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Moth hearing in response to bat echolocation calls manipulated independently in time and frequency

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We measured the auditory responses of the noctuid moth *Noctua pronuba* to bat echolocation calls which were manipulated independently in time and frequency. Such manipulations are important in understanding how insect hearing influences the evolution of echolocation call characteristics. We manipulated the calls of three bat species (*Rhinolophus hipposideros*, *Myotis nattereri* and *Pipistrellus pipistrellus*) that use different echolocation call features by doubling their duration or reducing their frequency, and measured the auditory thresholds from the Al cells of the moths. Knowing the auditory responses of the moth we tested three predictions. (i) The ranking of the audibility of unmanipulated calls to the moths should be predictable from their temporal and/or frequency structure. This was supported. (ii) Doubling the duration of the calls should increase their audibility by *ca.* 3 dB for all species. Their audibility did indeed increase by 2.1–3.5 dB. (iii) Reducing the frequency of the calls would increase their audibility for all species. Reducing the frequency had small effects for the two bat species which used short duration (2.7–3.6 ms) calls. However, the relatively long-duration (50 ms), largely constant-frequency calls of *R. hipposideros* increased in audibility by 21.6 dB when their frequency was halved. Time and frequency changes influence the audibility of calls to tympanate moths in different ways according to call design. Large changes in frequency and time had relatively small changes on the audibility of calls for short, largely broadband calls. Channelling energy into the second harmonic of the call substantially decreased the audibility of calls for bats which use long-duration, constant-frequency components in echolocation calls. We discuss our findings in the contexts of the evolution of both bat echolocation call design and the potential responses of insects which hear ultrasound.

Keywords: hearing; sonar; bat; moth

1. INTRODUCTION

Many insects have evolved defences against echolocating bats in order to reduce their chances of being preyed upon. Ears have evolved in at least seven insect orders (Fullard & Yack 1993; Hoy & Robert 1996) and moth hearing is generally most sensitive between 20 and 60 kHz (Fullard 1987), the bandwidth used by most species of echolocating bats (Fenton *et al.* 1998). Bats which eat many moths presumably use a range of echolocation specializations in order to make their calls less audible to eared moths. First, they emit calls of low intensity which are inconspicuous to auditory receptors (Faure *et al.* 1990, 1993) or they may even switch off echolocation during approaches to prey (Faure *et al.* 1990). Second, they often emit short-duration calls because the auditory receptor cells of moths (being energy detectors) are generally more sensitive to longer calls because they generally contain more energy than short ones (Surlykke *et al.* 1988; Waters & Jones 1996; Tougaard 1998). Finally, echolocating bats may capture eared prey by calling at frequencies outside of the range of best hearing of the insects (Jones 1992; Fullard 1998; Bogdanowicz *et al.* 1999). Bat species which emit very low frequencies (< 15 kHz) (Rydell & Arlettaz 1994; Fullard & Dawson 1997) and very high frequencies (> 60 kHz) (Pavey & Burwell 1998) capture large numbers of prey which are probably eared. In all of these cases, it is not clear

whether bats evolved echolocation characteristics which reduce their audibility to insect ears or whether their call characteristics evolved for other reasons (e.g. low frequencies travel over long ranges and high frequencies are more directional) and, consequently, they can capture eared prey (Rydell *et al.* 1995). These adaptations are of course not mutually exclusive. Only if bats evolve echolocation calls for specifically improving their chances of catching tympanate prey can the scenario be described as coevolution (Janzen 1980). Fullard (1998) suggested that the case for bat–moth coevolution is clear, but this can only be verified if the call structures used by bats which eat large numbers of eared moths are not advantageous for other reasons.

