time signal).

Stationary bats

After conducting the flight measurements, the bats were rested for between 2 h and 1 day. A ruler was taped to the sound pressure meter, which was placed in the centre of the sound-proofed room at a height of 1.5 m. Bats were held loosely in the hand at a distance of 10 cm from the microphone. Bats tended to produce very low-amplitude calls while being held, but just prior to take-off increased their call amplitude. It was assumed the bat did this to orientate over a greater range prior to flight. Only these higher-intensity calls were recorded onto the instrumentation recorder. Call intensity was analysed as above.

Calculation of energy flux density

Theory

The measurement of peak pressure of the echolocation calls provides little information on the power content of the call and, hence, little information on the metabolic costs necessary to produce it. The energy flux density, E , is a measure of the energy content of a sound pulse at 1 m from the source, assuming that the source is isotropic. There appears to be some ambiguity in the definition of E in terms of the units involved. Møhl (1988) uses the units of $\text{Pa}^2 \text{s}$, but Au (1993) interchanges these with J m^{-2} when E is compensated for the density and velocity of sound in the medium. In general, E can be calculated as:

$$E = \int_0^T P^2(t) dt \text{ (in Pa}^2 \text{ s)} \quad (1)$$

or:

$$E = 1/\rho c \int_0^T P^2(t) dt \text{ (in J m}^{-2}\text{)}, \quad (2)$$

where E is energy flux density, $P(t)$ is the time-varying sound pressure, T is the duration of the signal (s), ρ is the density of the medium (kg m^{-3}) and c is the velocity of sound in the medium (m s^{-1}).

Evaluation of the integral in the above equations presents some difficulty, since the function defining the pressure waveform is unknown. In practice, it could be evaluated from a digitised time series of the waveform, as in Troest and Møhl (1986) and Hartley *et al.* (1989), graphically from a print of the waveform (which is time consuming), or a measure of E could be produced from the measurement of the root mean square (rms) pressure of a signal. While a direct measurement using a digital time series is likely to be the most accurate,

software for this type of analysis may need to be specifically written and is only now becoming commercially available. For this reason, measurement of the rms pressure of the signal was chosen because of the availability of conventional analogue meters.

The rms pressure of a finite duration signal can be evaluated as:

$$P_{\text{rms}} = \sqrt{1/T \int_0^T P^2(t) dt}, \tag{3}$$

where P_{rms} is root mean square pressure (N m^{-2}).

From equations 1 and 3, it can be shown that:

$$E = P_{\text{rms}}^2 T \text{ (in Pa}^2 \text{ s)} \tag{4}$$

and:

$$E = 1/\rho c P_{\text{rms}}^2 T \text{ (in J m}^{-2}\text{)}. \tag{5}$$

Conventional sound pressure meters measure the rms of sound sources using long time constants (a few hundred milliseconds) and produce accurate rms measures of sound levels which vary little over time. When the duration of sound pulses is less than the duration of the time constant, the meter produces a readout which is less than the actual rms pressure of the sound pulse. Since this function is well defined when the duration of the pulse is accurately known, a compensation factor can be calculated and added to the meter reading to produce the rms pressure of the pulse. Prestwich *et al.* (1989) used this technique to calculate the rms pressure of calls of hylid frogs by using a meter with a time constant of 125 ms. Since bat echolocation calls are much shorter in duration, a Brüel and Kjær 2204 meter with a 35 ms time constant (=‘impulse response’) was used. The response of the meter to a short duration pulse is defined by:—

$$P_m = P_{\text{rms}} \sqrt{1 - e^{-T/RC}}, \tag{6}$$

where P_m is measured pressure reported by the meter (N m^{-2}), P_{rms} is actual rms pressure (N m^{-2}) and RC is the time constant of the meter (s).

The actual response of the meter was compared with the predicted response by broadcasting rectangular-enveloped 50 kHz sine-wave pulses at various durations at the meter equipped with a Brüel and Kjær 4135 6.35 mm microphone

(grid off). The results of the actual meter response and the predicted response (Fig. 2) differ by less than ± 0.5 dB, and our measurements were highly repeatable, differing by ± 0.1 dB at most.

Procedure

Sequences of calls from the bats in free flight were examined on a Kay DSP 5500 Sonagraph. We selected three calls with a good signal-to-noise ratio and high maximum frequency for each bat, produced when the bat was facing the microphone. The sequence of tape containing the calls was replayed in real time and digitally sampled at a rate of 400 kHz using an Ultra Sound Advice S-350 digital memory recorder. Sampled sequences were downloaded in analogue form at $10\times$ time expansion into the Sonagraph. The call of interest was edited out and digitally compiled with 11 s of silence either side of it. The call sequence was then downloaded onto a Sony DAT recorder TCD-D3. To replay the signal, the analogue DAT recording was sampled into the Ultra Sound Advice S-350 at a sampling rate of 40 kHz and recompressed back to real time. The signal was amplified and broadcast through an Ultra Sound Advice amplifier and loudspeaker. Examination of the broadcast call revealed no major changes in frequency or temporal structure from the original call, although low-frequency tape noise had increased and some high frequencies had been attenuated by the atmosphere (Fig. 3). The broadcast call was replayed at a rate of 0.5 Hz at the Brüel and Kjær 2204 sound pressure meter equipped with a 4135 6.35 mm microphone (grid off) at a distance of 1.3 m from the speaker. The impulse response [termed dB(I)] on the meter was noted. The peak-to-peak voltage from the a.c. socket of the meter and the duration of the call were measured on a Tektronix 5113 oscilloscope. A 50 kHz sine wave was then broadcast at the meter and the peak-to-peak voltage matched to that of the call. The dB SPL reading of this signal was then noted with the integration time of the meter set to 500 ms. A correction factor for the call was calculated from its duration and equation 6 and added to the dB(I) value to produce the rms value of the call. The peak pressure reading (dB SPL+3.01) minus the corrected dB(I) value yields the dB

