

THE ECHOLOCAION CALLS OF THE SPOTTED BAT *EUDERMA MACULATUM* ARE RELATIVELY INAUDIBLE TO MOTHS

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Summary

Previous studies of the spotted bat *Euderma maculatum* have demonstrated that this bat emits echolocation calls that are lower in frequency, shorter in duration and fainter in intensity compared with those of most other insectivorous bats, acoustic characteristics which should render it less conspicuous to eared moths. We tested this prediction by monitoring electrophysiologically the ears of sympatric noctuid (noctuid, arctiid and notodontid) moths in a site in western Canada. Auditory threshold curves demonstrate that most of the moths tested are less responsive to the calls of *Eu. maculatum* than to those of another sympatric bat, *Eptesicus fuscus*. Playbacks to moth ears of pre-recorded search- and approach-phase echolocation calls of *Eu. maculatum* and *Ep. fuscus* further

demonstrate that the calls of *Eu. maculatum* are poorly detectable to moths and, in some cases, completely inaudible. We estimate that, in the wild, an average noctuid moth would detect the calls of *Eu. maculatum* at distances of less than 1 m as opposed to the calls of *Ep. fuscus* which should be first heard at distances of 20–25 m. Although most moths are unable to adequately hear *Eu. maculatum*, the observation that two individuals possessed ears sensitive to this bat's calls suggests the existence of auditory pre-adaptation to this type of echolocation.

Key words: spotted bat, *Euderma maculatum*, echolocation, noctuid moths, auditory threshold curves.

Introduction

Many species of moths defend themselves against the attacks of hunting bats with simple ears that detect the bats' echolocation calls (Roeder, 1967; Miller, 1983; Fullard, 1987a; Surlykke, 1988). Moth ears are used primarily for bat detection (but see Surlykke and Fullard, 1989) and their frequency sensitivities are syntonically (Fullard, 1987a,b, 1988) with (i.e. matched to) the echolocation characteristics of those bats that comprise their main predatory threat (Fullard, 1982). Although insectivorous bats and their species-specific echolocation calls cover a wide range of frequencies (Fenton and Bell, 1981), moth ears are most sensitive from 20 to 50 kHz, the bandwidth used by most insectivorous bats (e.g. Roeder, 1970; Fenton and Fullard, 1979; Fullard, 1979, 1982, 1984a,b, 1987a; Fullard and Barclay, 1980; Fullard and Thomas, 1981; Fullard *et al.* 1983; Fullard and Belwood, 1988; Surlykke and Fullard, 1989; Faure *et al.* 1990, 1993). To frequencies below and above this range (allotonic frequencies) most moths are relatively insensitive and although bats could theoretically increase their foraging success on eared moths by evolving allotonic echolocation (Fenton and Fullard, 1979; Fullard, 1990; Jones, 1992; Rydell *et al.* 1995), there are costs associated with using such calls. The severe atmospheric attenuation of very high frequencies and the poor target resolution in the echoes of very

low frequencies (Griffin, 1971; Lawrence and Simmons, 1982) place limitations on the acoustic efficacy of allotonic echolocation. Nevertheless, some bats do use allotonic frequencies as the main component of their echolocation calls. Certain old-world hipposiderid bats emit very high frequencies (e.g. *Cloeotis percivali*, 212 kHz; Fenton and Bell, 1981) and feed heavily upon moths (Whitaker and Black, 1976) suggesting a benefit to allotonic echolocation. The North American vespertilionids, *Myotis evotis* and *M. septentrionalis* also emit high-frequency calls that sympatric noctuid moths (*Catocala* spp.) cannot detect as well as those of other bats (Faure *et al.* 1990, 1993) and it has been argued that this allows them to feed heavily upon moths. There is, however, another reason for using very high frequencies. Bats hunting in dense vegetation experience problems with acoustic 'clutter' (Neuweiler, 1990) resulting from the multiple echoes returning from such environments, and the use of very high frequencies improves the resolving power of the echoes for these bats. This acoustic consideration provides an alternative explanation for the use of allotonic high-frequency echolocation rather than as an evolved response to the auditory defences of moths (Rydell *et al.* 1995).

To date, few studies have examined the sensory ecology of

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eared moths and allotonic low-frequency bat species. Certain bats use very low frequencies for their echolocation calls (e.g. the molossids *Otomops martiensseni*: 13 kHz, Fenton and Bell, 1981; *Tadarida australis*: 12.6 kHz, Fullard *et al.* 1991 and *T. teniotis*: 11 kHz, Zbinden and Zingg, 1986) and some appear to feed heavily on moths (Jones and Rydell, 1994). The spotted bat *Euderma maculatum* is a western North American vespertilionid that echolocates using an extremely low (for bats) dominant frequency of 9–12 kHz (Woodsworth *et al.* 1981; Fenton and Bell, 1981; Leonard and Fenton, 1984; Obrist, 1995) and has been reported to prey heavily on moths (Easterla, 1965, Ross, 1967; Poché, 1981; Wai-Ping and Fenton, 1989). Woodsworth *et al.* (1981) and Barclay and Brigham (1991) hypothesized that *Eu. maculatum* is acoustically inconspicuous to eared moths and the purpose of our study was to test this to examine the possibility that allotonic echolocation is adaptive as an acoustic countermeasure against the auditory defences of moths.

