The Influence of Moth Hearing on Bat Echolocation Strategies

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Summary. The ears of moths we tested in Canada and Côte d'Ivoire are most sensitive to sounds between 20 and 40 kHz, and much less sensitive to sound over 65 kHz. The insectivorous bats most commonly encountered in these (and other) locations use high intensity, frequency modulated echolocation calls with frequency components in the 20–40 kHz range, making them detectable by the most sensitive tympanate moths up to 40 m away. In Africa bats such as species in the Nycteridae, Megadermatidae, and some in the Hipposideridae, use low intensity calls with high frequency components, and these species are not detectable by moths at over 2 m. The hearing ability of moths may significantly influence the feeding efficiency of bats, and changes in the intensity and frequency components of bat echolocation calls can drastically reduce the range at which bats are detected, and thus the time available to the moths for evasive behaviour (Fig. 4). The use of low intensity, high frequency echolocation calls may constitute a bat counter-maneuver against insects tuned to bat calls.

Introduction

The ability of some insects, notably many moths (Roeder, 1974a) and some lacewings (Miller, 1975) to detect the ultrasonic echolocation cries of bats, represents an example of an 'eye-opening' discovery about animal orientation behaviour (Griffin, 1977) and is famed in song and legend (Pye, 1968). Some moths and lacewings, when warned of an approaching bat by its echolocation calls, and appraised of its range by intensity cues, respond according to the proximity of the bat by either flying in the opposite direction (under low intensity stimulation), or commencing a series of complex flight maneuvers (un-

der high intensity stimulation). In either case, the insect reduces its chances of being caught by the approaching bat (Roeder and Treat, 1960; Miller, 1978). The range at which the bat is detected probably strongly influences the chances of the insect successfully evading the bat.

The fact that the ears of moths, like the ears of most animals, are more sensitive at some frequencies than they are at others (Adams, 1972; Roeder, 1974a; Fullard, 1979) extends research on the bat-moth interaction to the investigation of strategies echolocating bats might use to foil the warning systems of insects (apart from the obvious cessation of echolocation). The purpose of this study was to determine whether or not there was a differential response to the echolocation calls of some bats by tympanate moths.

Materials and Methods

We monitored the activity of echolocating bats at four field locations: the Queen's University Biology Station on Lake Opinicon in southeastern Ontario (44°34'N; 79°15'W); the Lamto Ecology Station on the Bandama River in Côte d'Ivoire (6°13'N; 5°02'W); the Southwest Research Station near Portal, Arizona (31°53'N; 109°02'W); and in the Sengwa Wild Life Research Area in Rhodesia (18°10'S; 28°13'E). Recordings of bat echolocation calls were made at the Ontario, Arizona and Côte d'Ivoire sites, and neural preparations of moths in Ontario and Côte d'Ivoire.

We recorded bats as they hunted for insects in the field in a variety of situations using broadband microphones (10–200 kHz; Simmons, Fenton, Ferguson, Jutting and Palin, in press) and a Lockheed Store 4D tape recorder operated at 76 cm/s. Tapes were played at reduced speeds (8–16 times) into a Princeton Applied Research Model 4513 FFT (Fast Fourier Transform) Real Time Spectrum Analyzer (2048 lines; flat weighting) to determine the power spectra of the bat calls. In the field we also used a zero-crossing period meter with the broadband microphone and an oscilloscope (Simmons, Fenton, Ferguson, Jutting and Palin, in press) to assess habitat use by bats with different echolocation call characteristics and frequency patterns. Bat activity was quantified by counting the number of passes past the microphone during periods of monitoring. In the field the feeding behaviour

of bats was observed directly, sometimes with the aid of a night vision scope, in conjunction with the broadband microphone and period meter.

We used modifications of techniques described by Roeder (1966, 1974 b) to expose the thoracic auditory nerve of noctuids, arctiids, thyretids, thaumetopoeids, and notodontids, or the thoracic-abdominal ganglionic connective of geometrids, to which we attached an extracellular stainless steel hook microelectrode. A tapered stainless steel wire placed in the partially dissected thoracic flight musculature served as a reference electrode. Amplification was by a single-ended Grass Instruments P16 Preamplifier connected to a Tektronix 212 dual-beam portable oscilloscope.

Acoustic stimuli were delivered to the moth in the form of continuous pure tones at stimulus frequency intervals of 5 kHz from 5 to 110 kHz. These stimuli were generated by an Exact VCF/sweep 126 Signal Generator, and amplified by a portable ultrasonic power amplifier (Simmons, Fenton, Ferguson, Jutting and Palin, in press) through one of two speakers, a T27 (KEF Electronics, Tovil Maidstone, Kent, England; 5 to 40 kHz) or a coated mylar, electrostatic (35–110 kHz) model (Kühl), 10 cm from the moth ear. Threshold values were determined by increasing the stimulus intensity until auditory nerve spike activity was first detected. Intensities were monitored by the oscilloscope after amplification, recorded then as mV, and subsequently converted to dB SPL r.m.s. re. 2×10^{-5} N/m², 10 cm. The intensities of stimulus sounds 10 cm from the speakers were measured before and after field observations using calibrated Brüel and Kjaer quarter inch microphones in an anechoic chamber. To reduce the effect of stimulus echoes, moths were placed during testing in a Faraday cage open at one side and lined with 4 cm of sound attenuating foam.

In Ontario and Côte d'Ivoire, specific bats (*Myotis lucifugus, Rhinolophus landeri, Hipposideros ruber, Nycteris macrotis*, and *Pipistrellus nanus*) were allowed to fly about in the room while we monitored the neural responses of moths to determine the approximate distances over which the moths could detect these bats. In Ontario bats could be as far as 4 m from the moth preparation, while in Côte d'Ivoire 3 m was the farthest the bats could be from the moths; in either case a function of the size of the laboratory.