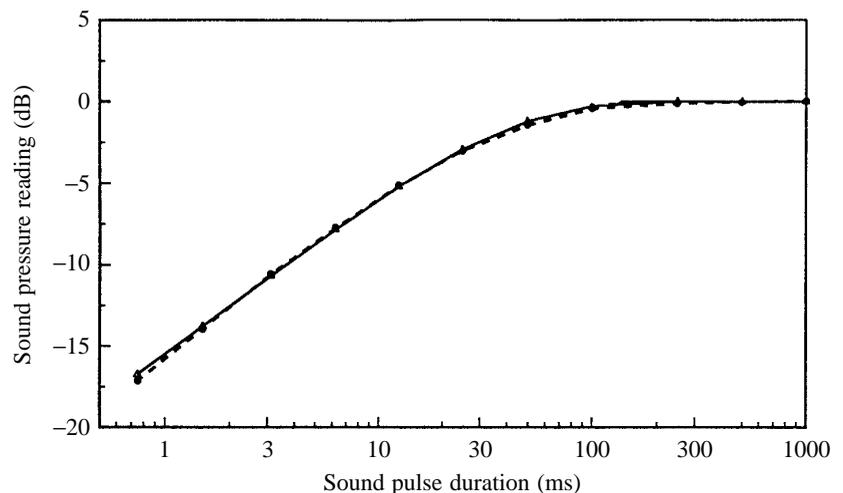


Fig. 2. Predicted (solid line) and actual (dashed line) responses of the Brüel and Kjær 2204 sound pressure meter impulse response with decreasing pulse durations. The y-axis is the reading on the meter scale below the actual dB SPL.

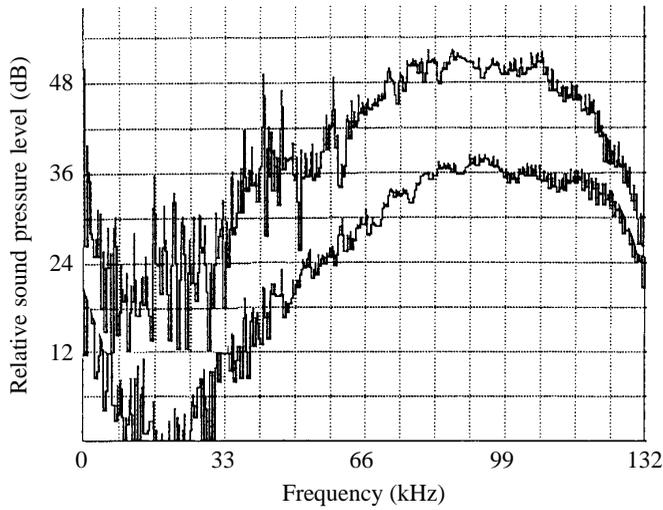


Fig. 3. Power spectrum of a recorded call of *Myotis nattereri* (lower trace), and the same call after sampling, editing, rebroadcasting and re-recording (upper trace). Traces are deliberately separated by 12 dB for clarity.

equivalent crest factor of the call, necessary for the calculation of the energy flux density from the free-flight call intensity data.

Results

Echolocation call intensity in free flight

Regressions of call intensity (dB peSPL re $2 \times 10^{-5} \text{ N m}^{-2}$) with distance (Fig. 4) are based on logarithmic transformations of distance since intensity is expected to depend on the inverse square law for distances and on the distance-linear effect of atmospheric attenuation. The former should have the highest relative influence over the short distances recorded. Since the distance could not be controlled,

least-squares regression is an inappropriate model (Sokal and Rohlf, 1981), and we used reduced major axis regressions to provide the least bias since the variances of the measurement errors could not be estimated (Rayner, 1985). Assuming the inverse square law for the intensity–distance relationship (and hence the inverse distance law for the pressure–distance relationship), a regression should result in the predicted 6.02 dB drop with doubled distance. The calls of two individuals did not show a significant relationship between call intensity and distance from the microphone, one *P. auritus* and the only flying *R. hipposideros* (Fig. 1; Table 1). The calls of all of the other bats showed a significant relationship, and the slopes of the regression line were steeper than the -6 dB predicted from the inverse square law.

Regression of the intensity data (Table 1) gave intensities at a distance of 1 m. For individuals whose calls showed a significant relationship between intensity and distance from the microphone, the value at 1 m is taken from the regression. For the two exceptions, the values are estimated from the sound pressure levels emitted close to 1 m. The calculation of peak intensities is usually performed to provide a measure of the intensity at a default distance of 10 cm from the bat’s mouth (Pye, 1980) using the inverse square law. Because this calculation takes no account of the effect of excess atmospheric attenuation, it produces only a rough estimate so, to provide values for comparison with the literature, the calculated values at 10 cm are also presented (Table 1) assuming the inverse square law alone.

Four species produced calls of similar intensities, while the calls of *P. auritus* were less intense by $\geq 7.1 \text{ dB}$ than that of the next quietest bat. There was a large discrepancy between the two *P. auritus* of about 9 dB. There was almost no overlap in the intensity measurements between these two individuals, though the calls for both bats were of lower intensity than those of the other species.

Table 1. Summary of call intensity data from bats in flight and while held in the hand

Bat	Flight: intensity at 1 m (dB peSPL)	Slope	r^2	P	E ($\text{Pa}^2 \text{ s}$)	E (J m^{-2})	Flight: equivalent dB peSPL at 10 cm	Stationary bats: dB peSPL at 10 cm	Difference dB
<i>P. pipistrellus</i> 1	83.2	-8.7	0.64	<0.001	8.38×10^{-5}	2.01×10^{-7}	103.2	85 ± 2.4	-18.2
<i>P. pipistrellus</i> 2	86.2	-14.3	0.51	<0.001	1.40×10^{-4}	3.39×10^{-7}	106.2	87 ± 2.4	-19.2
<i>M. brandtii</i> 1	88.9	-9.6	0.75	<0.001	1.26×10^{-4}	4.73×10^{-7}	108.9	101 ± 2.2	-7.9
<i>M. brandtii</i> 2	89.3	-11.3	0.36	<0.001	2.26×10^{-4}	5.45×10^{-7}	109.3	92 ± 2.4	-17.3
<i>M. nattereri</i> 1	89.8	-9.5	0.38	<0.001	2.53×10^{-4}	6.08×10^{-7}	109.8	96 ± 1.2	-13.8
<i>M. nattereri</i> 2	82.8	-11.3	0.44	<0.001	4.15×10^{-5}	3.29×10^{-7}	102.8	93 ± 2.1	-9.8
<i>P. auritus</i> 1	68.6	-8.1	0.02	NS	1.11×10^{-6}	2.68×10^{-9}	88.6	73 ± 1.5	-15.6
<i>P. auritus</i> 2	77.1	-11.6	0.28	<0.001	3.71×10^{-6}	1.18×10^{-8}	97.1	75 ± 1.8	-22.1
<i>R. hipposideros</i> 1	NA	NA	NA	NA	NA	NA	NA	95 ± 2.5	NA
<i>R. hipposideros</i> 2	85.4	-12.9	0.11	NS	2.62×10^{-3}	6.29×10^{-6}	105.4	100 ± 4.3	-5.4

Slope is the decibel decrease with doubled distance from the microphone.