Materials and methods

Study area and animals

We conducted this study in the southern Okanagan Valley near Oliver, British Columbia, Canada (42° 12'N, 119° 33'W). We collected eared moths (Noctuoidea: Noctuidae, Arctiidae and Notodontidae) using ultraviolet and mercury-vapour lamps erected in front of white cotton sheets facing 'open' (Fenton, 1990) habitats (fields and hillsides). These collection sites were chosen to select for moths that fly in the flight zones used by *Eu. maculatum* (Leonard and Fenton, 1983; Wai-Ping and Fenton, 1989). Examples of the moths used in our study were subsequently deposited in the Canadian National Collection (Ottawa). Echolocation signals from wild sympatric bats were recorded as they foraged near the Okanagan Falls provincial campground (*Ep. fuscus*) and on the banks of the Water Dog lake on the property of the Osoyoos Indian Band (*Eu. maculatum*). Auditory examinations were performed in the field at the Department of Geology station, University of British Columbia and subsequent data analyses including acoustic analyses of the bat calls were performed at the laboratories of the Queen's University Biological Station, Chaffey's Lock, Ontario, Canada.

Auditory sensitivity examinations

Auditory examinations were similar to those described in Fullard (1984a) and Faure *et al.* (1993) and are described briefly below. Moths collected each night were used the following day. After exposure of the moth's auditory nerve (IIIN1b; Nüesch, 1957) we used stainless-steel hook electrodes to record extracellularly the responses of the two auditory receptor cells (A1 and A2). The stimuli were 10 ms tone pulses (1–30 kHz in 1 kHz increments) generated by a Wavetek function generator (model 23), shaped to a 1 ms rise/fall time (Coulbourn S84-04), amplified (National Semiconductor LM1875T) and broadcast at 1 s⁻¹ from a low-frequency (InterTan 40-8428) (for stimulus frequencies of 1–5 kHz) or a

high-frequency (Technics EAS-10TH400B) (for stimulus frequencies of 5–30 kHz) loudspeaker mounted 30 cm from the moth (total system frequency response ± 3 dB, 1–40 kHz). The moth was oriented in a 'normal', wings-extended, dorsal-side-up position for these exposures and the loudspeaker was directed towards the postero-lateral margin of the moth (i.e. its most sensitive region; Payne *et al.* 1966). Thresholds were determined as those intensities that elicited three action potentials per stimulus pulse for four consecutive pulses (Faure *et al.* 1993). Intensities were recorded as millivolts peak-to-peak and were later converted to peak equivalent sound pressure levels (peSPL; Stapells *et al.* 1982) from equal-amplitude continual tones using a Brüel and Kjær (B&K) type 4135 1/4 inch microphone and type 2610 B&K measuring amplifier following calibration with a B&K type 4228 pistonphone. The playback system, including calibration equations for converting voltages into decibels, was controlled by a customized MS-DOS program written by J. W. D. A stimulus sound duration of 10 ms was chosen for these tests to obtain an estimate of the moths' best hearing abilities since this duration is in excess of the integration time of noctuid moth ears (Surlykke *et al.* 1988). Bats use a wide range of echolocation call durations (Novick, 1977; Fenton and Bell, 1981) so any particular stimulus duration will not match all those naturally encountered by flying moths.

Echolocation playback trials

Echolocation calls were recorded (see below) from wild bats as they foraged for insects over streams or lakes during the same period that the auditory examinations were performed. These recorded calls were played from a RACAL Store 4DS tape recorder (cf. Waters and Jones, 1996) running at 76 cm s⁻¹, amplified and broadcast from a Technics EAS-10TH400B loudspeaker mounted 30 cm from the moth auditory preparations (the low-frequency cut-off of this loudspeaker filtered out most of the recorded background noise). We recorded the moth's auditory receptor responses and the echolocation pulses onto separate channels of another RACAL tape recorder. One fly-by echolocation sequence from each bat ('bat pass'; Fenton, 1970) was chosen as the playback stimulus and played back at five amplification levels to provide a range of echolocation pulse intensities. Avoidance flight in moths commences in response to searching or cruising bats (Roeder, 1967) so we selected bat passes for playbacks that exhibited these phases and did not culminate in a terminal echolocation sequence. The voltages of the pulses were later converted to dB peSPL values by broadcasting a 10 kHz (for *Eu. maculatum*) or 30 kHz (for *Ep. fuscus*) continuous tone from the same loudspeaker while measuring intensities with the B&K measuring equipment described above.

The amplified bat echolocation pulses and corresponding auditory receptor spikes were digitized and stored using MS-DOS graphics analysis software (AxoTape 2.02, Axon Instruments, Foster City, CA, USA) by J. H. F. and later measured by a technician who was unaware of the acoustic characteristics of the two bat species chosen for the playbacks.