Several studies have shown that bat calls which are short in duration and outside the frequency range of best hearing in moths are not audible to moth ears (e.g. Fullard & Thomas 1984; Faure *et al.* 1990, 1993; Waters & Jones 1996; Fullard & Dawson 1997). However, the relative importance of frequency and time effects has not been investigated independently. This is important because in many taxa the frequency and time characteristics of echolocation calls covary—calls which are high in frequency are also of brief duration (Jones 1999)—so the relative importance of frequency and time factors in affecting the audibility of calls to moth ears is not clear. Moreover, moth audiograms are often constructed by using playbacks of constant-frequency (CF) pulses and bat calls almost always include some form of frequency modulation. In order to understand the evolution of signal designs in bats it is therefore of value to manipulate real bat signals and determine the relative effects of these

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manipulations on the audibility of insect prey. Our goal was to test whether echolocating bats may be able to reduce their call audibility to moth ears better by changing the duration or frequency of their calls. We did this by recording bat calls with a frequency-linear microphone and playing back the calls to neural preparations of a typical medium-sized noctuid moth, the large yellow underwing *Noctua pronuba*. Waters & Jones (1996) provided an audiogram of this species. The A1 sensory cell of the moth is maximally sensitive (threshold = 35 dB sound pressure level (SPL)) to 15 kHz, with the sensitivity falling to over 60 dB SPL at 120 kHz (Waters & Jones 1996).

We chose three bat species which use different echolocation features. The calls of the lesser horseshoe bat (*Rhinolophus hipposideros*) averaged 51.3 ± 4.6 ms (*n* = 6) in duration in our study (which is similar to durations recorded in the field) (Jones & Rayner 1989). These calls are dominated by a CF component with short frequency-modulated (FM) tails at the beginning and end. The CF component is the second harmonic of the calls and averaged 110.5 ± 1.1 kHz (*n* = 6) in this study. Brief FM sweeps (< 10 kHz bandwidth) occur at the beginning and end of the CF component. *R. hipposideros* calls at a high duty cycle (64%) (Jones & Rayner 1989). Because *N. pronuba* is relatively insensitive to the high frequencies emitted by *R. hipposideros*, its calls should be inaudible and, indeed, *R. hipposideros* often eats large numbers of moths (26% of their diet on average) (Vaughan 1997). The Natterer's bat (*Myotis nattereri*) emits brief calls (average 3.1 ± 1.3 ms (*n* = 6) in this study) which are broadband in structure with the first harmonics sweeping between 136 and 28 kHz. The peak frequency of the calls was at 70.3 ± 15.2 kHz (*n* = 6). The short duration and high peak frequency of the calls should render then relatively inconspicuous to moths. Because the calls of *M. nattereri* sweep into frequencies which moths are sensitive to but are of short duration and spread energy broadly over their bandwidth, we predicted that they would be of intermediate audibility. *M. nattereri* eats moderate numbers of moths (19% of their diet) (Vaughan 1997). The pipistrelle studied was the 45 kHz cryptic species (Jones & Parijs 1993), the scientific name of which is proposed as *Pipistrellus pipistrellus* (Jones & Barratt 1999). *P. pipistrellus* uses calls of 3.6 ± 0.6 ms (*n* = 6) duration which start with an FM sweep of up to 113 kHz and end in a narrowband sweep and which averaged 44.0 ± 1.3 kHz (*n* = 6) in this study. The peak frequency was 50.8 ± 3.5 kHz (*n* = 6). Because *N. pronuba* is relatively sensitive at 45–50 kHz, we predicted that these calls would be most conspicuous to the moths. Indeed, *P. pipistrellus* rarely eats moths in the wild (< 5% of their diet) (Barlow 1997). Both *M. nattereri* and *P. pipistrellus* echolocate at low duty cycles (typically 3–5%) (Vaughan *et al.* 1997). Sonagrams of the typical calls used in our experiments are summarized in figure 1. For power spectra of unmanipulated calls of the study species see Waters & Jones (1995). The calls resemble those of free-flying bats of these species recorded in the field (see Vaughan *et al.* 1997) except that *P. pipistrellus* typically emits longer duration calls when foraging away from clutter in the wild.