Results

The feeding bats that we observed and recorded in the field used the range of echolocation calls described for the location and pursuit of insects (Simmons et al., 1979) appropriate for the bat fauna in the area where we were working (see Table 1 for a list of bat species). In southeastern Ontario (Fig. 1 A) *Myotis lucifugus* and *Eptesicus fuscus* (Vespertilionidae) dominated the fauna at our study sites, and both used mainly frequency modulated (FM) echolocation calls with varying constant frequency (CF) components. At the Arizona site, we regularly observed 10 species of bats feeding (8 vespertilionids and 2 molossids), all of which used FM calls with varying CF components. The bats in the Arizona location used a broader range of frequencies (Fig. 1 B) than the bats in Ontario. In Côte d'Ivoire, both CF and FM echolocators (*sensu* Simmons et al., 1975) were observed, and the range of frequencies used for echolocation exceeded that which we had observed at either North American
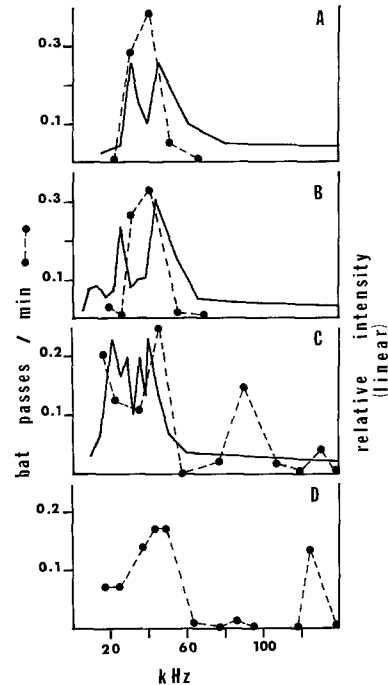

Fig. 1A–D. Incidences of bat echolocation calls at different frequencies (– – –) and power spectra (——) of echolocation calls, for four areas including, A Ontario, B Arizona, C Côte d'Ivoire, and D Rhodesia (for details of locations see text). Incidences of bat calls at different frequencies are presented as bat passes per min (a bat flying past the microphone and being detected is a 'bat pass'), derived by monitoring bat activity and scoring each pass for the frequency representing the longest part of the call (for rhinolophids or hipposiderids), or the lowest frequency (for FM echolocators). Power spectra were obtained by averaging signals recorded at field sites with an FFT spectrum analyzer on flat weighting. Period meter monitoring figures are based on 600, 600, 200 and 200 min, respectively, of field observation, while power spectra are derived from averages of 400 bat calls for each location. There are no recordings available for the Rhodesian site

location (Fig. 1 C). At the Rhodesian site, the range of frequencies (Fig. 1 D) and the variety of echolocation strategies resembled the Côte d'Ivoire site.

The bats we observed feeding in the field did not necessarily use all of the available habitats and some fed not only on flying, but also on stationary insects (Table 1). Low intensity or highly directional echolocators are under-represented in samples we acquired by monitoring echolocation calls, but we supplemented acoustic with visual monitoring of bat activity. In the North American locations we never saw bats that we were not also picking up on the microphones, high flying individuals notwithstanding, while at both African locations, we observed *Nycteris* spp. but never detected their echolocation calls and in the lab only picked up their calls when they were less than 0.2 m from the microphone. In Côte d'Ivoire we commonly saw *Hipposideros ruber* in gallery forest, but only occasionally detected them with micro-

Table 1. Habitat use by feeding insectivorous bats employing different echolocation strategies as determined by monitoring echolocation calls and by captures in mist nets and Tuttle traps (Tuttle, 1974). × denotes degree of habitat use; o denotes lack of habitat use; – denotes absence of this habitat at any site. Echolocation strategies include High Intensity Frequency Modulated (HIFM), High Intensity Constant Frequency (HICF) or Low Intensity (LI) orientation sounds

	Habitats							Means of prey capture	
	Small ponds	Open water (Lakes and rivers)	Grassland and fields	Savannah	Forest	Gallery or closed forest	Desert scrub	Aerial	gleaning
Ontario									
HIFM	× × ×	× ×	×	–	×	–	–	× × ×	× [a]
Arizona									
HIFM	× × ×	–	×	×	× ×	–	× ×	× × ×	× [a]
Côte d'Ivoire									
HIFM	× × ×	× × ×	× ×	× ×	–	o	–	× × ×	?
HICF	×	×	o	o	–	× ×	–	× ×	?
LI	×	o	o	o	–	× ×	–	×	× [a]
Rhodesia									
HIFM	× ×	× × ×	× ×	× ×	× ×	–	–	× × ×	× [a]
HICF	×	×	×	×	× ×	–	–	×	× [a]
LI	×	o	o	×	× ×	–	–	×	× [a]

[a] Bats encountered at these locations are as follows (gleaners, whether from rocks, foliage, ground, buildings, or water are marked '*'): Ontario *Myotis lucifugus* and *Eptesicus fuscus* (Vespertilionidae); Arizona *Myotis auriculus**, *M. volans*, *M. californicus*, *M. thysanodes*, *Lasionycteris notivagans*, *Eptesicus fuscus*, *Lasiurus cinereus*, *Antrozous pallidus* (Vespertilionidae), *Tadarida brasiliensis*, and *T. macrotis* (Molossidae); Côte d'Ivoire *Taphozous peli* (Emballonuridae – HIFM), *Nycteris arge**, *N. macrotis** (Nycteridae – LI), *Hipposideros abae*, *H. cyclops*, *H. ruber* (Hipposideridae – LI?), *Rhinolophus landeri* (Rhinolophidae – HICF), *Pipistrellus nanus*, *Scotecus albofuscus*, *Scotophilus gigas* (Vespertilionidae – HIFM), *Tadarida condylura*, and *Myopterus senegalensis* (Molossidae – HIFM); and Rhodesia *Nycteris woodi**, *N. thebaica** (Nycteridae – LI) *Hipposideros commersoni*, *H. caffer* (Hipposideridae – HICF), *Rhinolophus hildebrandti*, *R. fumigatus*, *R. landeri*, *R. denti*, *R. clivosus* (Rhinolophidae – HICF), *Miniopterus schreibersi*, *Myotis welwitschii*, *Pipistrellus nanus*, *P. rueppelli*, *P. rusticus*, *P. kuhlii*, *Glauconycteris variegata*, *Laephotis angolensis**, *Eptesicus capensis*, *Scotophilus viridis*, *S. nigrita*, *Nycticeius schlieffeni* (Vespertilionidae – HIFM), *Tadarida aegyptica*, *T. nigeriae*, *T. bivittata*, and *T. chapini* (Molossidae – HIFM)