Bat recordings and analyses

Foraging bats (see above) were recorded using a Larson–Davis type 2520 1/4 inch microphone preamplified by a type 2200C power supply connected to a RACAL Store 4DS tape recorder running at 76 cm s⁻¹. Calls were later examined using a customized Fast Fourier Transform (FFT) spectral analysis program written by J. W. D. (see Faure *et al.* 1993 for details). The following variables were measured: duration (ms), dominant frequency (the value, in kHz, of the maximum spectral peak), lowest and highest frequencies (the kHz values of the spectrum -18 dB below and above dominant frequency, respectively) and the spectral bandwidths at -6 and -18 dB below dominant frequency.

Results

Auditory analyses

Auditory sensitivity curves (audiograms) were derived for the following 18 noctuid moths caught in the field: *Apamea antennata* (Noctuidae), *N*=2; *Leuconycta lepidula* (Noctuidae), *N*=2; *Hyphantria cunea* (Arctiidae), *N*=3; *Clostera albosigma* (Noctuidae), *N*=3; *Gluphisia septentrionalis* (Noctuidae), *N*=6; *Nadata gibbosa* (Notodontidae), *N*=2. Fig. 1 illustrates the combined audiograms of these moths. For the present study, we chose frequencies relevant to the bats used in the playback experiments and exposed the moths to 5–30 kHz (for audiograms of British Columbian moths that extend beyond 30 kHz, see Fullard *et al.* 1983). The dashed lines in Fig. 1 indicate 12.4 and 27.8 kHz, the dominant frequencies emitted by *Eu. maculatum* and *Ep. fuscus*, respectively. Low-frequency thresholds in these moths were generally high, ranging (at 10 kHz) from 55 to 105 dB with most thresholds exceeding 70 dB. All but one moth had higher thresholds for the frequencies of *Eu. maculatum* (12 kHz) than for those of *Ep. fuscus* (28 kHz) and there was an average threshold difference across all of the moths of 27 dB (range 2–44 dB). One individual of *H. cunea* did show a lower threshold to 12 kHz than to 28 kHz but there was no evidence that these ears were most sensitive to (i.e. tuned to) the frequencies emitted by *Eu. maculatum*. Fig. 1 further illustrates that inter-individual auditory thresholds for most species are variable, particularly at low (allotonic) frequencies. Threshold variability, especially at frequencies outside the best frequency, is commonly observed in moths (Surlykke, 1986; Faure *et al.* 1993; Fullard, 1994) and does not appear to be an artifact of experimental conditions.

Playbacks

Five moths, one individual each of *Halysidota maculatum* (Arctiidae), *Nadata gibbosa* (Notodontidae), *Euxoa flavicollis* (Noctuidae), *Lacinipolia illaudabilis* (Noctuidae) and *Zotheca tranquilla* (Noctuidae), were exposed to the prerecorded echolocation calls of *Eu. maculatum* and *Ep. fuscus*. Fig. 2 illustrates the auditory nerve responses of an insensitive (*N. gibbosa*) and a sensitive (*E. flavicollis*) moth to the echolocation pulses of the two bats; the shorter duration of the

calls of *Eu. maculatum* will result in lower dB SPL levels for this species compared to *Ep. fuscus*, resulting in a conservative estimate of the difference between the moths' responsiveness to the two bats (see Discussion). Fig. 2 illustrates that the auditory receptors in both moths respond to the calls of *Ep. fuscus* more vigorously than to those of *Eu. maculatum* and with a difference as to which receptor neuron is activated. Whereas both A1 and A2 receptors respond to the calls of *Ep. fuscus*, the A2 cell responds only rarely to those of *Eu. maculatum*. The results illustrated in Fig. 2 are typical of those observed for most of the moths investigated, although some individuals (e.g. *Lacinipolia illaudabilis*) revealed only single receptor spikes to even the most intense of the calls of *Eu. maculatum* and these were never those of the A2 cell. The results from all the moths' receptor responses to the bat pulses in the playback experiments are shown in Fig. 3. For all moths tested, the auditory responses (calculated as the total number of A1 and A2 receptor cell spikes) were less to *Eu. maculatum* (mean number of spikes per pulse was 2.4) than to *Ep. fuscus* (mean of 7.3 spikes per pulse). We caution that the points in Fig. 3 arise from repeated measurements from single individuals and are therefore pseudoreplicates. Although quantitative statistical comparisons are not possible for these data, we contend that the differences between the responses to the two bats are obvious with the calls of *Eu. maculatum* eliciting fewer spikes than those of *Ep. fuscus* at all intensities used in the playbacks. In addition, the narrower bandwidths of the calls of *Eu. maculatum* (see below) will result in lower total energy levels per call, further reducing their conspicuousness to the moths.

Noctuid moth auditory receptors spontaneously fire in the absence of sounds, a random activity that presumably signifies a 'no-bat' condition (Roeder, 1967). We assume that, in the absence of other sensory cues to the presence of an approaching bat, a moth cannot distinguish between a single receptor spike arising spontaneously and one elicited by a faint echolocation pulse. We therefore tabulated the receptor

Table 1. Echolocation call characteristics of the *Euderma maculatum* and *Eptesicus fuscus* passes used in the playback experiments

	<i>Euderma maculatum</i>	<i>Eptesicus fuscus</i>
Duration (ms)	4.2±0.1	9.8±0.3
LF (kHz)	8.6±0.2	24.8±0.2
DF (kHz)	12.4±1.7	27.8±1.5
HF (kHz)	24.3±1.7	51.2±1.5
BW _{-6dB} (kHz)	6.0±0.2	7.4±0.8
BW _{-18dB} (kHz)	15.7±1.8	26.4±1.5

Values are means ± s.d. from 20 pulses per bat.

