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Auditory Components in the Defensive Behaviour
of Certain Tympanate Moths

by

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A thesis submitted to the Faculty of
Graduate Studies in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy.

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ABSTRACT

I used electrophysiological and behavioural techniques to analyze the tympanic organ responses of certain moths from a variety of families in south-eastern Ontario and west Africa. These analyses were used to compare the auditory characteristics of these moths as they relate to the echolocation/hunting cries of the sympatric, insectivorous bats that are their potential predators.

Moths have evolved simplistic auditory systems tuned to the frequencies most predominant in the acoustic emissions of their chiropteran predators. Moths exposed to higher densities and diversities of bat faunas exhibit increased sensitivities and wider ranges of frequencies to which they are maximally sensitive.

Arctiid moths from south-eastern Ontario that are sympatric with a limited diversity of echolocating bats possess tympana that are morphologically restricted to

be tuned to the cries of those bats. Compared with non-auditory sclerites, the arctiid ear remains more constant in size (radius) throughout the different sizes of species in the family.

Specimens of arctiid moths from this locality that I tested in early May to June possessed peripherally functional tympanal organs in the apparent absence of high levels of bat predatory activity. The relationships of audition and sound production in these moths during periods of low bat predation levels are discussed.

Two behavioural criteria show that the arctiid, Cycnia tenera Hübner, exhibits auditory threshold curves possessing maximal sensitivities at those frequencies predominant in the echolocation/hunting cries of the most common sympatric bats, Myotis lucifugus and Eptesicus fuscus. These audiograms offer a behavioural correlation to the neurological examinations of other tympanate species and illustrate the existence of behaviourally expressed intensity discrimination in these insects. The selective

advantage of the high levels of inter-individual variation present in this and another species of arctiid is discussed.

I used auditory threshold values to devise derivations which predict the distances at which the tympanic organ of a given moth will detect the echolocation cries of an approaching bat, based on certain acoustic and environmental parameters. These values, their predictions, and the neurological responses of an African moth, Desmeocraera graminosa, to the cries of sympatric bats illustrate the next possible step in bat-moth co-evolution: acoustic disguises employed by some bats to provide a countermeasure against the tympanate defenses of their lepidopteran prey.

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This thesis is dedicated to Kenneth D. Roeder

"I recognize

The moths; with great overpoise of wings

Which makes a mystery of them how at all

They can stop flying."

Elizabeth Barrett Browning

INTRODUCTION

INTRODUCTION

The lives of nocturnal creatures have fascinated and intrigued man for centuries and of all of these mysteries, the elusive and enigmatic behaviour of bats and their insect prey have provided him with one of the greatest sources of legend, fear and awe. Although the possible relationship of the seemingly chaotic flight of moths to the attacks of marauding insectivorous bats had been suggested since the 1700's (Bonsdorff, 1790; Kirby and Spense, 1826; White, 1877), and even though the tympanic organs of some moths had been described (Eggers, 1911; 1919; von Kennel and Eggers, 1933), their significance remained obscure until the present century. When the elegant experiments of Griffin and his associates (Griffin and Galambos, 1941; Galambos and Griffin, 1942) demonstrated, for the first time, the echolocation abilities of insectivorous bats, a possible source of acoustic input for these moths and their ears was provided.

Early recordings from tympanic nerves demonstrated

that the moth ear possessed a high sensitivity for ultrasonic (>20 kHz) sounds (Schaller and Timm, 1950; Haskell and Belton, 1956) but the purpose of these organs remained hidden until the studies of Kenneth D. Roeder, Asher E. Treat and their associates (reviewed in Roeder, 1967) revealed these ears for what they were: bat detectors.

The neurophysiological studies of the tympanic organ by these investigators revealed that the ears of noctuids were tympanic air sacs consisting of two acoustic sense cells (A1 and A2 cells) with one non-acoustic cell (B cell). Later studies revealed the characteristics of the ears of moths in other families (Roeder et al., 1968; Roeder, 1974a) and questioned the presumably non-acoustic role of the B cell in noctuids (Lechtenberg, 1971). Roeder and his associates demonstrated the efficient neural mechanisms used by the moths to code the acoustic input produced by hunting bats and the use of this afferent information to gauge the position and distance of the approaching predator. To these neurological studies, Roeder (1962)

added the direct observations of the free-flying behaviour of moths and the effects of bat cries on their elusiveness. The results and interpretations of these studies are well known (Roeder, 1967; 1974b; Sales and Pye, 1974; Villee and Dethier, 1976) and have served as a catalyst for investigations into auditory neural activity within the central nervous systems of tympanate moths as well as the bat-directed ears of non-lepidopterans (eg. Chrysopa spp. (Miller and Macleod, 1966; Miller, 1970; 1971). The diversity of these auditory organs within the insects studied is summarized by Roeder (1974b) and strongly suggests the polyphyletic origins of these ears.

The ears of moths and the cries of bats combine to form a uniquely simplified predator-prey relationship. By the nature of their nocturnal and volant habits, the sensory factors governing these interactions have been reduced to one: acoustic. Whereas the defensive systems of most arthropods rely on a mélange of sensory modalities (vision, olfaction), the flight response of alerted tympanate moths to bats is apparently based

solely on the auditory information contained in the signals of their chiropteran predators.

If we accept the premise that bats have served as a powerful selective force for the development and maintenance of high-frequency sound detectors in moths, we can begin to look more closely at the subtler ecological aspects of this relationship. Since the moth "sees" its predators not as distinct species nor as individuals but rather as particular acoustic images, we should expect that bats have, in some cases, evolved acoustic countermeasures to disguise their images. Just as an antennariid anglerfish has evolved methods of disguising its visual presence (Pietsch and Grobecker, 1978), some bats may have altered their acoustic presences to counteract the defenses of their tympanate prey.

Roeder (1967) demonstrated that, although there appears to be no frequency discrimination present in the acoustic sense cells of the noctuid tympanic organ, these cells do exhibit maximal frequency sensitivities.

Neurological examinations of the acoustic characteristics of a variety of moth species have revealed peak sensitivities ranging from 20 to 60 kHz (Roeder and Treat, 1957; Roeder, 1966a; Agee, 1969a; Roeder and Fenton, 1973; A. Michelsen, personal communication) corresponding to the frequencies in the echolocation signals of bats. Within the acoustic clutter of their environment, how do the sensitivities of these moths act to match these signals and what are the differences between moths living in habitats with low bat diversity as compared to those from areas of higher diversity and numbers?

Arctiid moths also possess paired tympanal organs superficially similar in morphology and innervation to those of noctuids (Eggers, 1919; Roeder, 1974b). The ears of arctiids, like those of other tympanate moths, afford a degree of protection to the insects from insectivorous bats (Agee, 1969b). Arctiid ears also respond to ultrasonic frequencies (Haskell and Belton, 1956) and, like noctuids, arctiids will execute similar evasive flight maneuvers when confronted by real or

artificial bat cries (Agee, 1969a; Roeder, 1974b; Goldman and Henson, 1977).