Table 2. Comparison of sensitivity of ears of different moths to signals of specific frequencies, based on those species for which our sample size is 3 or more individuals

Moths	Sample size	Frequency of maximum sensitivity kHz	Minimum intensity of signal required to ellicit Neural response, in dB SPL re 2×10^{-5} N/m², 10 cm					
			10 kHz	20 kHz	40 kHz	60 kHz	80 kHz	100 kHz
North American								
Spilosoma virginica[a]	3	15–40	74	51	49	73	73	78
Spilosoma congrua[a]	6	15–40	81	52	52	73	69	84
Halysidota caryae[a]	5	20–40	78	56	55	69	69	73
African								
Desmeocraera graminosa[b] *	10	40	85	59	44	54	50	58
Balacra inflammata[c]	4	45–95	96	91	75	72	65	73
Rhodogastria vitrea[b] *	3	30	72	57	40	50	48	62
Caryatis phileta[a] *	4	25–40	91	65	52	67	65	74
Estigmene unilinea[a]	4	30	82	62	49	61	56	71
Spilosoma penicillata[a]	6	25–40	75	48	43	57	54	68
Geolyces convexaria[d]	5	30	66	49	47	62	61	70
Colocleora potaenia[d]	5	25	64	48	49	59	64	76
Miantochora venerata[d]	4	30	66	49	45	62	64	75
Miantochora interrupta[d]	5	25–30	61	48	44	59	64	78
Megadrepana cinerea[e]	5	25–30	68	45	47	62	71	85
Anaphe ambrizia[e]	6	40	88	74	59	70	67	75

[a] Arctiidae; [b] Notodontidae; [c] Thyretidae; [d] Geometridae; [e] Thaumetopoeidae
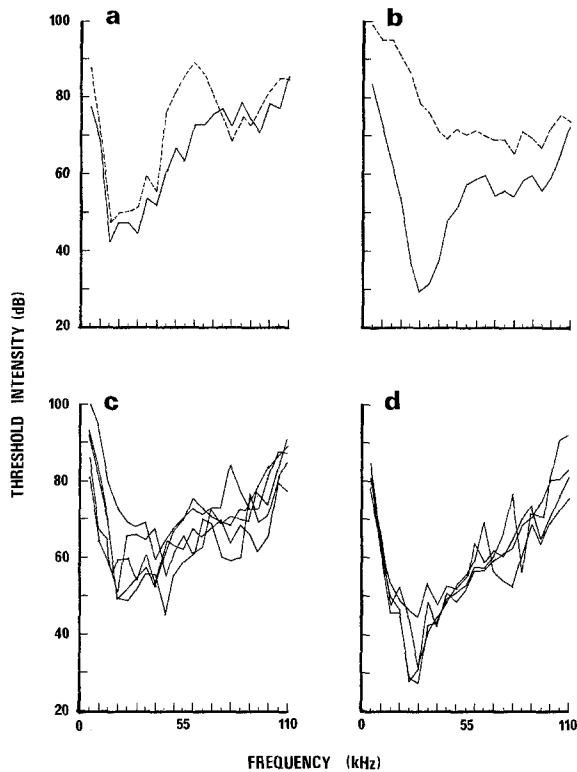* species identification near to or=

Fig. 2a–d. Audiograms of moths from Ontario (**a** and **c**) and Côte d'Ivoire (**b** and **d**) showing the most sensitive species (——— in **a** and **b**), the least sensitive species (–––– in **a** and **b**), and the variability in threshold curves for 4 (**d**) and 5 (**c**) individuals. From Ontario the following moths were used: *Phragmatobia assimilis* (——— in **a**), *Spilosoma prima* (– – – – – in **a**), and *Halysidota caryae* (**c**), while from Africa the data are from *Gorua apicata* (——— in **b**), *Balacra inflammata* (– – – – – in **b**), and *Miantochora interrupta* (**d**). Audiograms in **a** and **b** are average values for 5 individual moths each. dB values are re 2×10^{-5} N/m^2 at 10 cm

Fig. 3a–d. Tympanic nerve responses of the moth *Desmeocraera graminosa* to the echolocation calls of **a** – *Pipistrellus nanus*, **b** – *Rhinolophus landeri*, **c** – *Hipposideros ruber*, and **d** – *Nycteris macrotis*. The vertical deflection of the *p. nanus* pulse is attenuated relative to the other bat pulses. Characteristics of the bat calls and distances to the bats are provided in Table 3

phones, corresponding to times when the bats were within 1.5 m of the microphone. In both African locations, we rarely detected the echolocation calls of *Rhinolophus* spp., presumably because of their highly directional nature (Schnitzler and Grinnell, 1977). High intensity FM echolocating bats hunted insects in all of the habitats we sampled in Ontario, Arizona and Rhodesia, but were never encountered in the gallery forest in Côte d'Ivoire (Table 1) where they foraged along the margins of the gallery forest, over savannah, large rivers and small pools.