LF, low frequency (-18 dB from spectral peak); DF, dominant frequency (spectral maximum); HF, high frequency (-18 dB from spectral peak); BW_{-6dB}, bandwidth (-6 dB from spectral peak); BW_{-18dB}, bandwidth (-18 dB from spectral peak).

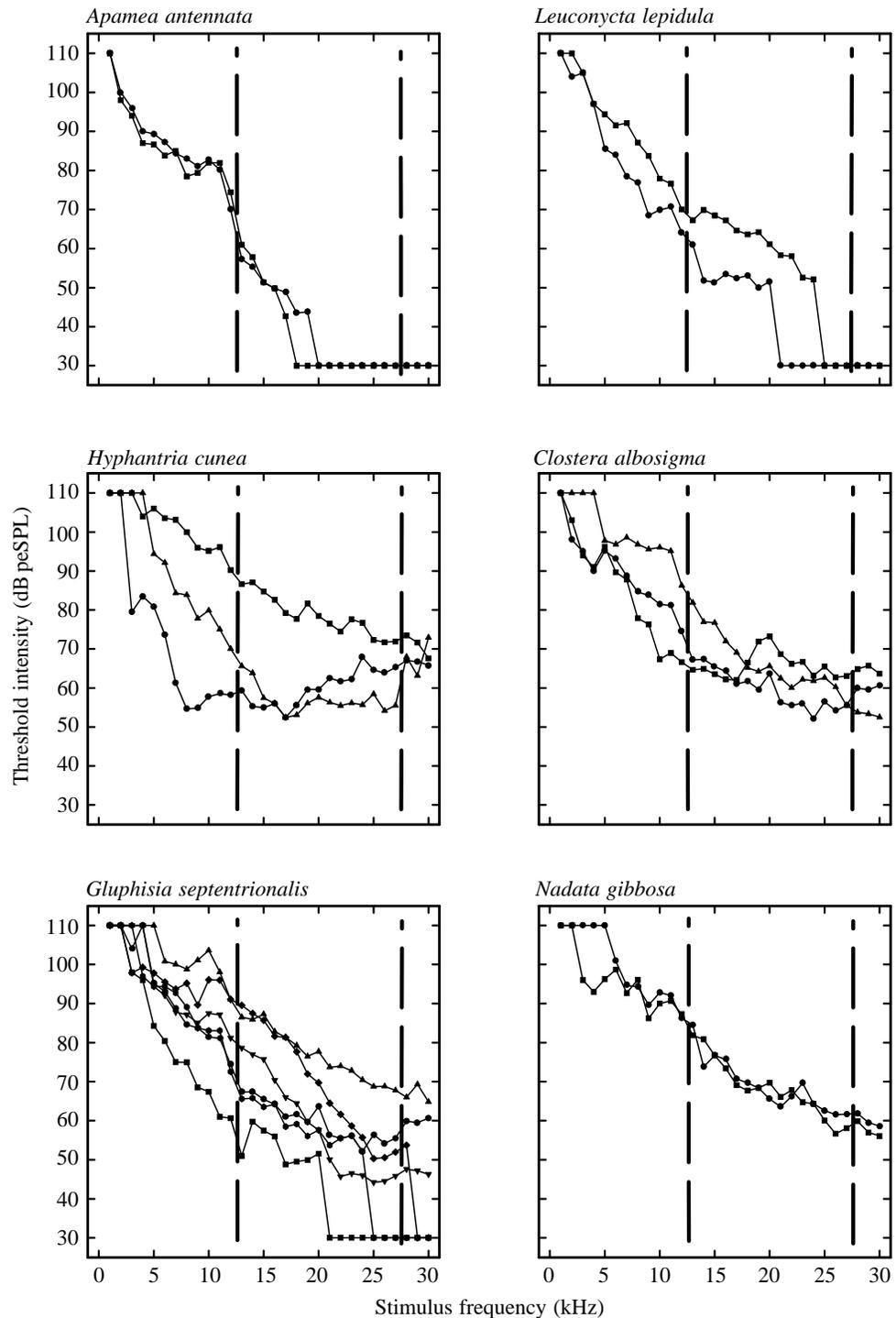


Fig. 1. Audiograms of British Columbian moths captured for this study. For frequencies where the maximum loudspeaker output could not obtain a threshold value, an arbitrary value of 110 dB is assigned; for frequencies where the lowest output of the loudspeaker still elicited receptor activity, an arbitrary value of 30 dB is assigned. For each audiogram, the approximate frequencies of the searching echolocation calls of *Eu. maculatum* (12.4 kHz) and *Ep. fuscus* (27.8 kHz) are indicated by dashed lines.

responses consisting of one spike per bat pulse as a proportion of the total response to each bat. The results (41.4% of *Eu. maculatum*'s pulses versus 10.1% of *Ep. fuscus*' pulses) indicate that a greater proportion of *Eu. maculatum*'s pulses elicited responses equal to spontaneous firing levels, and were presumably treated as 'no bat', than did those of *Ep. fuscus*.