Certain arctiids possess an additional form of acoustically mediated defense behaviour: ultrasonic clicks that are produced when the moth is stimulated by real or artificially produced cries of bats (Dunning and Roeder, 1965; Fullard and Fenton, 1977). The sounds produced by these moths serve to deter attacks from bats in a manner still not fully understood (Dunning and Roeder, 1965; Dunning, 1968; Fullard et al., 1979).

With certain exceptions (Swihart, 1967; Simmons et al., 1971; Miller, 1975) insects have not generally proven to be suitable subjects for the behavioural substantiation of neurological auditory investigations. The behavioural responses of arctiids (sound production and flight alteration) can be used to measure the auditory sensitivity of these insects and to provide a behavioural context for the expression of neural responses previously described.

Based on the preliminary observations of Roeder (1970) that tympanate moths are frequency matched to their chiropteran predators, the purpose of this study was to examine some of the subtler acoustic relationships between moths and bats. These relationships have been explored in three primary areas. First, I have examined how the tympanal morphology reflects the acoustic matching between moths of different sizes and the bats which prey on them. Second, the study has investigated the neurological auditory characteristics of moths from two localities of greatly differing bat fauna diversities and, third, I have endeavored to place these neurological observations in a behavioural perspective by examining the responses of moths to real and artificial bat signals and to suggest potential countermeasures that bats may be using against their tympanate prey. The acoustic inter-relationship of these animals and the resultant behavioural predator-prey interactions represents a chapter in co-evolution no less intriguing than the original eighteenth-century observation of Bonsdorff:

"...during the night, scarcely a voice could be raised than they would turn round very swiftly and the antennae appear to be, as it were, convulsed." (cited in Sharp (1833))

Echolocation in the Microchiroptera

Microchiropteran bats use a wide variety of acoustic signals in their hunting and orientation behaviour, the complexity of which has only recently been discussed (Simmons et al., 1979a). Without exception, all species of Microchiroptera studied to date, employ some form of echolocation, although for most bats this behaviour has only been cursorily examined.

Within this sub-order, two "strategies" of echolocation can be discerned: frequency modulated (FM) and constant frequency (CF) type calls. Although these terms have been used, in the past, to denote a particular ecological strategy, they are, more

correctly, phrases describing the prevalent acoustic patterning of the signals being emitted by the bats rather than a categorization of the bats themselves.

Frequency Modulated (FM) Signals

Most insectivorous bats rely heavily on this form of echolocation call. It is a generally short (<10 msec.) acoustic burst sweeping from a higher to a lower frequency. The frequencies emitted are usually ultrasonic (>20 kHz) although audible echolocators have been reported. Harmonics are often associated with these cries and appear to be related to the degree of fine-line discrimination of target distance and features that the bat is interested in. Harmonic inclusion also seems to be important for bats flying in areas of high background noise. The versatility of certain FM echolocators is exemplified by Tadarida spp. which adds or filters out harmonic components in its cries, depending on the nature of the airspace surrounding it.

Constant Frequency (CF) Signals

Certain species (primarily of the Hipposideridae and the Rhinolophidae) emit calls that are characterized by some portion of constant frequency. This unmodulated segment of the signal may be either preceded or followed by some FM portion and are usually not associated with harmonics. CF pulses are used primarily by bats for determining target velocities from the Doppler shift of the echoes. Although certain bats appear to use these signals almost exclusively (e.g. Rhinolophus ferrumequinum), CF or partial CF signals are also emitted by other, typically FM bats such as Tadarida brasiliensis and Eptesicus fuscus.

Although FM and CF signals are defined as distinct acoustic designs, recent evidence indicates that both types of calls are used by a variety of bats in particular foraging situations. The flexibility of individual species appears to rely partially on genetically determined constraints which may be related

to the foraging strategy of the particular species.

Tympanic Organ of Moths

The structure of thoracic organs in moths and their relation to the thoracic nervous system has been covered in considerable detail by Eggers (1919), von Kennel and Eggers (1933), Nüesch (1957) and Ghiradella (1971). The following is a brief summary of these findings.

The ears of moths can be subdivided into those species possessing them on the metathorax and those with them on some segment of the abdomen (Table 1). Although Swihart (1967) demonstrated a sound receptive area in Nymphalidae (butterflies) and Roeder et al. (1968) reported the acoustic receptors in the facial pilifers that abutt against the palps in choerocampine sphingids, true tympanal organs have only been reported in moths belonging to the superfamilies: Noctuoidea, Notodontoidea, Geometroidea Drepanoidea and Pyraloidea (Table 1).

The ear of a noctuid consists of a thin chitinous membrane set obliquely backwards in tympanic recesses on the metathoracic segment. The membrane is partially covered by the tympanic hood, a forward projecting fold of the first abdominal segment. The tympanum is bounded by skeletal sclerites and by the conjunctivum, a thickened section separated from the tympanum by a thin sclerite, the epaulette. The ear, itself, is an air chamber (tympanic air sac) thought to be a modification of the thoracic tracheal system and is connected to the outside via the metathoracic spiracle. Within the tympanic air sac, the two scoloparia (A cells) attach to the internal centre of the membrane and are enclosed in a tracheal epithelial sheath (sensillum). The A cells proceed to the anterior end of the air sac from which they are suspended by an epithelial ligament. From here they turn towards an internal skeletal support (Bügel) where they join the third tympanic neuron (B cell) and exit the air sac. The tympanic nerve proceeds from here as IIIN1b to the main metathoracic nerve trunk (IIIN1) and to the

metathoracic ganglion.

The tympanic organs of other moths are essentially the same and differ only in their location and in the number of sense cells that service the tympanic membrane. The radically different ears of choerocampine sphingids, however, represent a totally different evolutionary form of ear which have also been demonstrated as effective bat-detectors (Roeder and Treat, 1970).

MATERIALS AND METHODS

MATERIALS AND METHODS

Study Localities

Field studies were conducted at two localities: the Queen's University Biology Station in Leed's County, Ontario, Canada ($44^{\circ}34'N$; $79^{\circ}15'W$) (hereafter referred to as QUBS) and the Lamto Ecology Station on the Bandama River in Côte d'Ivoire ($6^{\circ}13'N$; $5^{\circ}02'W$) (hereafter referred to as Lamto). Moths were collected from ultraviolet neon lights and either tested on the night of capture or stored in plastic vials. I always tested moths within three days of their capture. Bats used in acoustic stimulus experiments were captured in Tuttle traps (Tuttle, 1974) or mist nets. Moths captured at QUBS were identified from Holland (1968), Forbes (1960), Rockburne and Lafontaine (1976) and Ward et al. (1975). African specimens were identified by Dr. A. Watson of the British Museum (Natural History) where vouchers now reside. For Lamto moths, in cases of species complexes, only the species name is used in the text. Complete identifications and sample sizes are

given in Appendix IV; Figure IVa. Dr. Eugene Monroe of the Biosystematics Institute, Department of Agriculture, Ottawa and Rev. J. C. E. Riotte of the Royal Ontario Museum (presently of the Bishop's Museum, Honolulu, Hawaii) assisted me with some of the identifications.