E , energy flux density; NA, data not available; NS, not significant.

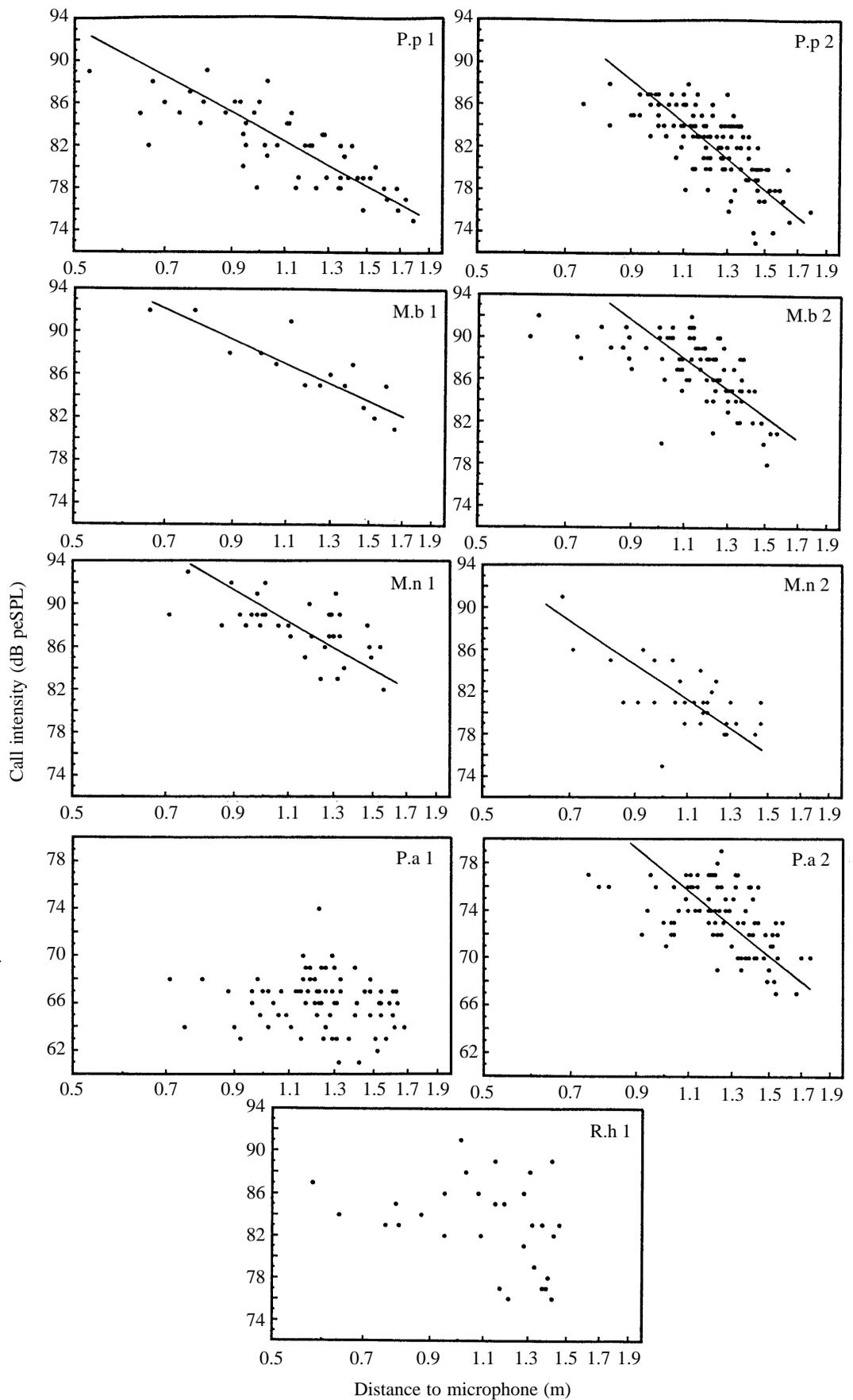


Fig. 4. Sound pressure level of echolocation calls with distance from the microphone for bats in free flight. Levels are converted into dB peSPL using a reference level of $2 \times 10^{-5} \text{ N m}^{-2}$. Note that for *Plecotus auritus* 1 and *P. auritus* 2 the y-axis scale is different. P.p 1, *Pipistrellus pipistrellus* 1; P.p 2, *P. pipistrellus* 2; M.b 1, *Myotis brandtii* 1; M.b 2, *M. brandtii* 2; M.n 1, *M. nattereri* 1; M.n 2, *M. nattereri* 2; P.a 1, *P. auritus* 1; P.a 2, *P. auritus* 2; R.h 1, *Rhinolophus hipposideros* 2. Regression equations and levels of significance are given in Table 1.

Echolocation call intensity in the hand

The dB peSPL values of the echolocation calls of stationary bats measured at 10 cm from the microphone (Table 1) are lower than those calculated for 10 cm from the free-flying bats. Averaged across species, this difference is 13 ± 5.5 dB, and the differences are statistically significant within species ($P < 0.05$, Student's *t*-test), with the exception of *P. pipistrellus*. The magnitude of these differences is generally small compared with across-species differences, however. The intraspecific differences in echolocation call intensity recorded in the hand are not consistent with those shown by the same individuals in free flight.