Our first prediction was that the ranking of the bat species according to audibility should be *Pipistrellus* >
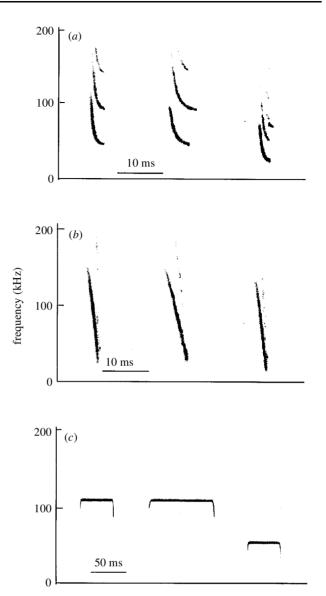

Figure 1. Sonagrams of the unmanipulated and manipulated calls of (*a*) *P. pipistrellus*, (*b*) *M. nattereri* and (*c*) *R. hipposideros*. The left-hand call is unmanipulated for each species. The middle call is manipulated in the time domain and the right-hand call in frequency. See § 2 for details. Note the different time axis for *R. hipposideros* calls.

Myotis > *Rhinolophus*, reflecting the temporal and/or frequency structure of their calls and the relative importance of moths in the diets of these species. Second, we predicted that doubling the duration of the signals would increase their audibility by 3 dB over the range of durations studied here assuming that the moth's peripheral system can be viewed as a leaky-integrator model (Tougaard 1998). The moths studied so far typically have integrating time constants of between 10 and 69 ms (as measured from time–intensity trade functions) (Surlykke *et al.* 1988; Waters & Jones 1996; Tougaard 1998). At durations below these, doubling the duration of the stimulus means that the amplitude of the stimulus can be reduced by 3 dB and still produce a threshold response from the moths' sensory cells. Finally, we predicted that reducing the frequency of calls would increase their audibility for all species because the moth is more sensitive to the reduced frequency for all species. The audibility of calls was predicted to increase by *ca.* 4 dB for *Myotis*, 6 dB for

Pipistrellus and 17 dB for *Rhinolophus* (approximations made from responses to pure tones used in constructing audiograms which correspond to peak frequencies of calls) (see Waters & Jones 1996). We expected the effect to be most pronounced for *Rhinolophus* since its relatively long duration calls may be made particularly audible when halved in frequency.

2. METHODS

The calls used in the playbacks (details in §1) were analysed on a Kay 5500 DSP Sonagraph (Kay Elemetrics Corporation, Pine Brook, NJ, USA) with a 512 point fast-Fourier transform with Hamming window, producing 400 Hz frequency resolution on the call in real time. The playback experiments were performed on the noctuid moth *N. pronuba* obtained from the wild using a mercury vapour light trap. All experiments were performed in a 4 m × 4 m × 2.6 m room lined with sound-attenuating foam. Determinations of the threshold sound intensity were made from recordings from the moth's tympanic nerve. The moth was fastened dorsal side up, decapitated and dealeated and the thorax dissected following the methods of Waters & Jones (1996). Once located, the tympanic nerve was hooked over the end of a bipolar silver hook electrode, the output amplified (CFP 8120 Preamplifier; Searle BioScience, Sheerness, UK) and passed to an audio amplifier and Tektronix 5113 dual-beam storage oscilloscope (Tektronix, Inc., Beaverton, OR, USA).

Echolocation calls of two individuals each of *P. pipistrellus*, *M. nattereri* and *R. hipposideros* were used as the playback stimuli. The echolocation calls were recorded from free-flying bats in the room using a Brüel and Kjær 4135 0.25 in (1 in = 0.025 m) microphone (Brüel and Kjær, Nærum, Denmark) (grid off) attached to a 2204 sound pressure meter, high-pass filtered above 15 kHz and recorded onto a Racal Store 4DS recorder (Racal Recorders Ltd, Hythe, UK) at 76 cm s^{-1} (total system response ± 3 dB at 15–120 kHz). Calls showing a high bandwidth and good signal-to-noise ratio (analysed on a Kay DSP 5500 Sonagraph) were sampled from the tape using an Ultra Sound Advice S-350 memory bat recorder sampling at a rate of 400 kHz and stored at × 10 time expansion on DAT tape (Sony TCD-D3 Sony Corporation, Tokyo, Japan). For broadcast, the calls were reloaded into the S-350 device sampling at 40 kHz and recompressed back to real time. The output was high-pass filtered at 18 kHz prior to amplification and broadcast through an Ultra Sound Advice ultrasound amplifier and electrostatic loudspeaker (frequency response ± 3 dB at 20–120 kHz). The sound level necessary for eliciting one to two stimulus-locked action potentials from the A1 cell was used as the threshold criterion except for the longer duration calls when the spontaneous activity of the A1 cell made this difficult. In this case, the first perceptible rise in activity of the A1 cell was used as the threshold criterion. The rise in the number of action potentials was very rapid within 1 or 2 dB of the threshold for long-duration stimuli (Waters 1996) and this should result in little error in the assessment of the threshold level due to the problem of probability integration (Tougaard 1998). The sound levels were recorded as loudspeaker voltages and converted to absolute decibels peak-equivalent (pe) SPL (after Stapells *et al.* 1982) after calibration.