We prepared audiograms for 147 moths of 38 species, 62 (16) from Ontario, and 85 (22) from Côte d'Ivoire (Table 2). There was variation in hearing sensitivies between species (Table 2) and individuals (Fig. 2), but in general the most sensitive African species were more sensitive over their whole range than their Ontario counterparts. Furthermore, the African moths tended to have broader ranges of frequencies over which they were most sensitive than the Ontario species (Fig. 2; Table 2), coinciding with
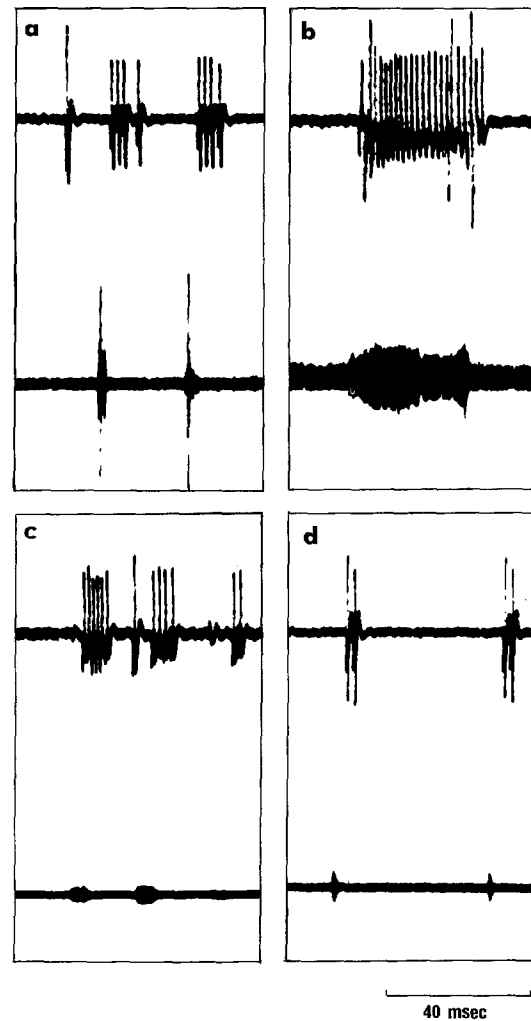
the broader ranges of echolocation call frequencies to which they were exposed (Fig. 1). With the exception of the two African species that showed relatively flat frequency responses (Fig. 2b; Table 2), most moths were much less sensitive to sounds above 65 kHz. The ears of moths from Ontario were most sensitive to the frequencies dominant in the echolocation calls of bats occurring there (Fig. 1A, and 2a, b; Table 2), but the situation in Africa was more complex. There moths exposed to wider ranges of frequencies in echolocation calls were most sensitive to the frequencies used most by the bats (Fig. 1C, and Fig. 2d, f, and Table 2), and relatively insensitive to frequencies less commonly used by the bats.

The auditory responses of moths to bats flying in the laboratory clearly demonstrated the effect of
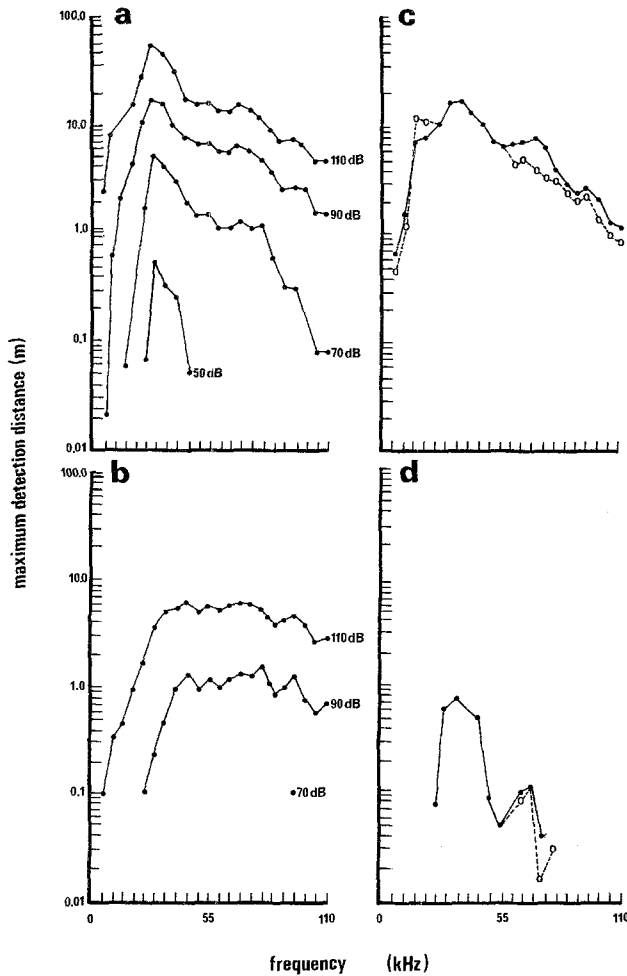
Fig. 4a–d. A representation of the maximum distances at which tympanate moths detect echolocation cries of bats based on auditory threshold values. Figures for maximum detection distances derived by transforming audiogram values with the data of Griffin (1971; pers. comm.). Data illustrate effects of different initial intensities of bat echolocation signals (dB re 2×10^{-5} N/m²; 10 cm), frequencies and relative humidity. Specific data are for **a** – *Scalmicauda bisecta* (Notodontidae), the most sensitive moths we studied in Côte d'Ivoire at 20% relative humidity, **b** – *Balacra inflammata* (Thyretidae), the least sensitive Ivorian moth we studied, at 20% relative humidity, **c** – *Rhodogastria vitrea* (Arctiidae) at 20% (●——●) and 100% (o——o) relative humidities (initial intensity 110 dB, and **d** – the same moth for an initial bat intensity of 70 dB

echolocation strategy on moth sensitivity to bats. In Ontario the moths *Phyrrharctia isabella* and *Phragmatobia assimilis* detected flying *Myotis lucifugus* when the bats were up to 4 m away, as long as the bat was not flying away from the moths. In Côte d'Ivoire the moth *Desmeocraera* sp. near to or = *graminosa* (hereafter *D. graminosa*) detected *Pipistrellus nanus* anywhere up to 3 m away, as long as the bat was not flying away from the moth (Fig. 3 a). The same species of moth also detected *Rhinolophus landeri* (Fig. 3 b) up to 3 m away, when the bat was flying directly

towards the moth. However, *D. graminosa* did not detect *H. ruber* (Fig. 3 c) until the bats were less than 1.5 m away and flying directly towards it, and was unable to pick up the calls of *Nycteris macrotis* (Fig. 3 d) as it flew around in the room unless the bat was less than 0.2 m away. A comparison of the acoustic characteristics of the calls of these bats (Table 3) emphasizes that frequency and intensities of the bats' calls are crucial to the moths' detection of a marauding bat. These effects are presented as a function of distance of detection in Fig. 4.