Energy flux density

Crest factors for the three calls from each bat are plotted in Fig. 5. Since the experimental design is unbalanced (only one *R. hipposideros* was recorded in flight), the data cannot be analysed to test for inter- and intraspecific differences. The data suggest that the constant-frequency (CF) calls of *R. hipposideros* appear have a lower crest factor than the frequency-modulated (FM) calls of the other bats. A higher crest factor indicates a shorter percentage of time at peak amplitude, which is consistent with the shapes of the waveforms (Fig. 6). The mean crest factor for the subsample of calls from each bat was subtracted from the peak call intensity in dB at 1 m obtained from the free-flight regression data presented above (Table 1). The energy flux densities were calculated using equations 4 and 5 (Table 1). There is some variation both between and within species, but two distinctions are clear. The energy flux density of the calls of *P. auritus* are much lower than those of the other FM bats and values for the calls of *R. hipposideros* are much higher. Since energy flux density is directly related to call duration and amplitude, and inversely related to the crest factor, the higher value in *R. hipposideros* is assumed to be the result of the longer call duration and lower crest factor. The lower values in *P. auritus* are the result of low amplitude, short duration and high crest factor.

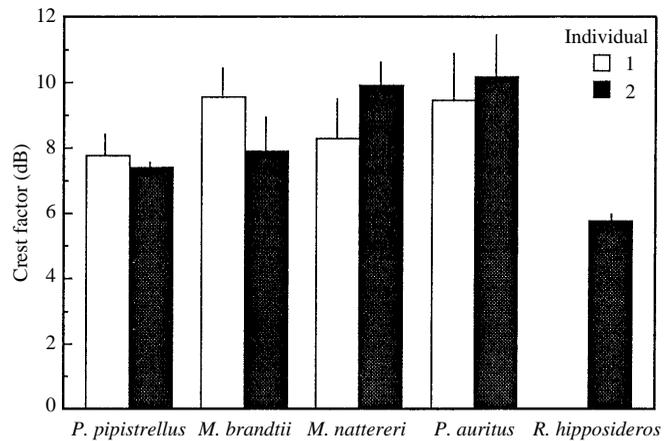


Fig. 5. Decibel-equivalent crest factors of calls taken from free flight calls ($N=3$ calls per individual bat). Values are mean \pm S.D.

General call characteristics

The call characteristics of the free-flying bats are presented in Table 2, and sonograms and power spectra of representative calls are illustrated in Fig. 7. The calls of *P. pipistrellus*, *M. brandtii*, *M. nattereri* and *P. auritus* are typical FM calls starting at a high frequency and sweeping down to a low frequency. Second harmonics are well developed in *P. pipistrellus*, *M. brandtii* and *P. auritus*. The call of *R. hipposideros* is a typical CF call, with a suppressed fundamental, long CF portion and short-duration low-bandwidth FM sweeps at either end. The call of *R. hipposideros* differs from those of the other species in that it calls with a high duty cycle of 52.3% (64% in the wild; Jones and Rayner, 1989b). The other bats studied echolocate with duty cycles of less than 7% (Table 2).

Data for calls from stationary bats are presented in Table 3. Calls from the bats when stationary differ in both timing and frequency from those emitted during flight, and there appears to be more variation within species. In general, calls emitted whilst bats are stationary were shorter in duration than those

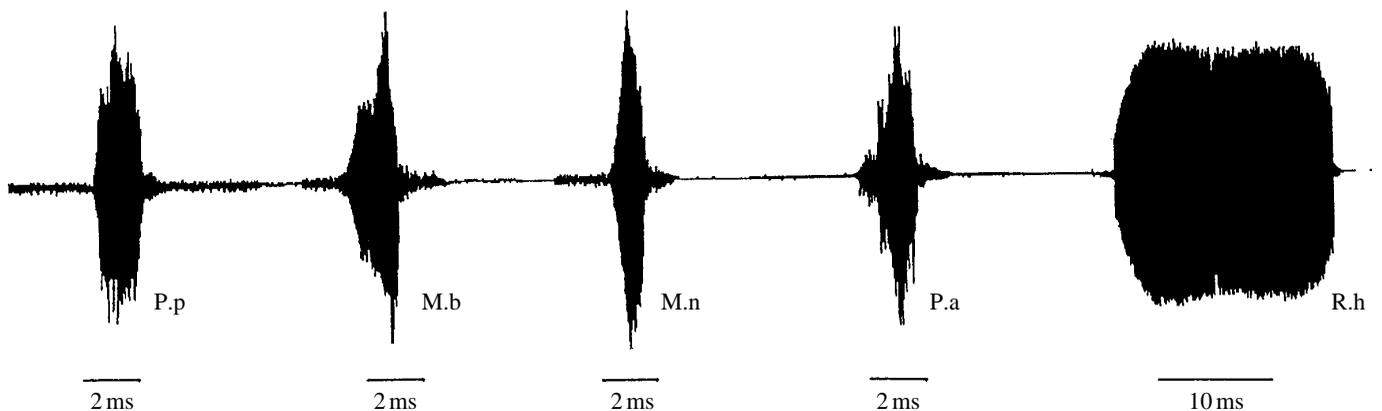


Fig. 6. Waveforms of representative calls for the five species of bats in flight (P.p, *Pipistrellus pipistrellus*; M.b, *Myotis brandtii*; M.n, *M. nattereri*; P.a, *Plecopus auritus*; R.h, *Rhinolophus hipposideros*).