The bat calls were presented as three treatments: (i) unmanipulated, (ii) maintaining the same frequency structure but doubling the call duration, and (iii) maintaining the same temporal structure but shifting the call down in frequency.

Rhinolophus calls were reduced in frequency by 55 kHz, effectively halving the frequency and mimicking a situation whereby the bat would be calling with most energy in the first rather than second harmonic. *Pipistrellus* calls were reduced in frequency by 20 kHz, again effectively almost halving the peak frequency. *Myotis* calls were more difficult to shift in frequency because some swept to relatively low frequencies and large frequency changes would have resulted in manipulated calls having frequencies below zero, thus truncating calls in the temporal and/or frequency structure. We therefore reduced the frequency of the *Myotis* calls by 15 kHz. The signals were manipulated digitally in SIGNAL/RTS (Engineering Design, Belmont MA, USA). Tonal sounds were represented as the time-varying frequency (spectral contour) and by an amplitude envelope (time-varying intensity). The spectral contour was passed through a voltage-frequency sinewave generator in order to produce a constant amplitude signal of time-varying frequency. This was multiplied by the amplitude envelope in order to provide appropriate amplitude characteristics. The process was justified by Hilbert's transformation theory which shows that a signal can be decomposed into amplitude and frequency functions and recovered without information loss. Consequently, duration and frequency can be manipulated independently (Beeman 1998).

Two controls were constructed in order to investigate whether variation in the tape noise could influence the results. One control was a short section of sample tape noise of the duration of a *M. nattereri* call. The other control was tape noise equivalent in duration to a *R. hipposideros* call. The tape noise was manipulated in the same way as the stimulus calls. Each of six moths was presented with 15 stimuli, i.e. the three treatments of the echolocation calls of each of the three species plus the two sets of controls. The stimulus echolocation calls and control sequences were different for each moth, three sets of the echolocation calls coming from each of two individual bats of each species (it was not possible to obtain recordings of six individuals of each species because of licensing restrictions). However, the intra-individual variation in call structure was large compared with the between-individual variation. The order of presentation of the stimuli was randomized both within and between moths.

Because the threshold data were not distributed normally and included a repeated-measures design whereby each moth was presented with the same call either unmanipulated, doubled in duration or halved in frequency, we analysed the data with the approximate test for trends and contrasts (Meddis 1984). There is no test for pairwise comparisons of treatments from this repeated-measures design, so differences between treatments were identified by Wilcoxon's signed-rank test with the probability level for rejection of the null hypothesis adjusted by Bonferroni corrections in order to allow for multiple contrasts.

3. RESULTS

The auditory threshold levels of the moth A1 cells to the tape controls were between 38 and 47 dB peSPL, a level similar to the threshold values recorded for most stimulus calls. Since the signal to noise ratio of the stimulus calls to tape noise was of the order of 40 dB, the tape noise would have to have been over 40 dB greater in magnitude to stimulate the moth ear during call playback. Therefore, we concluded that tape noise and its manipulation did not influence the threshold measurements.
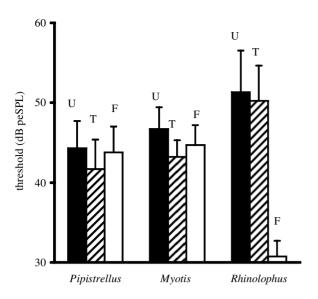
Figure 2. Thresholds necessary to elicit auditory responses in the A1 cell to unmanipulated and manipulated echolocation calls of *P. pipistrellus*, *M. nattereri* and *R. hipposideros*. Means + standard deviations are illustrated for six moths. Responses to control, unmanipulated calls (U) are illustrated by solid bars, responses to calls that which doubled in duration (T) are illustrated by hatched bars and responses to calls which were manipulated in frequency (F) are illustrated by open bars.