Bat echolocation analyses

Fig. 4 and Table 1 describe the characteristics of the

echolocation pulses used in the playback experiments with moth auditory preparations. We caution that, in both cases, only the approach sequence of one bat was used and that these data are not intended to provide species-specific characteristics (for a detailed treatment of the acoustic characteristics of *Eu. maculatum* see Obrist, 1995). The calls of *Eu. maculatum* are human-audible with a fundamental harmonic of 12.4 kHz and with a second harmonic of 25–30 kHz, 10–20 dB less than the fundamental. In contrast, the calls of *Ep. fuscus* possess a

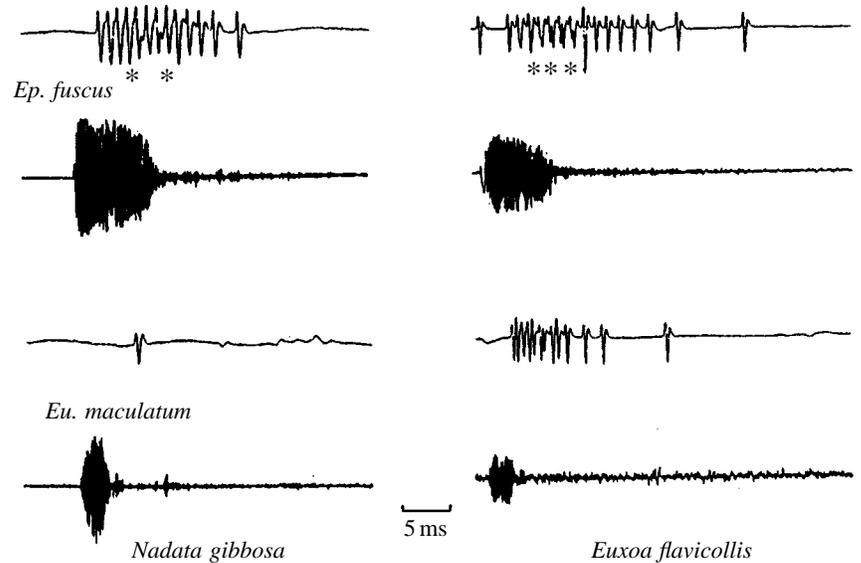


Fig. 2. Representative oscillograms (upper traces in each set) of the auditory nerve responses of an insensitive moth, *Nadata gibbosa* and a sensitive moth, *Euxoa flavicollis* to the echolocation calls (lower traces) of the two bat species (*Ep. fuscus* and *Eu. maculatum*) used in the playback trials. In both illustrations the most common spike is that of the A1 receptor while the less-sensitive A2 receptor (indicated by asterisks) responds more commonly to the calls of *Ep. fuscus* than *Eu. maculatum*.

fundamental dominant frequency of 27.8 kHz, also with upper harmonics. Furthermore, the spectral bandwidths at -6 and -18 dB of *Eu. maculatum* are narrower, with all frequencies lower than those of the calls of *Ep. fuscus*. The durations of the calls of the two species also differ, with those of *Eu. maculatum* being shorter (4.2 ms) than those of *Ep. fuscus* (9.8 ms). While our results reflect those reported for *Ep. fuscus* in the same region, our values for dominant frequency in *Eu. maculatum* were higher than those previously reported (Fenton and Bell, 1981; Leonard and Fenton, 1984; Obrist, 1995).

Discussion

Results from the auditory analyses and playback experiments in the present study demonstrate that moths are less responsive to the calls of *Euderma maculatum* than to those of *Eptesicus fuscus*, an insensitivity that appears to arise from a combination of the very low frequency and short duration of the echolocation calls of *Eu. maculatum*. Threshold *versus* stimulus-pulse-length relationships for other noctuid moths (Surlykke *et al.* 1988) suggest that the short calls of *Eu. maculatum* fall below the integration time of these ears (evoking a response equal to a longer pulse approximately 6 dB less intense) while the longer calls of *Ep. fuscus* will evoke the maximum response possible. The short durations of the calls of *Eu. maculatum* suggest that our use of a 10 ms stimulus tone resulted in higher thresholds than would be elicited by the calls themselves and the natural ability of moths to hear *Eu. maculatum* approach would be even less than we predict. Woodsworth *et al.* (1981) estimated the emitted natural intensities of the calls of *Eu. maculatum* to be 80–90 dB SPL at 10 cm as extrapolated from measured intensities at known distances, values considerably less than the 100–110 dB SPL at 10 cm computed for other vespertilionid bats (Griffin, 1958). Using estimates of moth auditory integration times from Surlykke *et al.* (1988), the calls of *Eu. maculatum* would be

treated as if they were 6 dB less than predictions from Woodworth *et al.* (1981), rendering the calls even less detectable to moths.