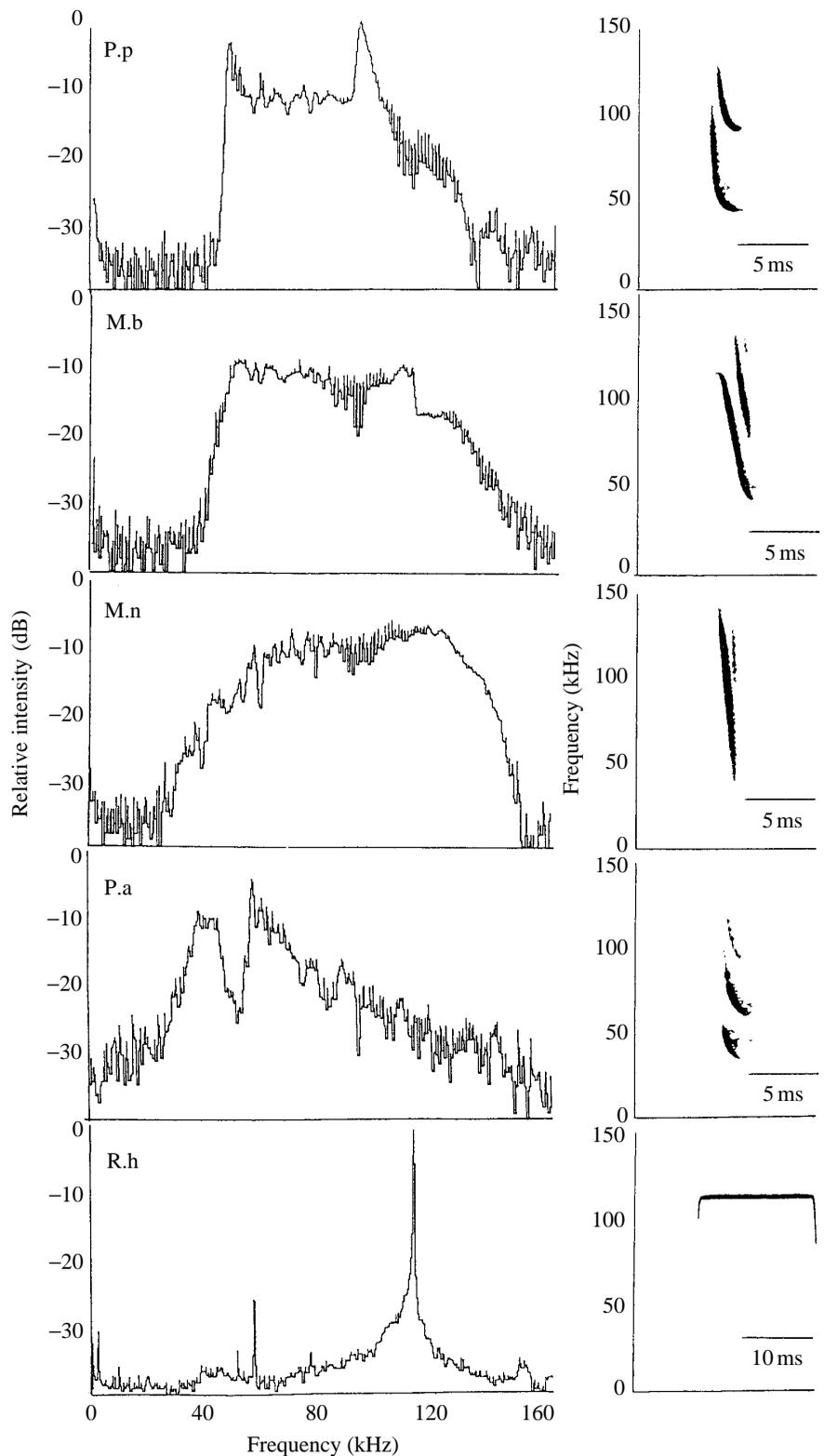


Fig. 7. Power spectra and sonagrams of representative calls for the five species of bats in free flight (P.p, *Pipitrellus pipistrellus*; M.b, *Myotis brandtii*; M.n, *M. nattereri*; P.a, *Plecotus auritus*; R.h, *Rhinolophus hipposideros*).

emitted during flight. There were no consistent cross-species effects in alteration of frequency structure between free-flying and stationary bats with the exception that the call of *M. nattereri* lost all traces of the second harmonic whilst stationary.

Time variables

The durations of the free-flight laboratory-recorded calls we obtained from *M. brandtii*, *M. nattereri* and *P. auritus* do not appear to differ from search phase calls obtained in the field (Ahlén, 1981). The calls of *P. pipistrellus*, however, appear to

Table 2. Call characteristics of bats in free flight

Bat	Number of calls	Duration (ms)	Peak F (kHz)	Peak F_0 (kHz)	Maximum F_0 (kHz)	Minimum F_0 (kHz)	Peak F_1 (kHz)	Maximum F_1 (kHz)	Minimum F_1 (kHz)	Duty cycle (%)
<i>P. pipistrellus</i> 1	55	2.7±0.44	77±21	52±2	115±17	43±1	96±2	149±7	88±2	4.0
<i>P. pipistrellus</i> 2	123	2.9±0.46	66±20	56±5	118±4	43±2	103±4	153±7	88±3	4.3
<i>M. brandtii</i> 1	15	3.8±0.51	58±3	68±18	166±3	31±2	96±8	153±8	64±3	6.6
<i>M. brandtii</i> 2	92	2.9±0.36	58±9	58±9	120±4	29±2	95±3	157±8	66±2	4.5
<i>M. nattereri</i> 1	36	3.6±0.55	84±17	75±13	150±5	21±2	106±10	156±8	58±8	4.1
<i>M. nattereri</i> 2	31	3.7±0.63	55±10	63±16	155±3	20±2	104±13	151±13	43±10	6.7
<i>P. auritus</i> 1	79	2.0±0.36	54±10	50±38	57±3	29±3	63±2	91±7	51±2	4.0
<i>P. auritus</i> 2	92	2.0±0.30	59±7	43±1	61±4	25±3	64±2	92±6	49±2	2.9
<i>R. hipposideros</i> 2	32	19±4	109±0.4	NA	NA	NA	109±0.4	117±3	80±2	52.3

F , frequency; F_0 , fundamental frequency; F_1 , second harmonic.
 NA, data not available.
 Data are means ± standard deviations.

be shorter in duration than even the FM calls of this species at 4–6 ms when recorded in the wild. The mean durations of calls in *R. hipposideros* (approximately 19 ms) are also shorter than those recorded in the wild (50 ms; Jones and Rayner, 1989b). At 2.0 ms, the calls of *P. auritus* were the shortest that we recorded. In the laboratory, the free-flying bats emitted pulses at rates comparable to those measured during the search phase in the field (Ahlén, 1981; Jones and Rayner, 1989b), though the variance appears to be higher in the laboratory measurements.

Frequency variables

The peak and maximum recorded frequencies in the FM bats from the free-flight experiments are consistently higher than those previously reported for these species (Ahlén, 1981).

Significant frequency components of the fundamental component in *M. nattereri* and the second harmonic in *P. pipistrellus*, *M. brandtii* and *P. auritus* were still being recorded up to 150 kHz, where the sensitivity of the microphone had dropped by 5 dB. This frequency also corresponded to the linear limit of the instrumentation recorder. The minimum recorded frequencies were highly consistent with those reported previously (Ahlén, 1981), with the exception of the call of *M. nattereri* which appears to reach lower frequencies than reported in the literature.