The auditory threshold data (figure 2) were analysed in order to investigate the predictions from our three hypotheses. The auditory thresholds of *N. pronuba* differed according to the treatment of the echolocation call for the *P. pipistrellus* ($L = 80$, $Z = 2.3l$, $n = 6$ and $p < 0.05$), *M. nattereri* and *R. hipposideros* playbacks ($L = 83.5$, $Z = 3.32$, $n = 6$ and $p < 0.001$ in both cases).

(i) Prediction 1. The audibility of unmanipulated calls should reflect the extent to which the three species fed on moths in the wild and the frequency and time characteristics of their calls. The ranking of the bat species, according to audibility, should therefore be *Pipistrellus* > *Myotis* > *Rhinolophus*. This hypothesis was supported and there were significant differences in the moth auditory thresholds for unmanipulated calls from the three bat species ($L = 84$, $Z = 3.46$, $n = 6$ and $p < 0.001$). Unmanipulated *Pipistrellus* calls were on average 2.4 dB more audible than *Myotis* calls, which in turn were 5.6 dB more audible than *Rhinolophus* calls.

(ii) Prediction 2. Doubling the calls' duration should increase their audibility by *ca*. 3 dB over the range of the manipulations. This hypothesis was supported. Doubling the duration of the calls increased their audibility by 2.6 dB for *Pipistrellus*, by 3.5 dB for *Myotis* and by 2.1 dB for *Rhinolophus*. The comparisons of the responses to increased duration calls versus the responses to the unmanipulated signals were significant for all species in Wilcoxon's signed-rank tests at $p = 0.03$. The increased duration stimulus elicited a lower threshold sound level for each moth and for each bat species. The *Rhinolophus* calls presumably showed the smallest threshold change relative to the unmanipulated calls because

the unmanipulated calls may have been close to or in excess of the A1 cell's integration time for single pulses.

(iii) Prediction 3. Reducing the frequency of the calls should increase their audibility for all bat species and the effect should be most marked for *Rhinolophus* calls. There was no effect of reducing the frequency by 20 kHz on the audibility of *Pipistrellus* calls (Wilcoxon's test comparison versus the response to unmanipulated calls $p > 0.05$). The audibility of the calls was increased by 2.0 dB in *Myotis* calls reduced by 15 kHz (Wilcoxon's test $p = 0.03$) and by 21.6 dB in *Rhinolophus* calls which were halved in frequency (Wilcoxon's test $p = 0.03$). Thus, large-frequency manipulations had marginal or non-existent effects on call audibility for the two bat species using short-duration calls at frequencies already within the window of high auditory sensitivity of *N. pronuba*. However, halving the frequency had a massive effect on the audibility of the calls of *Rhinolophus* bringing its calls into a frequency range where *N. pronuba* is highly sensitive. Because the calls of *Rhinolophus* are already long in duration, halving them in frequency elicited auditory responses in *N. pronuba* at a much lower threshold than for any other call type studied.

4. DISCUSSION

Our experiment showed that the frequency and time parameters of bat echolocation calls affect their call audibility to moth ears independently. Although the results were to some extent predictable from knowledge of auditory mechanisms, the complex nature of bat calls resulted in some findings which were more difficult to predict from the audiogram of the moths constructed by playbacks of pure tones. For example, *Myotis* calls are 5.6 dB more audible than *Rhinolophus* calls, whereas inspection of the audiogram of *N. pronuba* (Waters & Jones 1996) would predict a 12–13 dB difference based on the peak frequencies of the calls. Some of these difficulties will be the consequences of individual differences in hearing between the samples of moths used in the two studies and to measurement errors. Overall however, the considerable differences between the predictions and observations of audibility between *Myotis* and *Rhinolophus* were probably because the broadband calls of *M. nattereri* contain substantial energy at low frequencies (20–40 kHz) where *N. pronuba* has sensitive hearing. The longer duration calls of *R. hipposideros* would also increase their audibility. Hence, audiograms constructed from constant duration pure tones can generate reasonable predictions about the relative audibility of bat calls, but the more complex nature of bat calls in comparison to pure tones makes precise predictions more difficult.