Discussion

Roeder and Treat (1960) and L.H. Miller (pers. comm). have shown that in some cases insects that can hear bats have 40% less chance of being captured by bats as opposed to insects which do not. What is probably critical to the insect having detected an approaching bat is the time available to it for evasive action. Bats can reduce the escape time available to an insect in at least three ways: 1) increasing their flight speeds, and changing the 2) frequency and/or 3) intensity of their echolocation calls (Fig. 4).

There are few accurate data on the flight speeds of foraging bats. *Myotis lucifugus* fly 5 m/s through obstacle courses in the laboratory (Griffin, 1958), and may realize these speeds when feeding. Other data on flight speeds provide similar figures (Hayward and Davis, 1964; Patterson and Hardin, 1969), but do not pertain to the speeds of foraging bats. Some bats fly much more rapidly than others, and molossids are among bats specifically identified as having rapid, direct flight (Vaughan, 1959). By flying 10 m/s while hunting, a bat using high intensity echolocation calls can reduce the warning time for a moth from 6 to 3 s relative to a bat flying at 5 m/s, assuming that the moth detected the bat at 30 m. Increased flight speeds are probably effective counters to listening insects for bats hunting in open areas (Table 1).

Pipistrellus nanus and *Rhinolophus landeri* are two bats whose echolocation calls have most of their energy above 65 kHz. This reduces by a factor of 2 the distance over which either species can be detected by some moths, relative to bats using calls with most of their energy between 20 and 50 kHz (Fig. 4). *Rhinolophus landeri* may further reduce its profile to moths by producing very directional signals, as indicated by our observations of these bats in the lab. However, it remains to be determined if this type of echolocation signal provides any real benefit to the bat in terms of alerting prey, as moths not exposed to the echolocation calls are presumably not detected by the bat. Perhaps bats with very directional orientation

Table 3. Characteristics of the echolocation calls of some bats and the distances over which they were detected by moths in the laboratory. For *Myotis lucifugus*, the moths were *Pyrrharctia isabella* and *Phragmatobia assimilis*, for the other bats, *Desmeocraera graminosa*

Bats	Echolocation calls[a]					Minimum distance from moth for detection in m
	Duration ms	Frequency		Frequency with most energy kHz	Intensity	
		High kHz	Low kHz			
Myotis lucifugus	2.5±1.2	93.2	39.6	44.2	high	>8
Pipistrellus nanus	1.2±0.3	126.4	75.4	82.2	high	>3
Nycteris macrotis	0.6±0.2	116.2	57.3	84.0	very low	0.2
Hipposideros ruber	6.3±0.1	139.4	129.5	139.4	low	1.5
Rhinolophus landeri	25.0±1.0	104.0	91.7	100.6	high	>3

[a] characteristics determined by averaging analysis of 100 calls for each species using FFT for frequencies, and a storage oscilloscope for durations

Table 4. Average diets of insectivorous bats by echolocation strategy based on studies reported in the literature. The data base allows only approximations by diets, and this is a reflection of different methods of analysis (stomach contents or feces), sample sizes and durations of studies

Echolocation strategy	Number of species studied	Number of studies[a]	Diet incidence of Lepidoptera			Impression of diets
			Mean % by volume ±SD[b]	$N_{100\%}$[c]	$MN_{0\%}$[d]	
High intensity frequency modulated (HIFM)	35 (15)[e]	45	32.4±29	1	8	Highly variable
High intensity constant frequency (HICF)	9 (3)	15	77.2±21	4	1	Variable
Low intensity (LI)	5 (4)	11	25.8±28	0	2	Highly variable

[a] These data are drawn from the following literature which does not represent a comprehensive list of studies of diets of insectivorous bats, rather a sample which we consider representative: Anthony and Kunz, 1977; Belwood and Fenton, 1976; Black, 1972, 1974; Bradbury and Vehrencamp, 1976; Buchler, 1976; Darlington, 1977; Easterla and Whitaker, 1972; Fenton, 1975; Fenton and Thomas, in press; Fenton et al., 1977; Funakoshi and Uchida, 1975; Kunz, 1974; Pine, 1969; Poulton, 1926; Ross, 1961, 1967; Vestjens and Hall, 1977; Whitaker, 1972; Whitaker and Black, 1976; Whitaker and Mumford, 1978; Whitaker et al., 1977; Wilson, 1971. The number of studies indicates the number of estimates of diet for a a species; for example, some authors report data for several species in different seasons, and we have used the figures for each species and each season. Hence, for example, 45 studies arising from 23 citations
[b] SD – standard deviation of the mean
[c] Number of studies with 100% Lepidoptera
[d] Number of studies with 0% Lepidoptera
[e] Numbers in parentheses represent species for which something is known about echolocation calls, other species probably use calls of this nature

calls cause less general warning of tympanate insects where they are feeding than those which broadcast their calls more broadly, a situation that could allow a bat to feed more effectively in a small area without alerting all of the potential prey. The fact that *R. landeri* is known to feed heavily on one species of presumably tympanate moth (*Anua tirhaca;* Fenton, 1975) may support this suggestion.

Bats in the genera *Nycteris*, *Megaderma*, *Cardioderma* and *Micronycteris* use very low intensity echolocation calls (59–65 dB SPL re 2×10^{-5} N/m² at 10 cm) and reduce the distance over which they can

be detected by moths. Furthermore, when their calls have most of their energy above 65 kHz, the detection ranges are further reduced (Fig. 4). Other species such as *Hipposideros ruber* (this study) and *H. galeritus* (Griffin, 1971) produce slightly louder calls which are still much less intense than the calls of 'typical' high intensity (110 dB SPL re 2×10^{-5} N/m² at 10 cm) bats such as *Myotis*, *Eptesicus*, *Rhinolophus* or *Tadarida*. The detection range of *D. graminosa* for *H. ruber* was less than that for a high intensity bat (*P. nanus*), but greater than that for the low intensity *N. macrotis* (Table 3).

The cost of higher frequency and/or lower intensity echolocation calls to the bats is a reduction in the effective range of echolocation, in part a function of atmospheric attenuation of high frequency sounds (Fig. 4; see also Griffin, 1971). Bats using high frequency and lower intensity echolocation calls in some areas (e.g. Côte d'Ivoire) appear to be most abundant in more closed habitats where sacrificing effective range may be less important to the bats, given the plethora of targets at close range. It is hard to accurately determine the effective range of echolocation, but Griffin (1971) estimated that *H. galeritus* did not have an effective range of more than 2 m. When the effective range of a bat's echolocation $\geq$ the distance at which the bat is detected by a tympanate moth, the advantage to the insect is probably greatly reduced.