Laboratory studies on moths were conducted at Carleton University using either specimens of Scoliopteryx libatrix or Triphosa haesitata collected, as adults, from hibernacula near Ottawa. Lab-reared specimens of Pyrrharctia isabella provided by Dr. B. Philogène of the University of Ottawa and specimens of the Cinnabar moth (Hypocrita jacobaeae) collected, as pupae, from the property of Mr. Garner, Cinnabar Valley, Vancouver Island, British Columbia were also used for some of the acoustic experiments. Moths collected for laboratory studies were housed in plastic vials and stored at 5° C. Adult H. jacobaeae were allowed to emerge from pupae kept at room temperature and tested within 3 days of emergence.

Tympanal Morphology

The following measurements were made of 18 species of arctiid moths caught at QUBS (Figures 1 and 2): 1. Tympanal radius (TR), 2. Scutal length (SL), 3. Clypeal width (CW), 4. Mesothoracic meron width (MW) and, 5. Coxal (III) length (CL). Thoracic volume was chosen as an indicator of moth size and was measured as thoracic depth (tergum to coxal-trochanter junction) times thoracic width (wing joint to wing joint) times thoracic length (anterior scutal tip to scutellar-post-notum junction).

Auditory Analyses

Neurological and behavioural tests were conducted to determine auditory threshold values for acoustic stimuli of varying intensity, structure and frequency.

Stimuli generated by an Exact Model 126 VCF/Sweep Signal Generator were either a set of continual tones from 5 kHz to 110 kHz or acoustic bursts of predetermined duration and repetition rates. Frequency

modulated stimuli were generated by means of an echolocation signal synthesizer ("OMNIBAT", constructed by Mr. A. Mitz of the Computer Division, National Institutes of Health, Bethesda, Maryland). Signals from the generators were delivered through one of two speaker systems. Low frequency stimuli (5 kHz to 40 kHz), amplified by the signal generator, were presented through a KEF T27 speaker (KEF Electronics Ltd., Tovil Maidstone, Kent, England) (frequency range: 200 Hz to 40 kHz). High frequency stimuli (45 kHz to 110 kHz) were amplified by an AC or DC powered ultrasonic amplifier (Simmons et al., 1979b) and delivered through a 7 cm. aluminized mylar, electrostatic Khl speaker (McCue, 1961) (frequency range: 20 kHz to 125 kHz). Measurements of the signal voltage (mV) were made after amplification and later converted to dB (SPL r.m.s. re. 20 μ Pa, 10 cm) (unless otherwise indicated, all dB values in this study are relative to this value; 20 μ Pa = 2×10^{-5} N/m² = 0.0002 dynes/cm²). I made conversion measurements by generating continuous tones using the aforementioned equipment and recording dB values using a Brel and Kjaer (B&K) Type 4135 1/4 inch condenser

microphone and B&K Measuring Amplifier Type 2606 (system frequency range: 20 Hz to 100 kHz $\pm$ 2 dB) (Appendix III). Stimulus frequencies were verified at regular intervals using a General Radio Frequency Counter Type 1192-B.

(Neurological Analyses) (Figure 3A)

I exposed the tympanic nerves in experimental moths using techniques outlined in Appendix I. Most exposures employed a dorsal approach to reduce the obstruction to the tympanic membrane and to allow for recording from ipsi- and contralateral auditory nerves. Unanesthetized thoracic preparations were kept moist with amphibian Ringer's Solution during the operation and acoustic trials. I mounted tapered, stainless steel, thin gauge wire recording and reference electrodes in Narishige micromanipulators and used the partially dissected thoracic flight musculature as a reference site. Since single ended amplification was used in this study, the preparations were housed within a copper screen Faraday Cage lined with 4 cm. of

sound-attenuating foam. At Lamto, the Faraday cage and associated equipment were grounded to a metal pole driven into the earth.

I obtained auditory threshold values by gradually raising the intensity of the stimulus (continual pure tone) until the first detectable change in tympanic nerve activity was monitored. Values were recorded and a new stimulus frequency chosen. Trials were duplicated and only moths that yielded two complete sets of threshold values were used in subsequent audiogramic analyses. Values were converted to dB (Appendix III) and plotted with a Hewlett-Packard 9803A Computer and 9862A Calculator X-Y Plotter.

Audiograms were analyzed with respect to the following parameters: 1. minimal threshold frequency (best frequency), 2. total sensitivity (5 kHz to 110 kHz), 3. low frequency sensitivity (5 kHz to 25 kHz), 4. low mid-frequency sensitivity (30 kHz to 50 kHz), 5. high mid-frequency sensitivity (55 kHz to 75 kHz), 6. high frequency sensitivity (80 kHz to 110 kHz) and 7.

degree of tuning (Q10 value). Sensitivity values were computed in a similar fashion to those of Masterton et al. (1968). Auditory threshold values were linearized and expressed in N/m^2 to avoid logarithmic biasing from dB values. These values were then used to compute the audiogram areas (Figure 4). Q10 values were computed by the following formula:

$$Q10 (bf) = bf / bw (10 \text{ dB})$$

where:

$bw (10 \text{ dB})$ = bandwidth (kHz), 10 dB above threshold at
best frequency

bf = best frequency

Auditory comparisons were analyzed with non-parametric comparisons of means (Sokal and Rohlf, 1969) or parametric comparisons of means with heteroscedastic samples (Time Sharing Statistical Library- Carleton University Xerox Sigma 9 Computing Services).

Neural Response to Echolocation Cries

Moth ear preparations were exposed to the echolocation cries of sympatric, insectivorous bats, both recorded and live. Recordings of Myotis lucifugus and Eptesicus fuscus (Vespertilionidae) were made using an ultrasonic microphone (Simmons et al., 1979b) and a Lockheed Store 4D Instrumentation Tape Recorder operated at 76 cps (system frequency range: 10 kHz to 140 kHz). Recordings were then amplified and played to the ear preparations of Pyrrharctia isabella using the Khl speaker. Live bats (Myotis lucifugus) were released in the the laboratory at QUBS and allowed to fly near the preparation of Phragmatobia assimilis while tympanic nerve response was monitored. The dimensions of the lab room were 5 m. x 3 m. allowing a maximum distance attainable from the moth of 4-5 m. At Lamto, the following bats were allowed to fly in a 4 m. x 3 m. laboratory with the ear preparation of the notodontid, Desmeocraera graminosa: Pipistrellus nanus (Vespertilionidae), Hipposideros ruber (Hipposideridae), Nycteris macrotis (Nycteridae) and, Rhinolophus landeri (Rhinolophidae). In addition to the

lab studies in Côte d'Ivoire, moth ears of this species were also exposed to the cries of hunting bats on the banks of the Bandama River approximately 500 m from the station.

Nerve responses were recorded on a separate channel of the Lockheed tape recorder and analyzed with a Tektronix Dual-beam Storage oscilloscope Type 5103N.

(Behavioural Analyses) (Figure 3B)

Specimens of the arctiids, Cycnia tenera and Hypoprepia fucosa were captured at the Queen's University Biology Station from UV lights for the study. These species were chosen for the study because of their low level of habituation and high responsiveness (Fullard, 1976).