The large manipulations which were conducted had relatively small effects on the audibility of calls except in the case of *R. hipposideros* where a halving of their frequency increased the audibility of their calls by over 21 dB. By using the second harmonic, *R. hipposideros* is allotonic, calling outside of the window of maximum sensitivity in moth hearing (Novick 1977; Fullard 1987), thus enabling this species to approach eared prey by stealth. This huge increase in audibility may have

relevance for explaining why many rhinolophoid bats channel most of the call's energy into the second rather than first harmonic. Rhinolophoid bats which echolocate at high duty cycles reduce the frequency of calls emitted in flight to compensate for the Doppler shifts induced by their flight speed (Trappe & Schnitzler 1982). Echoes return at frequencies represented in an 'acoustic fovea' (Schuller & Pollak 1979) and, because pulses and echos are separated in the frequency domain, the bats can emit long-duration pulses at high frequencies without experiencing problems with pulse–echo overlap (Jones 1999). Pulse duration decreases with increasing call frequency in bat species which are intolerant of pulse–echo overlap (Waters *et al.* 1995; Jones 1999) because extreme excess atmospheric attenuation at high frequencies means that targets are often only detectable at close range. Therefore, short pulses are produced in order to avoid forward masking of the echo (which returns early from a close target) by the outgoing pulse (Kalko & Schnitzler 1993). Thus, although rhinolophoid bats which show Doppler-shift compensation can produce long pulses in order to improve target detection and classification at high frequencies (Schnitzler & Kalko 1998), these long pulses have a cost in that their duration makes them conspicuous to moth ears.

Many rhinolophoid bats emphasize the second harmonic of their calls (Heller & Von Helversen 1989). Their calls are therefore above the frequencies that most moth ears are sensitive to and rhinolophoid bats which call at higher frequencies tend to eat more moths (Jones 1992; Bogdanowicz *et al.* 1999). One benefit of using the second harmonic is clear from our experiment. If the first harmonic was used by *R. hipposideros*, the call's audibility to moth ears would increase by almost 15 times, even excluding the reduced excess atmospheric attenuation of the call at lower frequency. It is important to remember that our playbacks were of single calls. In nature, the higher duty cycle of rhinolophid compared with vespertilionid calls will result in greater potential acoustic stimulation of moth ears. The high duty cycles of rhinolophid bats may put a great selective pressure on individual calls being inconspicuous to moth ears.

Whether many rhinolophoid bats evolved use of the second harmonic specifically for allowing them to catch more moths is debatable. Higher frequencies also allow greater directionality of sound transmission (e.g. Simmons 1969; Schnitzler & Grinnell 1977), use of a frequency channel isolated from many other bats, an increase in energy reflected from very small targets (Pye 1993) and, perhaps, a reduction in the detection of distant clutter objects in complex habitats. There are therefore alternative (and non-exclusive) explanations not involving coevolution for why these bats may have shifted to using calls dominated by a second harmonic. Nevertheless, this study shows that, by using the second harmonic, the audibility of rhinolophid bat echolocation calls to moth ears becomes substantially reduced.

Our results show that the potential for coevolution by changing the frequency and temporal patterns of echolocation calls is limited in bat species which emit broadband (FM) signals. Large-scale manipulations of time and frequency in calls from these bats cause small changes in audibility. There is much greater potential for coevolution in bat species which emit narrowband or CF calls. Such potential may partly explain why rhinolophoid bats often emit calls with most energy on the second harmonic, which is often allotonic. Even greater potential for coevolution may occur in low-frequency (< 15 kHz) allotonic bat species because the low frequencies emitted by these bats reflect poorly from moths and impose a cost by reducing the detection distances by echolocation. Most moths hear low frequencies poorly, however and the benefits of reduced detection by moths outweigh the costs of reduced detection distances by echolocation (Norman & Jones 2000). It therefore seems likely that some bat species evolved low-frequency calls specifically to exploit the limited sensitivity to low frequency in moth hearing. This perhaps provides the strongest evidence for coevolution in interactions between echolocating bats and hearing moths.