Data on the diets of insectivorous bats do not provide a clear indication that species which should be more effective predators of tympanate moths because of their echolocation calls, actually take more moths than bats more conspicuous to these insects (Table 4). There have been no extensive dietary studies of rhinolophid, hipposiderid, megadermatid or phyllostomatine bats, although such analyses have been reported for some high intensity FM echolocators (e.g. Funakoshi and Uchida, 1975; Belwood and Fenton, 1976; Anthony and Kunz, 1977). Some of these studies have analyzed bat feces and attempted to identify as many insects therein as possible, whereas others (e.g. Black, 1972, 1974) have used only the presence of moth scales and beetle parts as markers. Studies which have examined the diets of bats over an entire season or year have shown considerable variability, but shorter studies with small sample sizes have occasionally shown very high levels of moths in the diets (Table 4). With the caveats about data on bats' diets mentioned above, and including the evidence that some insects which may have been eaten do not appear in the feces as recognizeable entities (Belwood and Fenton, 1976; Rabinowitz, 1978), there is some evidence that rhinolophids and *Hipposideros caffer* take more moths than high intensity FM echolocators. There is no indication that bats which use low intensity echolocation calls feed more on moths than other groups of bats (Table 4). Because part of the variability in the diets of insectivorous bats depends upon insect availability (Belwood and Fenton, 1976; Anthony and Kunz, 1977), on nights when moths are the most abundant prey items, bats less conspicuous to them may be more successful than those more easily detected by tympanate moths.

Insectivorous bats appear to select a mosaic of generalized and specific food types, and the rapidity with which bats exploit concentrations of insects (Fenton and Morris, 1976; Fenton et al. 1977; Gould, 1978) emphasizes the importance to bats of minimizing the time between capture of prey items, suggesting that bats are behaving as optimal foragers (sensu Pyke et al., 1976). Specializations for rapid feeding and turnover of food in bats include cheek pouches (Murray and Strickler, 1975), rapid mastication (Kallen and Gans, 1972), and short transit time for food through the digestive tract (Buchler, 1975). The first two adaptations contribute to capture rates for *Drosophila* in the laboratory of 12 per minute (Griffin et al., 1960). Bats which minimize their cost of foraging (flight time) by making short foraging sallies from a perch may be more selective in their feeding (e.g. *Hipposideros commersoni;* Vaughan, 1977) or they may not be (e.g. *Carioderma cor;* Vaughan, 1976).

The small hipposiderid *Cloeotis percivalli* whose hunting and echolocation habits are unknown, feeds extensively and almost exclusively on moths in Zambia (Whitaker and Black, 1976). Based on what is known about the echolocation calls of other hipposiderids, this species presumably uses at least high frequency, and perhaps also low intensity orientation calls when hunting and may represent an example of a specialist by virtue of the tuning of its calls.

Neurological studies have indicated that species in several families of Lepidoptera have ears sensitive to ultrasonic sound (Geometridae, Noctuidae, Pyralidae, Arctiidae, Notodontidae, Thyretidae), that some Sphingidae are similarly equipped, but that those in the families Lasiocampidae and Saturniidae lack tympanal organs (Roeder, 1974a). Our work in Africa produced no evidence of functional thoracic or abdominal ears in 5 species representing the Lasiocampidae, Saturniidae, Cossidae and Limocodidae. If all of the species of moths in families with tympanate representatives have functional ears, and vice versa, one can calculate the proportion of tympanate moths in an area. When doing this it is important to remember that only some sphingids have ears (Roeder et al., 1970). At the Ontario location where we worked, 731 of 778 species of recorded Macrolepidoptera belong to families known to have functional ears (94%), whereas in southern Africa (Pinhey, 1975), 798 of 1182 species (68%) are in families about which we have some neurophysiological data, and 240 species are in families for which no such data exist. This means that 85% of the moths in families that have been examined may have functional ears. Apart from Miller's work on lacewings, it is not known how many other groups of nocturnal insects have ears that are sensitive to bat echolocation calls. Many Orthoptera use calls with high frequency components (Sales and Pye, 1974) and may also use bat

echolocation calls to avoid being caught by bats. Rentz (1975) has suggested that some tettigoniids have special defense mechanisms directed towards bats.

Bats that use high intensity FM echolocation calls appear to comprise at least 65% of the insectivorous species, and in some regions, for example most of temperate North America, all of the insectivorous bats fall into this category. In tropical faunas insectivorous bats, primarily in the Nycteridae, Megadermatidae and Phyllostomatinae, and some Hipposideridae use low intensity echolocation calls while hunting, and some other species, primarily in the Hipposideridae and Rhinolophidae, use higher intensity calls over 65 kHz. In the Neotropics one mormoopid uses echolocation calls that are similar to those of rhinolophids, but the calls are not especially high in frequency (most of the energy below 65 kHz; Simmons et al., 1979). Some vespertilionids use low intensity calls when negotiating obstacle courses in the lab (*Plecotus townsendii*; Griffin, 1958), but it is not known if this species uses low intensity calls while hunting in the field. Gary P. Bell (pers. comm.) found that *P. townsendii* in Arizona used high intensity echolocation calls, albeit not necessarily while hunting, and similar observations are available for *Plecotus phyllotis* (Simmons and O'Farrell, 1977).

Therefore, in any region bats which use high frequency and/or low intensity orientation calls are in a minority, although they may be the most common species within some habitats. Bats using these calls for hunting appear to be absent from most of temperate North America, but the lack of data on the calls used by most species of bats when hunting precludes definite conclusions at this time. Furthermore there are few data on the flexibility of echolocation systems within species or individuals. *Tadarida brasiliensis* adjusts its echolocation calls by adding or deleting harmonics, depending upon the situation in which it is foraging (Simmons et al., 1978; Simmons, pers. comm.), but there is little information about manipulations of call intensity. In some parts of Africa *Hipposideros ruber* and *H. caffer* are considered to be conspecific (K.F. Koopman, pers. comm.), but the *H. caffer* we observed feeding in Rhodesia used high intensity calls (detectable at 10 m with a broadband microphone), and the *H. ruber* we observed in Côte d'Ivoire did not.