Discussion

Call intensity

Griffin (1958) and Novick (1958) were the first to describe

Table 3. Call characteristics of stationary bats

Bat	Number of calls	Duration (ms)	Peak F (kHz)	Peak F_0 (kHz)	Maximum F_0 (kHz)	Minimum F_0 (kHz)	Peak F_1 (kHz)	Maximum F_1 (kHz)	Minimum F_1 (kHz)
<i>P. pipistrellus</i> 1	10	1.7±0.19	91±10	78±8	115±6	48±4	118±7	158±4	100±7
<i>P. pipistrellus</i> 2	10	2.7±0.34	61±20	52±6	95±9	28±3	88±13	147±12	61±6
<i>M. brandtii</i> 1	10	3.3±0.43	81±17	57±11	120±3	30±1	101±5	155±8	66±3
<i>M. brandtii</i> 2	10	2.3±0.27	87±4	56±9	106±6	29±1	92±6	147±4	64±2
<i>M. nattereri</i> 1	10	1.5±0.16	120±2	120±2	157±2	24±3	NA	NA	NA
<i>M. nattereri</i> 2	10	2.1±0.24	82±29	82±29	147±8	19±2	NA	NA	NA
<i>P. auritus</i> 1	10	1.5±0.16	61±9	42±1	50±1	28±3	64±1.2	94±4	51±2
<i>P. auritus</i> 2	10	1.6±0.23	42±7	40±1	56±2	23±1	63±2.6	95±6	50±1
<i>R. hipposideros</i> 1	10	43±6	116±0.2	NA	NA	NA	116±0.2	131±6	88±1
<i>R. hipposideros</i> 2	10	20±5	110±0.3	NA	NA	NA	110±0.4	122±4	83±3

F , frequency; F_0 , fundamental frequency; F_1 , second harmonic.
 NA, data not available.
 Data are means ± standard deviations.

Table 4. Data on echolocation call intensity in a variety of bat species taken from the recent literature

Species	dB at 10 cm	Units	Flight (F) or stationary (S)		Notes	Source
<i>Myotis evotis</i>	77	dB peSPL	F		Gleaning sequence	Faure <i>et al.</i> (1990)
<i>Myotis grisecens</i>	100–110	dB SPL	S		Electrically induced	Shimozawa <i>et al.</i> (1974)
<i>Myotis lucifugus</i>	100–110	dB SPL	S		Electrically induced	Shimozawa <i>et al.</i> (1974)
<i>Myotis lucifugus</i>	95	dB peSPL	F		In a cage	Faure <i>et al.</i> (1993)
<i>Myotis nigricans</i>	82.5	dB SPL	F		Flying in a large cage	Fullard (1987b)
<i>Myotis septentrionalis</i>	78	dB peSPL	F		In a cage	Faure <i>et al.</i> (1993)
<i>Myotis septentrionalis</i>	102	dB peSPL	F		In the field	Miller and Treat (1993)
<i>Myotis siligorensis</i>	100	dB peSPL	F		In the field	Surlykke <i>et al.</i> (1993)
<i>Myotis siligorensis</i>	90	dB peSPL	F		In a cage	Surlykke <i>et al.</i> (1993)
<i>Pipistrellus pipistrellus</i>	100–106	dB peSPL	S		Ranging (start calls)	Surlykke and Miller (1985)
<i>Pipistrellus pipistrellus</i>	82–86	dB peSPL	S		Ranging (approach)	Surlykke and Miller (1985)
<i>Eptesicus fuscus</i>	100	dB peSPL	S			Kick (1982)
<i>Eptesicus serotinus</i>	84–104	dB peSPL	S		Intensity range	Troest and Møhl (1986)
<i>Eptesicus serotinus</i>	104	dB peSPL	S			Miller (1991)
<i>Rhinolophus ferrumequinum</i>	100–123	dB	F			Schnitzler (1968)
<i>Rhinolophus ferrumequinum</i>	97–109	dB	S			Schnitzler and Grinnell (1977)
<i>Rhinolophus ferrumequinum</i>	121	dB	F			Konstantinov <i>et al.</i> (1973)
<i>Craseonycteris thonglongai</i>	110–115	dB peSPL	F		In the wild	Surlykke <i>et al.</i> (1993)
<i>Craseonycteris thonglongai</i>	90–95	dB peSPL	F		In a cage	Surlykke <i>et al.</i> (1993)
<i>Pteronotus parnelli</i>	106	dB SPL	F		In a large cage	Fullard (1987b)
<i>Tonatia silvicola</i>	96	dB SPL	F		In a large cage	Fullard (1987b)
<i>Megaderma lyra</i>	80–85	dB SPL	F		Taking off	Möhres and Neuweiler (1966)
<i>Desmodus rotundus</i>	110	dB SPL	F		In a flight tunnel	von Joermann and Schmidt (1981)

Where methods are described adequately, units are converted into dB peSPL. Where it is not possible to establish units, they are given as described in the source material.

the intensity of the echolocation calls of bats. Griffin (1958) coined the phrase 'whispering bats' to describe the low-amplitude calls of carnivorous or frugivorous bats. Surlykke (1988) divided bats into three call intensity classes depending on the dB SPL measured at 10 cm; 'low intensity' <75 dB SPL, 'intermediate intensity' 75–90 dB SPL, and 'high intensity' >90 dB SPL. Qualitative descriptions of call intensity are widely published, and Novick (1977) presents a list of such accounts. In general, bats using high call intensities can be found in the genera *Rhinolophus*, *Hipposideros*, *Taphozous*, *Saccopteryx*, *Rhynchonycteris*, *Pteronotus*, *Noctilio* and *Natalus* and in most vespertilionids and molossidids. Bats using low-intensity calls include species in the families Phyllostomidae, Nycteridae and Megadermatidae. Among the vespertilionids, some *Myotis* and most *Plecotus* produce calls in the intermediate intensity range.

The accuracy of early measurements by Griffin (1958) and Novick (1958) was limited by the technology available at the time, and most of their absolute values have been discounted (Pye, 1980). Novick (1977) has withdrawn his earlier maximum measurements of over 125 dB peSPL at 10 cm (Novick, 1958). More recent measurements have used a variety of techniques, including solid dielectric as well as air dielectric microphones, but the values suffer from improperly defined units (Møhl, 1988), making direct comparison difficult when methods are not fully detailed. Most studies also only estimate

distances of the bat from the microphone as opposed to using multiframe stereophotogrammetry (this study) or acoustic tomography (Surlykke *et al.* 1993; Miller and Treat, 1993) to establish distance accurately. A synopsis of recent call intensity measurements from the literature is presented in Table 4.