REFERENCES

Barlow, K. E. 1997 The diets of two phonic types of the bat *Pipistrellus pipistrellus* in Britain. *J. Zool. Lond.* **243**, 597–609.

Beeman, K. 1998 Digital signal analysis, editing and synthesis. In *Animal acoustic communication* (ed. S. L. Hopp, M. J. Owren & C. S. Evans), pp. 59–101. Berlin: Springer.

Bogdanowicz, W., Fenton, M. B. & Daleszczyk, K. 1999 The relationship between echolocation calls, morphology and diet in insectivorous bats. *J. Zool. Lond.* **247**, 381–393.

Faure, P. A., Fullard, J. H. & Barclay, R. M. R. 1990 The response of tympanate moths to the echolocation calls of a substrate gleaning bat, *Myotis evotis*. *J. Comp. Physiol.* A **166**, 843–849.

Faure, P. A., Fullard, J. H. & Dawson, J. W. 1993 The gleaning attacks of the northern long-eared bat, *Myotis septentrionalis*, are relatively inaudible to moths. *J. Exp. Biol.* **178**, 173–189.

Fenton, M. B., Portfors, C. V., Rautenbach, I. L. & Waterman, J. M. 1998 Compromises: sound frequencies used in echolocation by aerial-feeding bats. *Can. J. Zool.* **76**, 1174–1182.

Fullard, J. H. 1987 Sensory ecology and neuroethology of moths and bats: interactions in a global perspective. In *Recent advances in the study of bats* (ed. M. B. Fenton, P. A. Racey & J. M. V. Rayner), pp. 244–272. Cambridge University Press.

Fullard, J. H. 1998 The sensory coevolution of moths and bats. In *Comparative hearing: insects* (ed. R. R. Hoy, A. N. Popper & R. R. Fay), pp. 279–326. Berlin: Springer.

Fullard, J. H. & Dawson, J. W. 1997 The echolocation calls of the spotted bat *Euderma maculatum* are relatively inaudible to moths. *J. Exp. Biol.* **200**, 129–137.

Fullard, J. H. & Thomas, D. W. 1984 Detection of certain African, insectivorous bats by sympatric, tympanate moths. *J. Comp. Physiol.* A **143**, 363–368.

Fullard, J. H. & Yack, J. E. 1993 The evolutionary biology of insect hearing. *Trends Ecol. Evol.* **8**, 248–252.

Heller, K.-G. & Von Helversen, O. 1989 Resource partitioning of sonar frequency bands in rhinolophoid bats. *Oecologia* **80**, 178–186.

Hoy, R. R. & Robert, D. 1996 Tympanal hearing in insects. *A. Rev. Entomol.* **41**, 433–450.

Janzen, D. H. 1980 When is it coevolution? *Evolution* **34**, 611–612.

Jones, G. 1992 Bats vs. moths: studies on the diets of rhinolophid and hipposiderid bats support the allotonic frequency hypothesis. In *Prague studies in mammalogy* (ed. I. Horáček & V.

Vohralik), pp. 87–92. Prague, Czech Republic: Charles University Press.

Jones, G. 1999 Scaling of echolocation call parameters in bats. *J. Exp. Biol.* **202**, 3359–3367.

Jones, G. & Barratt, E. M. 1999 *Vespertilio pipistrellus* Schreber, 1774 *and V. pygmaeus* Leach 1825 (currently *Pipistrellus pipistrellus* and *P. pygmaeus*; Mammalia, Chiroptera): proposed designation of neotypes. *Bull. Zool. Nomencl.* **56**, 182–186.

Jones, G. & Rayner, J. M. V. 1989 Foraging behavior and echolocation of wild horseshoe bats *Rhinolophus ferrumequinum* and *R. hipposideros* (Chiroptera, Rhinolophidae). *Behav. Ecol. Sociobiol.* **25**, 183–191.

Jones, G. & Van Parijs, S. M. 1993 Bimodal echolocation in pipistrelle bats: are cryptic species present? *Proc. R. Soc. Lond.* B **251**, 119–125.