Unanesthetized moths were manually restrained while their thoracic terga were brushed free of scales and hair in preparation for mounting. The moths were fastened to the head of a dissecting pin with a drop of

adhesive wax (Cenco Softseal Tackiwax) so as to ensure the free movement of the wings. The specimen was then suspended in a normal, head-forward position 10 cm. above a 7 cm. Kühl speaker. Stimulus for the trials consisted of a train of 10 msec. bursts delivered at a rate of 10/sec from the Exact Signal Generator (spectral analyses of the pulses revealed negligible side-band energies in stimulus frequencies of 25 kHz and greater). The pulse train was amplified by a AC amplifier and fed to the speaker. Trials were conducted at night in red-light conditions to minimize observer interference. I used two forms of response (sound production and flight cessation) as the behavioural criteria in the tests.

(Sound Production)

Sound production by the moth was monitored with a Brüel and Kjaer 1/4 inch condenser microphone Type 4135 mounted within the sound field of the speaker. The clicks from the specimen were amplified by a Brüel and Kjaer Measuring Amplifier Type 2606 and displayed on a

Tektronix 5103N Oscilloscope (cf. Fullard and Fenton, 1977). This system was later used to determine the intensity (dB SPL) of the stimulus. Six Cycnia tenera and four Hypoprepia fucosa were tested using the following procedure: A specimen was prepared and mounted above the speaker and left for 5-10 min. Stimulus frequency for the trial was chosen in a random order between 20 and 100 kHz before the trial began. With the generator set at maximum attenuation, the stimulus was initiated and the intensity increased by 5 dB/sec until sound was produced by the moth (Figure 5). The intensity was then decreased until the moth ceased to respond. Threshold intensity was taken to be the average between the two values.

(Flight Cessation)

Four different specimens of C. tenera used for the flight cessation trials were mounted as previously described and directed towards a low-noise fan which generated an air flow of approximately 7-8 cm/sec. Moths were shielded from the air stream until the trial

began. The trials employed the following procedure: With the specimen facing the shielded air stream, the stimulus frequency was chosen and set on the signal generator. I then removed the shield which generally induced stationary flight in the moth (only those specimens which initiated sustained flight were further tested). The stimulus was applied as for the sound production trials and flight cessation was determined as that point at which wing movements completely ceased. This was preceded by a period of erratic fluttering flight associated with extensive antennal and abdominal movements and sound production. Upon lowering the stimulus the specimen would generally resume flight permitting the determination of a lower value. After threshold was determined the barrier was replaced and the specimen allowed to rest while a new frequency was chosen.

Echolocation Signal Analyses

The echolocation cries of temperate and tropical bats were recorded onto the Lockheed tape recorder with

an ultrasonic microphone (Simmons et al., 1979b). A 10 kHz high pass filter was used at QUBS to eliminate low-frequency background interference.

Signals from the bats were analyzed by a Princeton Applied Research Fast Fourier Transform (FFT) Real Time Spectrum Analyzer Type 4513. The PAR analyzer is a digital FFT instrument able to capture and analyze the short duration, high frequency signals of the bats when played into the machine at 1/8 tape speed. Spectra were individually analyzed or were automatically averaged and displayed on a linear or logarithmic intensity scale and reproduced from a Tektronix 604 Monitor Screen with a Nihon Koehden PC-3A Oscilloscope Camera.

Echolocation signals of hunting bats in both localities were monitored with a portable zero-crossing meter and a Non-linear Systems MS-15 "Miniscope" oscilloscope (Simmons et al., 1979b). Bat activity was monitored from the oscilloscope and recorded as bat passes/minute (Fenton et al., 1973).

RESULTS

RESULTS

Tympanal Morphology

A comparison of the relative dimensions of tympanal and non-auditory sclerites is shown in Figure 6. The proportionate increase in size for each of the sclerites as a function of the smallest species measured is plotted against the natural logarithm of the thoracic volume for each of 18 species measured at QUBS. The four non-auditory sclerites (mesothoracic meron width, clypeal width, coxal (III) length and scutum length) increase in size at a significantly greater rate with body size than tympanal radii which retains a greater degree of uniformity within the different sizes of moths measured ($p < .001$, analysis of covariance, Sokal and Rohlf, 1969).

Certain large species (eg. Apantesis nais) possessed tympana with radii that were slightly smaller than the smallest moth measured while exhibiting a greater than two-fold increase in meron width.

Uniformity in tympanal size was not limited to arctiid moths. The largest species measured was a noctuid, Catocala amatrix (Hübner) which had a thoracic volume nearly 23 times that of the smallest moth yet possessed a tympanal radius of only 1.5 times the size of that of the small species.

Measurements taken of arctiid specimens collected in Africa could not determine conclusively whether or not a similar degree of uniformity exists within moths exposed to a greater diversity of echolocation signals.

Auditory Analyses

(Neurological)

The main difficulties associated with the neurological techniques (Appendix I) pertained to the viability of the tympanic nerve, although suitable preparations could be maintained from 20 to 90 minutes

depending on the age and size of the specimen tested. Older moths and smaller species tended to give weaker signals, usually associated with a higher level of background interference. Preparation viability was best ensured by reducing to a minimum the time that the nerve spent exposed to the air and could be accomplished by returning the draped nerve to the physiological saline solution between stimulus trials and by keeping the tension on the nerve as low as possible. The tympanic nerve of very small species would generally tolerate no more than one to two minutes exposure to the air and even with repeated bathings in saline solution yielded less than 15 minutes of recording time.

Neurological preparations of Pyrrharctia isabella produced reliable results owing to its large size and good condition (lab-reared specimens). The types of response were typical of those I obtained from other North American species and included spontaneous tympanic nerve activity from specimens under no acoustic stimulation. Spontaneous activity was

characterized by the regular firing of the B cell (Figure 7a) and the less regular activity of the smaller amplitude A1 cell. The large spikes in Figure 7a represent B cell activity which had a spike rate, in one specimen, of 12-18/sec. This rate was usually remarkably constant over periods of time up to 60 minutes and changed only when tension was applied to the nerve or to the skeletal sclerites surrounding the tympanic membrane (Treat and Roeder, 1959). Different specimens exhibited large variation in this A1 cell activity with values ranging from 5 to 30 spikes/sec. B cell activity, as well, was variable between specimens and in some preparations, B cell spikes were not observed. Spontaneous A1 cell activity could be inhibited in P. isabella by very intense acoustic stimuli which elicited A2 spikes (smaller in amplitude than A1 cell spikes). Figure 7b shows the decrease in spontaneous A1 activity following the exposure to an A2-evoking stimulus. After the stimulus was terminated, spontaneous A1 activity resumed its pre-stimulus level after a period of about 6 seconds.

A1 cell activity was easily evoked by varying forms of acoustic stimuli ranging from jingling keys to pure tone continual or pulsed ultrasonic stimuli. Adaptation was evident and typical in A1 response to continual pure tones as illustrated in Figure 8. A1 response to pulsed stimuli is shown in Figure 9. The duration and intensity of the stimulus were coded by the A1 spike pattern which appeared to accomodate to increasing durations of stimuli (Figure 10), with stimulus durations of approximately 70 msec. eliciting A1 cell responses of almost equal duration. Although no precise measurements were taken, the A2 cell appeared to be 10-20 dB less sensitive than its A1 companion. There was no obvious response of the B cell to prolonged or intense stimuli as reported by Lechtenberg (1971) nor was there evidence of hysteretic patterning (Suga, 1961) on the part of the A1 cell although the acoustic trials in the present study were not specifically designed to detect these subtler nervous responses.