From our data, the five species investigated could be classified as high-intensity bats (*sensu* Surlykke, 1988), with the possible exception of *P. auritus*. Many qualitative studies have classified the genus *Plecotus* as producing low-intensity echolocation calls, e.g. Ahlén (1981) and Anderson and Racey (1991) for *Plecotus auritus* and Griffin (1958) for *Plecotus auritus* and *P. rafinesquii*. For these two species, Griffin (1958) claimed call intensities of 79–85 dB peSPL at 10 cm. However, Simmons and O'Farrell (1977) claim 'moderate' call intensities in *Idionycteris (=Plecotus) phyllotis* of 2–5 N m⁻² at distances of less than 1 m in the laboratory for an FM call type, and 10 N m⁻² at distances of over 7 m in open spaces for a CF call type. It may be that the latter signal was a social call used in communication, rather than an echolocation signal. Since the units are undefined (peak, peak-to-peak or rms), this could correspond to a number of dB peSPL values. Taking a conservative estimate, this corresponds to minimum values of 91–99 dB peSPL at less than 1 m for the FM call and 105 dB peSPL flying in the open at more than 7 m for the CF call. Even allowing for error arising from the use of solid dielectric

microphones, these values cannot be classified as low intensity, and the latter measurement (105 dB) must be considered an error.

The energy flux data presented for the high-intensity FM bats are consistent with the only other measurements of this variable of $2.4 \times 10^{-7} \text{ J m}^{-2}$ for *Eptesicus serotinus* calculated by Au (1993) from data presented in Troest and Møhl (1986) and between 1×10^{-5} and $1 \times 10^{-8} \text{ J m}^{-2}$ also for *E. serotinus* using automatic gain control echolocating at a target (Hartley, 1992). The measurements correspond to the amount of energy passing through a 1 m^2 surface of a sphere of 1 m radius from the sound source. The calculations assume that the sound field is isotropic, i.e. that the bat is acting as a point source. Since this is not the case when the wavelength of the emitted sound is similar to or less than the diameter of the source, this measure cannot be used directly as a measure of the total radiated energy of the sound field. A directivity index can be used to compensate for an anisotropic sound field (Au, 1993), but in practice this proves mathematically too complicated for complex emission shapes such as a bat's mouth or nostrils and/or frequency-modulated call structures. However, since the -6 dB intensity angle for most species appears to be between 30° and 60° , and the angle subtending a 1 m^2 surface area of a sphere of radius 1 m is 65° , the calculation for 1 m^2 probably provides a reasonably accurate estimate of the acoustic energy contained within one call. Only limited work has been conducted on the energetics of echolocation in the Chiroptera. Speakman *et al.* (1989) state that the cost of producing a single echolocation call in a 6 g *P. pipistrellus* is 0.067 J. Since the mean calculated energy flux density is $2.7 \times 10^{-7} \text{ J m}^{-2}$ for this species, it suggests a conversion efficiency of less than 0.0005%. Even allowing for a greater directional spread, and hence a greater acoustic energy contained within a call, the conversion efficiency is still orders of magnitude below efficiencies stated for invertebrates, anurans and birds (Prestwich *et al.* 1989; Forrest, 1991; Bailey *et al.* 1993). Comparison with data for invertebrates and other vertebrates shows that the acoustic power output is comparable with the data calculated for echolocating bats. The interspecific range of average power outputs is 0.0013 mW for *P. auritus* to 0.331 mW for *R. hipposideros*, assuming one call per second. This is within the ranges stated for Orthoptera (Forrest, 1991; Bailey *et al.* 1993), hylid frogs (Prestwich *et al.* 1989) and passerine birds (Brackenbury, 1979). The reduced conversion efficiency appears to be due to the energetic costs of call production being higher in echolocating bats.

The failure of the results from two individuals to show a significant correlation between call intensity and distance from the microphone could reflect echo-levelling (Kobler *et al.* 1985; Neuweiler, 1990; Hartley, 1992) or calls being off-axis. The latter possibility is most likely, given the difficulty of ensuring that the bat flew a straight course without constraining it within a cage. The high-frequency calls of *R. hipposideros* at 113 kHz are likely to be much more directional and would give a greatly reduced sound pressure level if off-axis. Individuals of *P. auritus* were especially manoeuvrable by

virtue of their low wing loading and, because of this, they seldom flew directly towards the microphone. This may be the reason why the results for individual 1 failed to show a significant relationship, but cannot explain why the results for individual 2 did or why the data from these two individuals are so different.

The slope of call intensity against distance shown by the data is higher than the predicted -6.02 dB with doubled distance from the microphone, as predicted from the effects of excess atmospheric attenuation (Griffin, 1971; Lawrence and Simmons, 1982). Over the 2 m width of the stereo window, the sound intensity of a 100 kHz pulse would be reduced by 26 dB as a result of spherical spreading alone and by a further 6.3 dB as a result of excess atmospheric attenuation (Bazley, 1976). Since excess atmospheric attenuation is frequency-dependent, the overall reduction in the intensity of an FM call is difficult to predict with any accuracy. Excess attenuation would also be expected to alter the peak frequency and the highest frequency recorded, producing an altered sound spectrum with distance to the microphone. A reduction in apparent call duration in FM bats would also be expected, since the upper frequency in the FM sweep would be attenuated the most, reducing the call duration measured. Since we could establish no such clear relationships, it seems likely that an additional factor has caused the slopes to deviate from the predicted -6 dB per doubled distance. If the bats were using automatic gain control to echolocate at the microphone, the pressure level of incident sound would be held constant and the slope would be predicted to be zero (Hartley, 1992). Since the slope of the line is significantly different from zero in seven out of nine individuals, this is clearly not the case. It seems likely that the increased slopes are due to errors in assessing whether the bat was facing the microphone and the possible effects of an initially lower-intensity echolocation call caused by the bat taking off and then flying into the stereo-view window of the cameras.