The variability in the hearing acuity of moths is striking, especially between species (Table 2). Add to this the "evitability" of the moths' behavioural responses (Roeder, 1975), and it is difficult to predict just when or how a tympanate moth will respond to an approaching bat. Echolocating bats can likely distinguish moths from other insects by the information available in the echoes they receive (Goldman and Henson, 1977; Schnitzler, 1978). Variability in the moths' responses is therefore adaptive as it produces a protean effect (=unpredictability; *sensu* Humphries and Driver, 1970) by not permitting an approaching bat to predictably associate targets they identify as moths with particular defensive reactions. Protean displays are probably also central to the responses of bats to sounds produced by arctiid moths (Fullard, Fenton and Simmons, 1979).

Thus most moths and some other nocturnal insects have ears tuned to the orientation calls of bats, allowing these insects to avoid many hunting bats. Success for bats or insects in the predator-prey game obviously involves other factors, including at least flight maneuverability which will influence the outcome of any interaction. By landing a moth may foil an attacking bat, but for a moth flying over water, this maneuver could be suicidal. At the same time, for a gleaning bat, a sitting moth may be an easier target than a flying one.

The interactions between bats and their insect prey provide a complex example of co-evolution that involves varability both in evasive behaviour where it serves a protean function, and in prey selection where it is associated with energetic demands. Hearing by moths or other nocturnal insects may represent an important selective pressure on the design of echolocation calls by bats.

References

Adams, W.B.: Mechanical tuning of the acoustic receptor of *Prodenia eridania* (Cramer) (Noctuidae). J. Exp. Biol. **57**, 297–304 (1972)

Anthony, E.L.P., Kunz, T.H.: Feeding strategies of the little brown bat, *Myotis lucifugus*, in southern New Hampshire. Ecology **58**, 775–786 (1977)

Belwood, J.J., Fenton, M.B.: Variation in the diet of *Myotis lucifugus* (Chiroptera: Vespertilionidae). Can. J. Zool. **54**, 1674–1678 (1976)

Black, H.L.: Differential exploitation of moths by the bats *Eptesicus fuscus* and *Lasiurus cinereus*. J. Mamm. **53**, 598–601 (1972)

Black, H.L.: A north temperate bat community: structure and prey populations. J. Mamm. **55**, 138–157 (1974)

Bradbury, J.W., Vehrencamp, S.L.: Social organization and foraging in emballonurid bats I. Field studies. Behav. Ecol. Sociobiol. **1**, 337–381 (1976)

Buchler, E.R.: Food transit time in *Myotis lucifugus* (Chiroptera: Vespertilionidae). J. Mamm. **56**, 252–255 (1975)

Buchler, E.R.: Prey selection by *Myotis lucifugus* (Chiroptera: Vespertilionidae). Am. Nat. **110**, 619–628 (1976)

Darlington, N.E.: Some aspects of the feeding habits of *Eptesicus fuscus* (Chiroptera: Vespertilionidae). Unpublished B.Sc. Thesis Department of Biology, Carleton University (1977)

Easterla, D.A., Whitaker, J.O., Jr.: Food habits of some bats from Big Bend National Park, Texas. J. Mamm. **53**, 887–890 (1972)

Fenton, MB.: Observations on the biology of some Rhodesian bats, including a key to the Chiroptera of Rhodesia. Life Sci. Contr., R. Ont. Mus. **104**, 1–27 (1975)

Fenton, M.B., Boyle, N.G.H., Harrison, T.M., Oxley, D.J.: Activity patterns, habitat use and prey selection by some African insectivorous bats. Biotropica **9**, 73–85 (1977)

Fenton, M.B., Morris, G.K.: Opportunistic feeding by desert bats (*Myotis* spp.). Can J. Zool. **54**, 526–530 (1976)

Fenton, M.B., Thomas, D.W.: Dry season overlap in activity patterns, habitat use and prey selection by sympatric African insectivorous bats. Biotropica (in press) (1979)

Fullard, J.H.: Behavioral analyses of auditory sensitivity in *Cycnia tenera* Hubner (Lepidoptera: Arctiidae). J. Comp. Physiol. **129**, 79–83 (1979)

Fullard, J.H., Fenton, M.B., Simmons, J.A.: Jamming bat echolocation: the clicks of arctiid moths. Can. J. Zool. **57**, 647–649 (1979)

Funakoshi, K., Uchida, T.A.: Studies on the physiological and ecological adaptation of temperate insectivorous bats. I. Feeding activities in the Japanese long-fingered bats, *Miniopterus schreibersi fulginosus*. Jap. J. Ecol. **25**, 217–134 (1975)

Goldman, L.J., Henson, O.W. Jr.: Prey recognition and selection by the constant frequency bat, *Pteronotus parnellii parnellii*. Behav. Ecol. Sociobiol. **2**, 411–420 (1977)

Gould, E.: Opportunistic feeding by tropical bats. Biotropica **10**, 75–76 (1978)

Griffin, D.R.: Listening in the dark. New Haven: Yale Univ. Press 1958

Griffin, D..R.: The importance of atmospheric attenuation for the echolocation of bats (Chiroptera). Anim. Behav. **19**, 55–61 (1971)

Griffin, D.R.: Expanding horizons in animal communication behavior. In: How animals communicate. Sebeok, T.A. (ed.). Bloomington: Indiana Univ. Press 1977

Griffin, D.R., Webster, F.A., Michael, C.R.: The echolocation of flying insects by bats. Anim. Behav. **8**, 141–154 (1960)

Hayward, B., Davis, R.: Flight speeds in western bats. J. Mamm. **45**, 236–242 (1964)

Humphries, D.A., Driver, P.M.: Protean defence by prey animals. Oecologia **5**, 285–302 (1970)