The tympanic nerve response of Scoliopteryx

libatrix (Noctuidae) and Triphosa haesitata (Geometridae), species taken from hibernacula near Ottawa during the winter, are illustrated in Figure 11 a and b. These observations demonstrate that T. haesitata possesses a peripherally functional tympanic organ that exhibits similar auditory threshold characteristics (Appendix IV, Figure IVa; o) to those described for Scoliopteryx libatrix (Roeder and Fenton, 1973). As the baseline level in Figure 11b shows, there is generally more background interference encountered when recording from the tympanic nerve of geometrids. Coupled with this low signal/noise ratio is the added neural input of the two additional acoustic cells in geometrids (Roeder, 1974a). Threshold curves were measured from the first cells to respond to the stimulus (presumably the A1 cell). In most of the tests, T. haesitata proved to be too small a species to tolerate detailed analyses of the spike activity from its tympanic nerve. In addition to the arctiids tested at QUBS, the thyaterid moth, Euthyatira pudens was captured and tested. This uncommon species possesses a geometrid-like tympanic nerve response with at least 4

cells responding to high intensity stimuli (Figure 12). The tympanic nerve of this species is not a separate fiber that runs alongside the abdominal connective as in geometrids. Rather, it appears to join the thoracic-abdominal connective immediately upon exiting from the tympanic air sac. This necessitated recording from the connective which resulted in a substantial amount of afferent abdominal neural interference.

Table 2 describes the audiogram characteristics of those moths surveyed at QUBS and Lamto during the spring and summer of 1978. As Figure 13 illustrates, all of the arctiid moths surveyed in the spring at QUBS possessed peripherally functional tympanic organs that exhibited similar auditory curves (Appendix IV, Figure IVa; a-j). The audiogram analyses of the moths surveyed at QUBS and Lamto and the comparisons between the two localities are summarized in Table 3. Moths from QUBS were tuned to a significantly lower frequency (30.4 kHz) than were those from Lamto (37.8 kHz) and Ivorian moths revealed a much higher interspecific variability in their best frequencies. Some moths from

Lamto possessed best frequencies as high as 100 kHz whereas no species nor individual tested in QUBS was tuned to frequencies higher than 50 kHz.

Computation of sensitivity values for moths from both localities indicate that, over the total frequency range tested, Ivorian moths possessed a significantly higher sensitivity than those surveyed at QUBS, the difference being greatest at the high mid-frequency and high frequency ranges (Table 3; Figure 14). Moths from both localities exhibited the lowest degree of variation at those frequency ranges that contained their best frequencies and for Ivorian moths this low variance remained at higher frequency ranges than for those species surveyed at QUBS.

Sensitivity appears to be related to the number of acoustic sense cells servicing the tympanic organs for those species tested in Côte d'Ivoire (Figure 15, Tables 4 and 5). This increase in sensitivity is due to a proportionately greater sensitivity for lower

frequencies than for any other part of the spectrum. I was able to analyze only geometrids as representative of species possessing four A cells from the moths sampled at Lamto. Geometrids were generally the most sensitive of the species that I analyzed although background nervous interference and the contribution of the four cells made some analyses difficult and many specimens would not yield enough data for two complete trials. Certain unineuronated species (eg. Thyretidae) characteristically possessed very low sensitivities over the entire frequency range. Specimens from this family also exhibited the highest incidence of total and partial deafness. There is no conclusive way, however, in the present study to ascertain that the innervation in the tympanic organs of Ivorian moths necessarily follow the taxonomic extrapolation of those species studied in North America.

The degree of tuning or the sharpness of the A1 cell audiogram is expressed as a function of its Q10 value. As this value decreases, the audiogram broadens out at its best frequency (minimum threshold). Q10

values (Figure 16) reveal that moths of both localities possess broad tuning curves with the specimens from QUBS exhibiting somewhat lower values than those from Lamto. Again, certain families tested revealed characteristic Q10 values with geometrids and arctiids generally possessing the sharpest tuning and african thyretids and notodontids exhibiting the broadest curves.

Neural Response to Echolocation Cries

Figure 17 shows the response of Pyrrharctia isabella to the recorded echolocation cries of the sympatric bat, Myotis lucifugus as played from a 7cm. Khl speaker held 30cm. from the preparation. In responding to the cries of M. lucifugus, P. isabella exhibited a latency of approximately 14 msec. with a slight afterdischarge. The response to double pulses appears to be in the form of longer duration spike bursts. An interesting response is given to a feeding buzz (Figure 17c). As the bat begins its buzz, the amplitude of its individual pulse envelopes decrease as

the repetition rate increases. These lower intensity pulses are reflected in the reduced spike numbers elicited in the tympanic nerve. The arctiid, Phragmatobia assimilis, could monitor the echolocation cries of this species as it flew 4 m. from the moth (maximum distance obtainable in the laboratory).

In Côte d'Ivoire, ear preparations of the notodontid, Desmeocraera graminosa, exhibited a differential ability to detect the echolocation cries of four species of insectivorous bats (Figure 18; Table 6). Pipistrellus nanus was detected as it flew anywhere within 4 m. (maximum distance obtainable) from the preparation as was Rhinolophus landeri. Desmeocraera graminosa detected the cries of P. nanus as the bat flew in most directions relative to the moth but was less able to detect the signals of R. landeri when this bat was not flying directly towards the ear preparation (a phenomenon also exhibited by the ultrasonic microphone monitoring the echolocation signals of the bats (Figure 19)). Desmeocraera graminosa could detect the cries of Hipposideros ruber

less frequently and only when the bat was flying directly towards the moth within a distance of 1.5-2.0 m. Nycteris macrotis was the least detectable bat and was picked up by the tympanic preparation only when the bat was 20 cm. from the moth and flying directly towards it.

Audiograms derived from each of the D. graminosa specimens used in the four playback trials indicated no gross differences in sensitivity that might have accounted for the differential ability to detect the different bats in the trials (Figure 20; Table 6).

A specimen of D. graminosa was also taken to the banks of the Bandama River near Lamto and monitored to assess its ability to detect the low frequency cries of unidentified bats (possibly molossids) hunting over the river. Figure 21 shows that these cries were detected by the moth as the bats flew approximately 5-10 m. from the preparation. FFT analyses of these signals indicated at least two species, one with a predominant spectral peak at 18 kHz and another with a

peak at 16 kHz. In addition to differences in frequencies, pulse envelope differences can be seen in the microphone traces in Figure 21.

Behavioural Analyses

Figures 22 and 23 illustrate the resultant auditory curves for both behavioural criteria used in the trials with Cycnia tenera. The reliably low incidence of intra-individual variability coupled with the higher levels of inter-individual variation suggest that lumping the data together to construct a "typical" audiogram for both criteria would obscure the observation that individual moths possess, in most cases, individually distinct tuning curves.