It is possible to estimate a moth ear's maximum detection distance for a particular bat if the moth's auditory thresholds to the dominant echolocation call frequencies of the bat are known (Fenton and Fullard, 1979; Surlykke, 1988). Fig. 5 plots the mean maximum detection distances predicted from the moths' thresholds (Fig. 1) to 10 kHz (i.e. *Eu. maculatum*) and 30 kHz (i.e. *Ep. fuscus*) against a range of emitted echolocation intensities (the estimated echolocation intensities for the two bats are indicated by arrows and, in the case of *Eu. maculatum*, two predicted dB values are given, one with and one without the correction factor from the integration time results of Surlykke *et al.* (1988)). The maximum detection distances predict that whereas *Ep. fuscus* will be detected at 20–25 m, *Eu. maculatum* will not be detected until it is less than 1 m from the moths. Assuming that bats must be within 1–5 m of their intended targets (Kick and Simmons, 1984; Kalko, 1995) before they can detect their echoes (indicated by the dashed line in Fig. 5), only *Eu. maculatum* appears to be able to achieve this distance before moths have heard its calls. Whereas most moths we tested would be subject to increased predation from *Eu. maculatum* (certain species, such as *Nadata gibbosa* appear to be completely deaf to it), others (e.g. *Euxoa flavicollis*) have ears that should be able to hear this bat in time to effect a 'take-cover' (Roeder, 1967) evasive response. Leonard and Fenton (1983) observed *Eu. maculatum* diving to within 1 m of the ground in pursuit of unidentified insects. If the insects in these encounters were moths, it would suggest that some possess ears that are at least capable of evoking take-cover defensive responses to attacking *Eu. maculatum*.

Does *Eu. maculatum* eat more moths as a result of having inconspicuous calls? Although stomach and faecal analyses of this bat suggest that it feeds extensively on moths (Easterla, 1965; Ross, 1961, 1967; Poché, 1981; Wai-Ping and Fenton,