Kalko, E. K. V. & Schnitzler, H.-U. 1993 Plasticity in echolocation signals of European pipistrelle bats in search flight: implications for habitat use and prey detection. *Behav. Ecol. Sociobiol.* **33**, 415–428.

Meddis, R. 1984 *Statistics using ranks. A unified approach*. Oxford, UK: Blackwell.

Norman, A. P. & Jones, G. 2000 Size, peripheral auditory tuning and target strength in noctuid moths. *Physiol. Entomol.* (In the press.)

Novick, A. 1977 Acoustic orientation. In *Biology of bats*, vol. 3 (ed. W. A. Wimsatt), pp. 74–289. New York: Academic Press.

Pavey, C. R. & Burwell, C. J. 1998 Bat predation on eared moths: a test of the allotonic frequency hypothesis. *Oikos* **81**, 143–151.

Pye, J. D. 1993 Is fidelity futile? The 'true' signal is illusory, especially with ultrasound. *Bioacoustics* **4**, 271–286.

Rydell, J. & Arlettaz, R. 1994 Low-frequency echolocation enables the bat *Tadarida teniotis* to feed on tympanate insects. *Proc. R. Soc. Lond.* B **257**, 175–178.

Rydell, J., Jones, G. & Waters, D. A. 1995 Echolocating bats and hearing moths: who are the winners? *Oikos* **73**, 419–424.

Schnitzler, H.-U. & Grinnell, A. D. 1977 Directional sensitivity of echolocation in the horseshoe bat, *Rhinolophus ferrumequinum*. I. Directionality of sound emission. *J. Comp. Physiol.* **116**, 51–61.

Schnitzler, H.-U. & Kalko, E. K. V. 1998 How echolocating bats search and find food. In *Bat biology and conservation* (ed. T. H. Kunz & P. A. Racey), pp. 183–196. Washington, DC: Smithsonian Institution Press.

Schuller, G. & Pollak, G. D. 1979 Disproportionate frequency representation in the inferior colliculus of Doppler-compensating greater horseshoe bats: evidence for an acoustic fovea. *J. Comp. Physiol.* **132**, 47–54.

Simmons, J. A. 1969 Acoustic radiation patterns for the echolocating bats *Chilonycteris rubiginosa* and *Eptesicus fuscus*. *J. Acoust. Soc. Am.* **46**, 1054–1056.

Stapells, D. R., Picton, T. W. & Smith, A. D. 1982 Normal hearing threshold for clicks. *J. Acoust. Soc. Am.* **72**, 74–79.

Surlykke, A., Larsen, O. N. & Michelsen, A. 1988 Temporal coding in the auditory receptor of the moth ear. *J. Comp. Physiol.* A **162**, 367–374.

Tougaard, J. 1998 Detection of short pure-tone stimuli in the noctuid ear: what are temporal integration and integration time all about? *J. Comp. Physiol.* A **183**, 563–572.

Trappe, M. & Schnitzler, H.-U. 1982 Doppler-shift compensation in insect-catching horseshoe bats. *Naturwissenschaften* **69**, 193–194.

Vaughan, N. 1997 The diets of British bats (Chiroptera). *Mamm. Rev.* **27**, 77–94.

Vaughan, N., Jones, G. & Harris, S. 1997 Identification of British bat species by multivariate analysis of echolocation call parameters. *Bioacoustics* **7**, 189–207.

Waters, D. A. 1996 The peripheral auditory characteristics of noctuid moths: information encoding and endogenous noise. *J. Exp. Biol.* **199**, 857–868.

Waters, D. A. & Jones, G. 1995 Echolocation call structure and intensity in five species of insectivorous bats. *J. Exp. Biol.* **198**, 475–489.

Waters, D. A. & Jones, G. 1996 The peripheral auditory characteristics of noctuid moths: responses to the search-phase echolocation calls of bats. *J. Exp. Biol.* **199**, 847–856.

Waters, D. A., Rydell, J. & Jones, G. 1995 Echolocation call design and limits on prey size: a case study using the aerial-hawking bat *Nyctalus leisleri*. *Behav. Ecol. Sociobiol.* **37**, 321–328.