In the sound production trials, Cycnia tenera was highly responsive to acoustic stimuli for extended periods. Habituation, whether due to fatigue or other factors, became apparent after approximately 45 minutes of testing and was marked by a sudden drop in responsiveness. It was this constraint which limited

testing to two trials per specimen (for sound production) and one trial per specimen (for flight cessation). The audiograms suggest that most of the specimens were maximally sensitive to frequencies between 30-50 kHz although one specimen revealed a threshold minimum at 56 kHz (Figure 22).

Flight cessation was generally a less reliable criterion in the trials. Some moths would not cease flying under the maximum intensity that the amplifier was capable of while others fatigued quickly and would not resume flight when re-exposed to the air stream. Of the four moths that yielded sufficient data, the audiograms (Figure 23) do not convincingly reveal any particular tuning although one specimen was markedly sensitive at 40 kHz. What these audiograms do illustrate, however, are higher threshold values (13-25 dB) than those obtained using sound production as the criterion. Since sound production was observed during the response behaviour leading to flight cessation, it can be assumed that the differing stimulus intensities required to elicit the two criteria are representative

of differences required to elicit the respective behaviors under natural conditions.

The lithosiinid arctiid, Hypoprepia fucosa yielded sufficient data from sound production trials to construct auditory threshold curves. Although the lumped data (Figure 24) show high levels of variation for each frequency, there appears to be a maximum sensitivity at 40 kHz. Flight cessation trials were not possible with H. fucosa owing to its reluctance to resume stationary flight under experimental conditions.

Echolocation Signal Analyses

Table 7 summarizes the acoustic parameters of the echolocation signals emitted by those bats that were sympatric with the moths tested at QUBS and Lamto. Myotis lucifugus and Eptesicus fuscus emit cries with maximally intense spectral peaks between 25 and 45 kHz (Figures 25 and 26) but species recorded in Côte d'Ivoire exhibited a far greater range of dominant

frequencies and structural parameters (Figures 27 and 28). In-field monitoring of hunting bats indicates echolocation activity with a maximum energy at QUBS of 30-40 kHz which is similar for sites monitored at Lamto. Spectra from Lamto, however, possess considerably more echolocation activity at lower (<20 kHz) and higher (>70 kHz) frequencies (Figure 29).

Maximum Detection Distances

The maximum theoretical distance at which moths could detect the echolocation cries of bats (MDD's) were computed for certain Ivorian moths (Figure 30) and illustrate the effects of 1) initial bat intensity, 2) signal frequency and 3) relative humidity on the detection ability of those moths. As the dominant signal frequency moves farther from the threshold minima of the moth, there is a corresponding decrease in the MDD for that moth. This effect can be compounded by lowering the initial bat intensity (stimulus dB) until at some point the MDD becomes of such low value as to be of no use to the moth. High

relative humidity (Figure 31) has the effect of increasing low frequency MDD's and decreasing high frequency MDD's due to the differential attenuation rates of these frequencies under the same relative humidity. These effects are most apparent for species exhibiting low sensitivities and do not affect the centre frequency ranges to the same degree.

DISCUSSION

DISCUSSION

Tympanal Morphology and Resonance Characteristics

The uniformity of tympanal radii within the species of arctiids surveyed at QUBS (Figure 6) may indicate some of the biophysical features of the moth ear. Michelsen (1971) analyzed the resonance characteristics of the tympanum of the locust in an attempt to correlate the vibrational properties of the tympanal membrane with the auditory sensitivities exhibited by the tympanic nerve. Michelsen (1971) argued that a tympanum acts like an approximation of a circular membrane and its resonance characteristics should be predictable and indicative of the frequencies at which the tympanum vibrates at its maximum amplitude (Johnstone et al., 1970; Loftus-Hills et al., 1971; Dragsten et al., 1974; Paton et al., 1977). Reasonably accurate predictions of the locust ear sensitivities were computed using the formula for circular membrane vibrations (Morse, 1948):

$$f(01) = 0.383 \times 1/a(\sqrt{T/\sigma})$$

where:

$f(01)$ = fundamental resonance
frequency (Hz)

a = tympanal radius (m.)

T = tympanal tension (N/m^2)

σ = tympanal mass (kg/m^2)

with second, third and fourth resonance frequencies at 2.296, 3.599 and 4.903 times $f(01)$, respectively.

If we assume that within a closely related group of insects the cuticular characteristics will not substantially vary (Morris and Pipher, 1967; Michelsen, personal communication), we should expect that the tympanal radius will be one of the principle components of its resonance characteristics. Simply put, the larger a circular membrane is, other parameters being equal, the lower its fundamental frequency becomes. For a group of insects possessing similar auditory organs, larger species should possess larger tympana and be correspondingly tuned to lower frequencies. This should not be the situation, however, for moths with ears selectively tuned to the same

signals (echolocating bats). Where a common predator is the source of selection pressure for the ears of a group of prey, the predominant frequencies to which the tympana are tuned should change less with the size of the species. This may explain the observation that non-auditory sclerites (body parts not associated with acoustic reception) increase in size with the average body size (thoracic volume) but tympanal radius does not. Although this is a relationship that should apply to all tympanate moths, there may be other factors influencing the tuning curves of more distantly related species. By examining the relationships of body size to tympanal radii within the Arctiidae captured at QUBS, one can be more confident in assuming other parameters are likely to be constant.

If we use Morse's (1948) resonance formula and substitute both known and extrapolated values for an arctiid tympanum the following calculation can be made:

$$f(01) = 0.383 \times 1/a(\sqrt{T/\sigma})$$

where (for Spilosoma prima):

$$a = 0.00023 \text{ m. (average, } n=10)$$

$T = 0.28$ (assume similar value as
for locust, Michelsen (1971))
 $\sigma = 0.00292$ (locust x proportionate
decrease in tympanum size
for S. prima)

therefore:

$$\begin{aligned} f(01) &= 0.383 (1/.00023) (\sqrt{.28/.00292}) \\ &= 16,306.42 \text{ Hz} \end{aligned}$$

The computed resonance frequency for this species would therefore be 16-17 kHz. This value agrees with averaged audiogram for S. prima (Appendix IV; Figure VIa; b)

If we compute the second, third and fourth harmonic resonance frequencies from this value we derive:

$$f(02) = 37.4 \text{ kHz}$$

$$f(03) = 58.7 \text{ kHz}$$

$$f(04) = 79.9 \text{ kHz}$$

The audiogram for S. prima shows a prominent increase in sensitivity at 80 kHz and may represent the fourth harmonic resonance for this species. Similar double-troughed audiograms are present for the

congenerics, S. congrua and S. virginica and are also evident in some Ivorian species. A more detailed frequency analysis at 1 or .5 kHz increments might serve to better illustrate the subtler sensitivity increases related to harmonic resonances.

The vibrational properties of the tympanum are not the only source of tuning for the ear that has been investigated. Adams (1972) demonstrated that the mechanical tuning of the scoloparium within the tympanic air sac of the noctuid, Prodenia eridania accounted for a maximal sensitivity at 2, 14 and 60-70 kHz. Michelsen (personal communication) has examined the vibrational characteristics of a European noctuid tympanum with laser vibrometric measurements and has found a correlation between neurological and vibrational parameters with a maximum sensitivity at 25 kHz. Adams (1972) suggested that resonance characteristics of the moth tympanum might serve to dampen the low frequency sensitivity exhibited by the scoloparium (a 2 kHz sensitivity being of little use in detecting echolocation signals) and would play a major

role in determining the frequency curve for the whole tympanic organ.