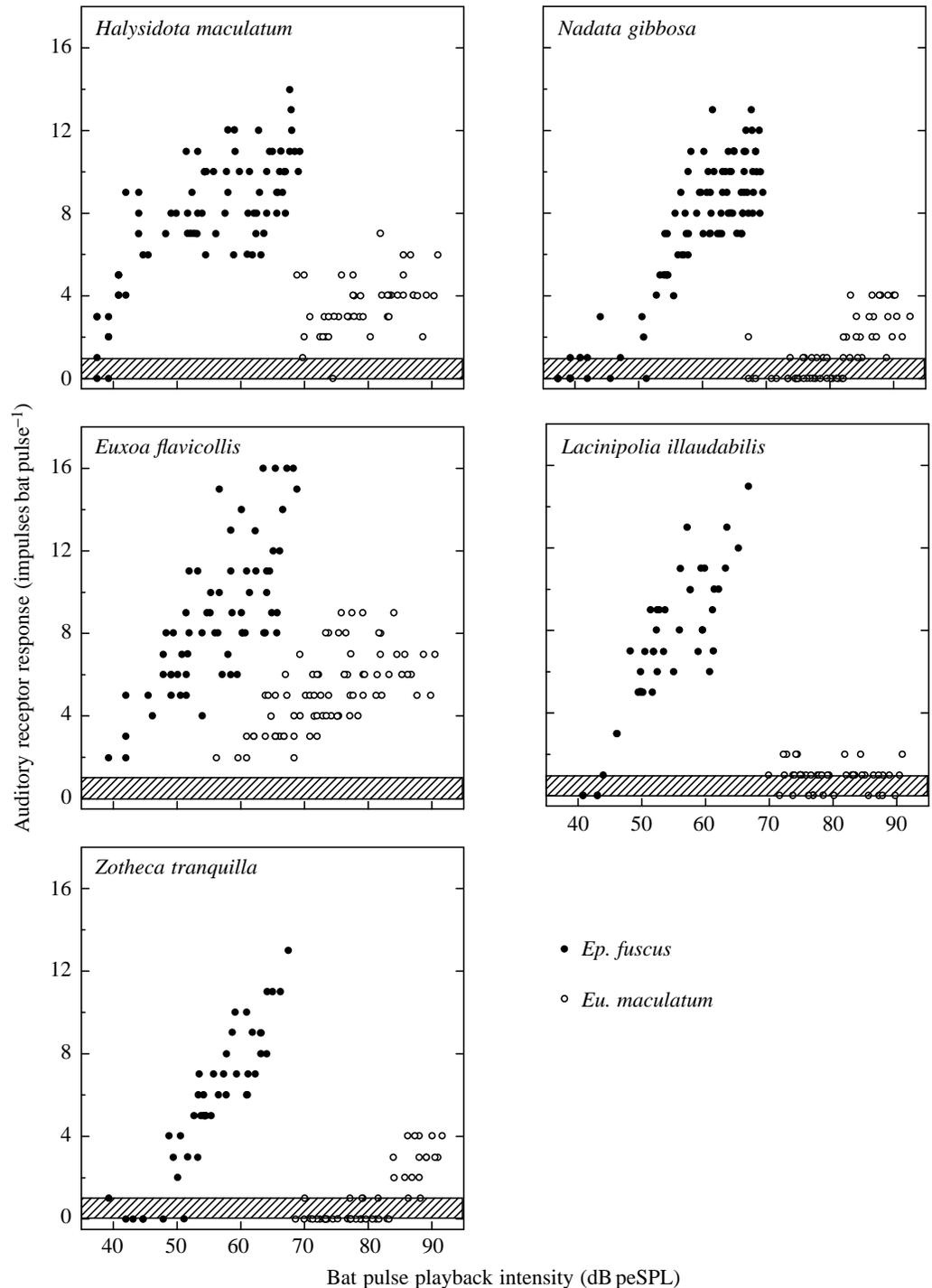


Fig. 3. Auditory receptor responses of the moths used in the playback trials to varying intensities of echolocation pulses from the two bat species (*Ep. fuscus* and *Eu. maculatum*) used in the playback trials. Each moth ($N=1$) was exposed to a number of echolocation pulses whose peSPL was determined from the recorded voltages. The shaded zone from 0 to 1 spike per bat pulse indicates spontaneous firing activity.

1989), caution is warranted in correlating these results with ours since some moth taxa are earless (Roeder, 1974; Fullard and Yack, 1993) and these may be the species fed upon by *Eu. maculatum*. The flight characteristics of earless moths, however, suggest that this is not the case. Morrill and Fullard (1992) and Lewis *et al.* (1993) observed that earless moths fly less often, more erratically and closer to the ground than eared moths, traits that presumably serve earless moths as passive defences against the attacks of bats whose echolocation calls

they cannot hear. These observations suggest that earless moths do not inhabit the open zones where *Eu. maculatum* hunts (Woodworth *et al.* 1981; Leonard and Fenton, 1983). Our collecting lights sampled from open habitats and the scarcity of earless species among those that we gathered there suggests that it is eared moths that fly with *Eu. maculatum* and subsequently become their prey. *Eu. maculatum* presumably benefits from preying on moths over other insects (e.g. caddisflies; Belwood and Fenton, 1976) since the greater body

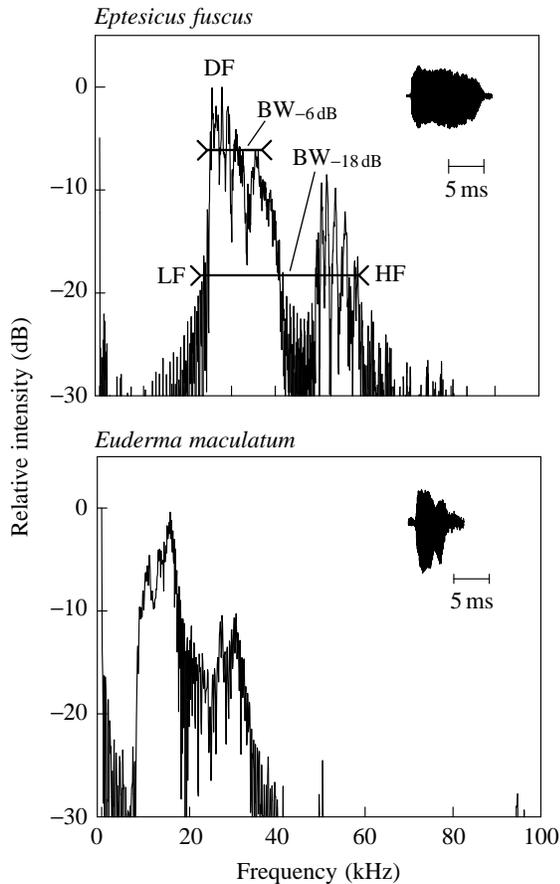


Fig. 4. Acoustic analyses of the echolocation pulses of the bats used in the playback trials. For both species a time/amplitude oscillogram (inset) is shown with its Fast Fourier Transform. The following call characteristics (values given in Table 1) are defined in the upper panel: BW_{-6dB}, bandwidth (-6 dB from spectral peak); BW_{-18dB}, bandwidth (-18 dB from spectral peak); DF, dominant frequency (spectral maximum); HF, high frequency (-18 dB from spectral peak); LF, low frequency (-18 dB from spectral peak).

mass of moths would result in greater foraging efficiency for these bats. This suggests that *Eu. maculatum* may be an authentic candidate for the title of moth 'specialist' since this bat appears to have evolved sensory and acoustic methods to maximize its capture success of moths while sacrificing its ability to prey on other insects.

These conclusions lead to two questions: first, if *Eu. maculatum* poses a threat to moths because of its echolocation calls, why have these insects not evolved ears that can effectively detect them? Second, if *Eu. maculatum* benefits from its specialisation on moths, why is it (and other bat species that use allotonic echolocation) not more common? Fullard (1982) and Fullard and Belwood (1988) hypothesised that the tone-deaf ears of moths (Roeder, 1967) are not tuned to specific bats but to the acoustic assemblage of the echolocation frequencies of *all of the echolocating bats* that present a significant predation risk (i.e. selection force) and whether a particular bat species is listened for by a moth is