Kallen, F.C., Gans, C.: Mastication in the little brown bat, *Myotis lucifugus*. J. Morphol. **136**, 385–420 (1972)

Kunz, T.H.: Feeding ecology of an insectivorous bat. Ecology **55**, 693–711 (1974)

Miller, L.A.: The behaviour of flying green lacewings *Chrysopa carnea*, in the presence of ultrasound. J. Insect. Physiol. **21**, 205–219 (1975)

Miller, L.A.: Interactions between bats and green lacewings (*Chrysopa*, Insecta) in free flight. Paper presented at the Fifth International Bat Research Conference in Albuquerque, New Mexico, 8 August 1978

Murray, P.F., Strickler, T.: Notes on the structure and function of cheek pouches within the Chiroptera. J. Mamm. **56**, 673–676 (1975)

Patterson, A.P., Harding, J.W.: Flight speeds of five species of vespertilionid bats. J. Mamm. **50**, 152–153 (1969)

Pine, R.H.: Stomach contents of a free-tailed bat, *Molossus ater*. J. Mamm. **50**, 162 (1969)

Pinhey, E.C.G.: Moths of southern Africa. Capetown: Tafelberg Publishers 1975

Poulton, E.B.: British insectivorous bats and their prey. Proc. Zool. Soc. London **1929** I, 277–303 (1929)

Pye, J.D.: How insects hear. Nature **218**, 797 (1968)

Pyke, G.H., Pulliam, H.R., Charnov, E.L.: Optimal foraging: a selective review of theory and tests. Q. Rev. Biol. **52**, 137–154 (1977)

Rabinowitz, A.: Fecal analysis and its validity in determining gray bat prey preferences. Paper presented at the Fifth International Bat Research Conference in Albuquerque, New Mexico, 8 August 1978

Rentz, D.C.: Two new katydids of the genus *Melanonotus* from Costa Rica with comments on their life history strategies (Tettigoniidae: Pseudophyllinae). Entomol. News **86**, 129–140 (1975)

Roeder, K.D.: Acoustic sensitivity of the noctuid tympanic organ and its range for the cries of bats. J. Insect Physiol. **12**, 843–859 (1966)

Roeder, K.D.: Acoustic sensory responses and possible bat evasion tactics of certain moths. Can. Soc. Zool. Annu. Meeting Proc., Univ. New Brunswick, Fredricton, pp. 71–78 (1974a)

Roeder, K.D.: Responses of the less sensitive acoustic sense cells in the tympanic organs of some noctuid and geometrid moths. J. Insect. Physiol. **20**, 55–66 (1974b)

Roeder, K.D.: Neural factors and evitability in insect behavior. J. Exp. Zool. **194**, 75–88 (1975)

Roeder, K.D., Treat, A.E.: The acoustic detection of bats by moths. Paper presented at the XI International Entomological Congress, Vienna (1969)

Roeder, K.D., Treat, A.E., Berge, J.S.V.: Distal lobe of the pilifer: an ultrasonic receptor in choerocampine hawkmoths. Science **170**, 1098–1099 (1970)

Ross, A.: Notes on the food habits of bats. J. Mamm. **42**, 66–71 (1961)

Ross, A.: Ecological aspects of the food habits of insectivorous bats. Proc. Western Found. Vert. Zool. **1**, 205–263 (1967)

Sales, G., Pye, J.D.: Ultrasonic communication by animals. London: Chapman and Hall 1974

Schnitzler, H.-U.: Echolocation in Neotropical bats. Paper presented at the Fifth International Bat Research Conference in Albuquerque, New Mexico, 7 August 1978

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

Simmons, J.A., O'Farrell, M.J.: Echolocation by the long-eared bat, *Plecotus phyllotis*. J. Comp. Physiol. **122**, 201–214 (1977)

Simmons, J.A., Howell, D.J., Suga, N.: Information content of bat sonar echoes. Am. Sci. **63**, 204–215 (1975)

Simmons, J.A., Lavender, W.A., Lavender, B.A., Childs, J.E., Hulebak, K., Rigden, M.R., Sherman, J., Woolman, B., O'Farrell, M.J.: Echolocation by free-tailed bats (*Tadarida*). J. Comp. Physiol. **125**, 291–299 (1977)

Simmons, J.A., Fenton, M.B., O'Farrell, M.J.: Echolocation and pursuit of prey by bats. Science **203**, 16–21 (1979)

Simmons, J.A., Fenton, M.B., Ferguson, W.R., Jutting, M., Palin, J.: Apparatus for research on animal ultrasonic signals. Life Sci. Misc. Pub., R. Ontario Mus. (in press) (1979)

Tuttle, M.D.: An improved trap for bats. J. Mamm. **55**, 475–477 (1974)

Vaughan, T.A.: Functional morphology of three bats: *Eumops, Myotis, Macrotus*. Pub. Univ. Kansas Mus. Nat. Hist. **12**, 1–153 (1959)

Vaughan, T.A.: Nocturnal behavior of the African false vampire bat (*Cardioderma cor*). J. Mamm. **57**, 227–248 (1976)

Vaughan, T.A.: Foraging behaviour of the giant leaf-nosed bat (*Hipposideroscommersoni*). East Africa Wildl. J. **15**, 237–249 (1977)

Vestjens, W.J.M., Hall, L.S.: Stomach contents of forty-two species of bats from the Australasian region. Aust. Wildl. Rev. **4**, 25–35 (1977)

Whitaker, J.O. Jr.: Food habits of bats from Indiana. Can. J. Zool. **50**, 877–884 (1972)

Whitaker, J.O., Jr., Black, H.L.: Food habits of cave bats from Zambia, Africa. J. Mamm. **57**, 199–204 (1976)

Whitaker, J.O., Jr., Maser, C., Keller, L.R.: Food habits of bats of western Oregon. Northwest Sci. **51**, 46–55 (1977)

Whitaker, J.O., Jr., Mumford, R.E.: Foods and ectoparasites of bats from Kenya, East Africa. J. Mamm. **59**, 632–634 (1978)

Wilson, D.E.: Food habits of *Micronycteris hirsuta* (Chiroptera: Phyllostomidae). Mammalia **35**, 107–110 (1971)