The relative simplicity of the moth tympanum offers an ideal model for the correlation of vibrational and neurological characteristics. Orthoptera and certain vertebrates are favoured subjects for analyzing these relationships (Michelsen and Larsen, 1978; Larsen and Michelsen, 1978; Moffatt and Capranica, 1978) but these systems suffer the major disadvantage of being multineuronal. Notodontid moths possess almost completely circular tympanic membranes with only one acoustic sensillum attached to the centre and would offer an opportunity to examine one of the closest approximations to a circular membrane in nature. The problems associated with moth ears are primarily related to accessibility of the membrane. The use of large species and recent developments in inexpensive vibration analyses (Masters, 1979) strongly favour the unineuronal tympana of moths as subjects for these investigations.

Auditory Comparisons

The relationship between the auditory characteristics of tympanate moths and the echolocation/hunting signals of sympatric, insectivorous bats is largely one of frequency matching although this aspect has not been extensively investigated. In eastern North America, this relationship is comparatively simple with moths exhibiting auditory sensitivity curves matched to the spectra present in the cries of the most common bats encountered by those moths (eg. Myotis lucifugus and Eptesicus fuscus). Frequency analyses of the cries of these bats (Figures 25 and 26) reveal spectra with maximum energy at 25-45 kHz, corresponding to the audiograms (neurological) (Roeder, 1970; present study) and behavioural (present study) of moths sympatric with these bats. Comparisons of the acoustic characteristics between moths from an area of low bat (i.e. echolocation strategy) diversity and those from localities with higher diversities may suggest something of the co-evolution of this relationship.

Total acoustic sensitivity is higher in Ivorian moths, presumably, as a result of two factors. First, the higher density of the Ivorian bat fauna places a greater predation pressure on sympatric moths and increased auditory sensitivity should occur in moths having to cope with greater numbers of potential predators. Second, where the increased diversity of bats is coincident with a greater array of echolocation strategies (eg. the Old World tropics), moths face additional problems associated with this more diverse acoustic output. At Lamto, the incidence of bats echolocating at very high and relatively low frequencies is much greater than for analysis made at temperate study sites (Figure 29). The increased energy present in higher frequency ranges appears to be countered by the significantly increased sensitivities of Ivorian specimens at these ranges. The lack of difference in sensitivity at low frequencies for moths from both localities presents somewhat of a contradiction. On one hand, the similarity in sensitivities may be due to the fact that low frequency

bats appeared to hunt exclusively over the Bandama River, a habitat not likely to be used extensively by lepidopterans. On the other hand, confounding this hypothesis is the observation that, in Ivorian moths, sensitivity at low frequencies increased with the number of acoustic sense cells servicing the tympanum. The reasons why geometrids, the species possessing the greatest number of A cells, favoured low frequency sensitivity is unclear but may be related to the degree of sympatry between bats and their potential moth prey. Although no obvious preference of moths for a particular habitat (savannah over forest) was observed, there may be subtler tendencies for moths to remain in habitats where their particular auditory characteristics are best matched to the echolocating bat community in that area. By this reasoning, we might expect more geometrids in areas frequented by lower frequency bats.

Another factor contributing to increased sensitivity in Ivorian species may be the presence of low intensity (i.e. <60 dB, 10 cm) echolocating bats

(eg. Nycteris spp.). Frequency analyses of hunting bats were biased in Côte d'Ivoire by the high numbers of presumably echolocating species that were visually, but not acoustically monitored (Fenton and Fullard, in preparation). A higher incidence of low intensity signal emitters may be important in selecting for increased sensitivity in moths. Since low intensity bats are also known from some North American localities (eg. Macrotis spp. (D. R. Griffin, personal communication); Myotis auriculus (Fenton and Bell, in press), it might be reasonable to expect higher sensitivities in moths sympatric with these species if these bats are numerous enough to form a significant selection pressure.

A reflection of the response of tympanate moths to the variability of echolocation calls encountered may be evident in the broad tuning curves observed for moths tested at both localities. The average Q10 values computed for moths with best frequencies at 30 kHz (QUBS: 1.00; Lamto: 1.51) are considerably less than those reported from some vertebrate single units with

the same best frequency (Antrozous pallidus: 3.4-4.9 (Brown et al., 1978); Myotis lucifugus: 2.5-5.0 (Jen, 1978)). For moths of both localities, selection would favour ears with broad enough tuning curves to detect the widest possible bandwidth of echolocation frequencies. An important question arising from this is the variability and flexibility of echolocation signals used by individual bats. Figure 25 illustrates the difference in harmonic composition in the echolocation cries of two recordings of Myotis lucifugus. Variation in frequency spectra have also been reported for Plecotis phylotis (Simmons and O'Farrell, 1977); Eptesicus fuscus (Simmons, 1971); Tadarida spp. (Simmons et al., 1978) and individual signal variability may be widespread. Increased tuning broadness should occur in moths that are exposed to bats using higher levels of individually expressed signal flexibility as well as greater interspecific variation.

Roeder (1970) described the acoustic relationships between the auditory threshold curves of noctuids and

the spectral peaks of the echolocation cries of unidentified insectivorous bats (probably Myotis lucifugus). The audiograms prepared from both neurological and behavioural frequency trials with moths collected at QUBS also reveal this matching. There are eight species of bats recorded in the vicinity of QUBS with Myotis lucifugus and Eptesicus fuscus comprising over 95% of the bats during the summer (M. B. Fenton (personal communication), T. M. Harrison (unpublished data)). In southeastern Ontario, dominance by two species (and their similar echolocation spectral patterns) of the bat predator community corresponds to the auditory tuning of potential moth prey and to their ability to detect sympatric predators. If the spectra of orientation calls of M. lucifugus and E. fuscus are similar throughout their range, the dispersion of tympanate moths would not be limited by the lowered fitness of individuals more poorly equipped to detect these species. Although the individual echolocation cries of a number of North American bats (Simmons et al., 1979a) have been analyzed, there are few data on the

collective spectra exhibited by different bat faunas. This accumulative spectrum of individual habitats is the acoustic "Umwelt" of the tympanate moths that live there. Regardless of the fact we can ascertain what the spectral peaks of a given species are, this information becomes meaningless when interpreting the audiograms of moths if the bat is not sympatric with the moth in question. By assessing all of the potential predator acoustic patterns in an area, one is able to determine the spectral pattern to which a tympanate moth should tune itself. Conversely, by determining the audiogram of a moth one has, to a degree, defined that moth's acoustic environment and therefore, to which bat calls it is most sensitive. Although tympanate moths possess broad tuning curves and are able to detect a wide range of ultrasonic frequencies, there are peak sensitivities at which selection has maintained these moths to avoid the greatest number of echolocating predators.