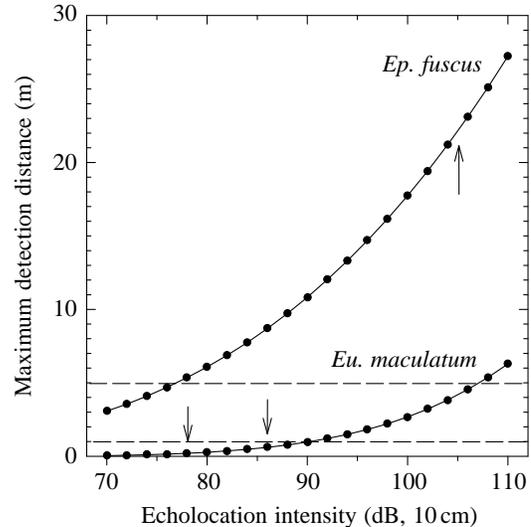


Fig. 5. Predicted maximum detection distances for the two species of bat recorded for all of the moths whose audiograms were derived (Fig. 1). The proposed in-flight intensities for both bats [*Eu. maculatum*: 85 dB SPL (Woodsworth *et al.* 1981) and 79 dB (as attenuated by the moth's integration time; Surlykke *et al.* 1988); *Ep. fuscus*: 105 dB (Griffin, 1958)] are indicated by arrows. The dashed line indicates 5 m, the point at which both bats may first detect echoes returning from the moths. The moths detect *Ep. fuscus* at a distance of 20–25 m, *Eu. maculatum* will not be detected until less than 1 m.

determined by that species' contribution to the total predator community. To a moth, common bats such as *Ep. fuscus* form a heavy predation potential because of the high probability of encountering them during the night. Where censuses have been taken, *Eu. maculatum* is a relatively rare species (Findley and Jones, 1965) and would not participate in many of the total nightly encounters a moth would make with bats. We contend that *Eu. maculatum* and its echolocation calls have not imparted a strong enough selection pressure on moths to have resulted in the evolution of auditory defences specific to this bat. Paradoxically, although *Eu. maculatum* feeds heavily on moths, moths have not evolved ears that can detect its calls. We believe that a similar situation exists for the short, faint, allotonic high-frequency calls of the gleaner bat, *Myotis septentrionalis* in eastern Ontario. This bat preys on moths as they sit on vegetation and uses echolocation calls which are also relatively inaudible to moths (Faure *et al.* 1993). *Myotis septentrionalis*, like *Eu. maculatum*, is an uncommon bat (Fullard *et al.* 1983) relative to the total bat community, and we contend that its predation pressure has not been intense enough to have favoured moths able to hear its approach. These bats, and other rare species with specialised foraging habits, have therefore exploited the sensory ecology that exists between moths and most bats and are consequently better able to prey heavily upon these insects.

The second question, why bats such as *Eu. maculatum* are not more common, may be answered by re-examining the problems associated with these types of echolocation systems. The low-frequency calls of *Eu. maculatum* suggest that this bat

has limited itself to large prey items (Leonard and Fenton, 1984) and a foraging zone that contains relatively few insects, constraints that may have favoured the southern portions of this bat's North American range and in which insect densities may be higher throughout the year. The primarily tropical and subtropical distributions of other low-frequency bats (e.g. *Tadarida* spp.) (Fenton and Bell, 1981) further suggests that populations of allotonic bats in general are determined by the insect prey base to which their echolocation signals have constrained them.

Although most of the moths we tested were insensitive to the calls of *Eu. maculatum*, some (e.g. *Euxoa flavicollis*) had thresholds that indicated that they could detect this bat in time to commence effective avoidance behaviours. High threshold variability at allotonic frequencies is common for moths (Fullard, 1984b; Surlykke and Fullard, 1989) and is likely to be a result of random variation in receptor sensitivities at these values. In the present study, we are confident that threshold variation was not a result of experimental error since low frequencies are not susceptible to confounding acoustic effects such as high reflectivity. We conclude, therefore, that some moths possess low thresholds at these frequencies because of naturally occurring character variability and not as a result of selection from low-frequency bats. If this is true, the rare allotonic sensitivity of these moths may represent a sensory preadaptation to low-frequency bats. It is unlikely that the pleiomorphic dominant frequency of echolocating bats was lower than 10 kHz (Simmons and Stein, 1980) so the occurrence today of allotonically sensitive moths is not likely to be an evolutionary hold-over from those times.

Whether or not the poor detectability of the calls of *Eu. maculatum* represents a co-evolved countermeasure (Fenton and Fullard, 1979) or simply a fortuitous coincidence remains speculative. The existence of extremely low-frequency echolocation in bats such as *Eu. maculatum* is rare and we suggest that the use of these frequencies (acoustically less efficient than typical echolocation for most insect prey sizes) serves primarily to confound moth ears. Simmons and Stein's (1980) proposed phylogeny of echolocation also suggests that low-frequency allotonic echolocation is rare and likely to be an apomorphic (i.e. derived) trait. Regardless of the evolutionary origins of this type of echolocation, it is not employed by most of the bats in the world. Anti-defence countermeasures should work best when they are not expressed by the majority of predators (Edmunds, 1974) and it is reasonable to expect that certain bats (i.e. a minority of species in any given community) have evolved inconspicuous echolocation calls as a countermeasure to prey more effectively on eared moths.

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