Frequency data

The high values of the peak and maximum frequencies recorded from the FM bats are above the maximum frequencies reported previously for these species and those for most other FM bats (Ahlén, 1981; Obrist *et al.* 1993). While flying in enclosed conditions can affect call structure, the correlation of call durations and lower frequencies with bats flying in the field implies that the call structure in this case is little altered from that of normal search-phase calls. Field recordings usually under-represent the high frequencies present in calls because of the greater distance of the bat from the microphone and its position relative to the microphone. Furthermore, solid dielectric microphones are non-linear in their frequency response. High-frequency components will enhance the ability of the bat to detect smaller targets, but it is unclear whether these frequencies can actually be used by the bat. Most audiograms of FM bats show a marked decrease in auditory sensitivity above 60 kHz (Brown *et al.* 1978; Neuweiler, 1983; Neuweiler *et al.* 1984; Guppy and Coles, 1988; Coles *et al.*

1989), although some FM bats do show high pinna gain at frequencies above 100 kHz (Obrist *et al.* 1993). It remains to be seen whether these high-frequency components are important for target discrimination or are simply a physiological consequence of the mechanism of sound production.

Implications for foraging

P. auritus is a gleaner, taking prey from surfaces, and this is reflected by its wing morphology and flight characteristics (Norberg, 1976), its diet (Swift and Racey, 1983; Rydell, 1989) and its foraging behaviour (Anderson and Racey, 1991). Gleaning species typically use calls of short duration, high frequency and low intensity (Norberg and Rayner, 1987; Neuweiler, 1990) in accordance with the intensity, duration and frequency data for *Plecotus auritus* presented here. *M. nattereri* is also considered to be a gleaner species from its wing morphology (Norberg and Rayner, 1987) and from dietary analysis (Poulton, 1929; Shiel *et al.* 1990). However, this species does not exhibit the short call durations or low call intensities predicted for a gleaner. Faure *et al.* (1993) report that the gleaner species *Myotis septentrionalis* uses calls of 1 ms duration and 97 kHz peak frequency at an intensity of 78 dB peSPL at 10 cm during gleaning attacks. Faure *et al.* (1990) also report that another gleaner species, *Myotis evotis*, using calls of 0.7 ms and 77 dB peSPL at 10 cm during gleaning attacks. Many species are known to exhibit a degree of call plasticity; the call duration of *M. evotis* was significantly longer during search-phase calls than during gleaning sequences. It is well known that, during the transition from the search phase to the approach and terminal phase, the call duration is reduced, the repetition rate is increased and the amplitude is reduced (Griffin *et al.* 1960; Schnitzler *et al.* 1988; Kalko and Schnitzler, 1989). Data are available for the first two variables, but the reduction in amplitude remains unquantified. von Joermann and Schmidt (1981) reported that *Desmodus rotundus* reduced its call intensity by 25 dB during the transition from free-flight search-phase calls to the terminal buzz associated with reaching a landing site. Kobler *et al.* (1985) and Neuweiler (1990) propose that the intensity of the echo from a target is levelled to provide an amplitude optimally suited for auditory analysis. This is achieved by the bat reducing the amplitude of its call as the target is approached. Such an effect would be predicted to be especially marked in gleaner bats, since the echo intensity from the surfaces of vegetation would be especially intense. It is not inconceivable that gleaner bats may use relatively high-intensity calls during orientation or aerial hawking and adopt much lower-intensity calls during gleaning. This is supported by Miller and Treat (1993), who found that *Myotis septentrionalis* reduced its call intensity on approaching a prey item during a gleaning attack.

Dietary studies show that *P. auritus* feeds primarily on moths (Thompson, 1982; Swift and Racey, 1983; Rydell, 1989; Barataud, 1990). Members of the moth families Noctuidae, Notodontidae, Geometridae and Pyralidae are sensitive to

ultrasound and exhibit escape manoeuvres in response to echolocating bats (Roeder, 1967). Fullard (1987a) calculates that a reduction in echolocation call intensity from 100 dB SPL to 70 dB SPL at 10 cm from the bat's mouth would result in a 90% reduction in detection distance of the bat by the moth. Call duration has also been shown to reduce the potential acoustic apparency of the echolocation call (Faure *et al.* 1993; Waters, 1994). Since *P. auritus* uses calls which are quieter than those of other bats and shorter in duration, this may allow it to approach tympanate moths more closely before being detected. It has also been suggested that *P. auritus* occasionally catches insects by aerial hawking without using echolocation (Anderson and Racey, 1991).

Although strenuous efforts were made to mimic the relatively anechoic conditions encountered in the wild, the bats may have responded to flying in an enclosed space by reducing their call intensity. Studies such as those by Surlykke *et al.* (1993) have shown that flying in a confined space can reduce the bat's emitted call intensity and thus one must concede that calls emitted in the wild may be more intense than those recorded in the experiments presented here. Data showing that stationary bats echolocate more at lower intensities than do flying ones support the suggestion that flight and echolocation are energetically coupled, and this has been suggested as a reason why echolocation systems have not arisen in many terrestrial animals (Speakman and Racey, 1991). This does not explain why some bats hunt from perches, since this would not reflect a significant energy saving as they continue to echolocate, although duty cycle and intensity are lower in perch-hunting bats (Schnitzler *et al.* 1985; Neuweiler *et al.* 1987; Jones and Rayner, 1989b). The CF bat *Rhinolophus ferrumequinum* has been shown to hunt from perches (Jones and Rayner, 1989b) and has a diet which contains a very high proportion of tympanate moths (Jones, 1990). It may be that perch-hunting, with a consequential loss of call intensity, reduces the range at which passing tympanate moths can detect the bat. The bat could then employ this reduced call intensity to gain a predation advantage. A bat using reduced call intensities in flight would need to fly more slowly and to be more manoeuvrable because the reduced ranging ability would increase the risk of collision.

In conclusion, the orientation call intensities reported here are consistent with those reported previously from the literature, and new data are presented on call intensity in free flight. The call intensities reported from the stationary bats are lower than those from the same bats in free flight; this may be due to the coupling of echolocation and the action of the flight muscles in reducing the cost of echolocation in flight. The gleaner species *P. auritus* uses orientation calls that are significantly less intense than those of the other species, which may allow it to approach tympanate moths more closely. A second gleaner species, *M. nattereri*, does not use the short-duration low-intensity calls predicted. This species may be able to alter its call structure and intensity dynamically depending on the foraging situation and it is predicted to use shorter, less-intense calls during gleaning.

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