There are complications inherent in the matching of moth audiograms to echolocation spectra. The cries of the piscivorous bat, Noctilio leporinus, would not

likely bear much importance to the ears of moths volant during periods when N. leporinus preys exclusively on fish (Howell and Burch, 1974). Nevertheless, these cries may comprise the largest proportion of the acoustic energy generated in certain habitats (eg. flight paths to feeding sites). Noctilio leporinus emit CF calls with fundamental frequencies at 58 to 61 kHz (Suthers, 1965). Sympatric with this species but possibly outnumbered by it in the aforementioned localities is Tadarida braziliensis that echolocates with search cries at around 40 kHz (Simmons et al., 1978). If we assume that T. braziliensis would be feeding more heavily on insects than N. leporinus, moths sampled from this area should possess audiograms appropriately matched to the signals of T. braziliensis (and any other insectivorous species echolocating at similar frequencies). These audiograms, however, would be considerably mismatched to the accumulative spectra exhibited in those localities heavily populated with N. leporinus. Similarly, the most commonly monitored signals in a given locality may be from bats not likely to prey on moths but may be of the same spectral design

as those to which the moths are tuned and may therefore mask the true predators of those moths (eg. the 38 to 42 kHz cries of the sanguivorous species Desmodus rotundus (Novick, 1963) in the previously described situation). Generally, it appears that the broad tuning exhibited by moths is an acoustic compromise to detect as many potential predators as possible and that moth ear audiograms can serve as a valuable bio-assay in assessing the predator community of those moths.

Maximum Detection Distances

The maximum detection distances (MDD's) reveal something of the relationship that echolocation signal parameters have with the bat's conspicuousness to a particular moth ear. Using the conversion formulae outlined in Appendix II, the arctiid, Phragmatobia assimilans, will possess a MDD of 27.4 m. for a bat whose spectral peak is at 30 kHz (one of the assumptions of MDD computation is that tympanic response is representative of a perceived response). This value is close to those reported by Roeder (1966a)

for noctuid moths monitored in the field (28-40 m. for one specimen; 32-40 m. for another). MDD's are subject to a variety of factors, only three of which (frequency, initial intensity and environmental relative humidity) have been explored here.

Lowering the emitted intensity has the effect of reducing the acoustic signal or cue that the moth has to respond to. As the emitted intensity is reduced, there is a corresponding logarithmic reduction in the distance that the ear will first detect the cry. Using the previously described bat-moth interaction, if the 30 kHz bat were to reduce its emitted cry from 110 to 90 dB the MDD reduces from 27.4 m. to 10.0 m. Corresponding to this MDD shift, however, the detection distance of the bat will also be reduced. If we assume that 2 m. is the average perception range for a high intensity echolocator (Griffin, 1958), this reduction in the moth's MDD would still maintain it outside of the perception range of the bat. A poorly understood component in these interactions is the distance at which echolocating bats detect their prey and how this

range is affected by their initial signal intensity. If the perception range of the bat reduces at a lower rate than the corresponding MDD of the moth, there will be an optimal signal intensity for the bat that would reduce the moth's MDD to within the range of the bat. The absence of "whispering" bats from southeastern Ontario may be a function of prey availability. Since the largest proportion of the diet of Myotis lucifugus consists of dipterans (Ross, 1967; Whitaker, 1972; Belwood and Fenton, 1976; Anthony and Kunz, 1977) or ephemeropterans (Buchler, 1976), it appears that this species of temperate bat has maintained its high intensity signals and relies heavily on non-tympanate prey.

By employing an echolocation cry with frequency components that are substantially mismatched to the auditory sensitivity curve of a moth, a bat can also theoretically reduce the MDD of its prey. Selection might therefore, favour bats that tended to minimize their MDD's by employing signals of higher frequencies than the average bat (the acoustic spectral peak of the

given habitat).

There are counter-selective forces stemming from the same parameters that govern the MDD's, however. Since high frequencies attenuate more rapidly in air (Griffin, 1971), a bat using them would expend more energy in both producing the signal and in perceiving the attenuated echo. Very low frequency signals, on the other hand, possess the disadvantage of containing less detailed information in the echoes. The same general spectral peaks for both QUBS and Lamto (25-50 kHz) suggests that for most echolocating bats, these frequencies are the compromise and, correspondingly, the frequencies to which the majority of moths are tuned to. There are therefore, limitations or physical restrictions that have been placed on the evolution of echolocation signal parameters of bats. Bats employing atypical or "difficult" forms of signals could forage in areas of high prey density where the reduced perception ranges and echo information content would not seriously reduce their foraging success. A bat employing a low-intensity cry should exhibit a high

degree of flight maneuverability paralleling the caution that visually orienting animals use in a darkened environment.

These two potential acoustic disguises of bats (low intensity and very high frequencies) are illustrated by the differential tympanic nerve responses of the African moth, Desmeocraera graminosa, to the echolocation cries of the four species of sympatric, insectivorous bats used in the playback experiments in Côte d'Ivoire. Of the species tested, Pipistrellus nanus emitted the most acoustically detectable cries, with the high intensity and mid-frequency range characteristics (for the auditory sensitivity of D. graminosa) of its signals rendering the bat detectable at most positions within the airspace surrounding the moth while Nycteris macrotis, an extremely low intensity bat, was the least conspicuous species tested. The predictions regarding intensity and frequency appear to be supported by the response of the moth to these bats. Nycteris macrotis, the "whispering" species exhibited an extremely adept flight capability

while in the lab and while flying in the field. Low intensity appears to be an important factor in allowing Nycteris macrotis to come within 20 cm. of the moth while its own reduced perception range has been counteracted by an increased flight maneuverability. Using parameters measured for the cries of N. macrotis and auditory threshold values for D. macrodonta, the computed MDD for a signal resembling that of N. macrotis would be 0.38 m. (Table 6) which is close to those distances observed. A signal resembling P. nanus, on the other hand, (80 kHz, 100 dB) generates a MDD of 6.3 m which would be beyond the distance possible in the laboratory where the trials were held but was substantiated by the maximum distances that the moth could detect P. nanus. The factors influencing D. graminosa's perception of Hipposideros ruber are not as clear, however. H. ruber uses very high frequencies in its cries, presumably beyond the threshold minima of D. graminosa. Since the highest frequency tested on Ivorian moths was 110 kHz, it cannot be assumed that the moth is deaf at these frequencies. In fact, its tympanic response to the almost pure tone 140 kHz CF

signals of H. ruber (Figure 21) would suggest that the moth could detect these frequencies. The reduced MDD for H. ruber may be a combination of two acoustic parameters, intensity and frequency. Hipposideros ruber emitted a signal intermediate in intensity between those of P. nanus and N. macrotis which may be partly responsible for its reduced observed detection distance of 1.5 m. The Hipposideridae contains other species that emit pure tone CF pulses of extremely high frequency (H. caffer; 160 kHz (Pye, 1972); H. galeritus; 145 kHz (Grinnell and Hagiwara, 1972)). The feeding habits of most of these species are not well understood although H. caffer has been described as preying heavily on moths (Whitaker and Black, 1976; Fenton and Thomas, 1979). Whether these species use very high frequency signals as a means of facilitating the capture of moths remains unknown.

Spring Arctiids

The existence of adult moths possessing functional tympanic organs, emerging in early spring poses some

interesting questions regarding the differential responses in defense behaviour to levels of bat activity (i.e. predation potentials). Moths emerging as adults in the spring (late April to early June) are exposed to lower levels of bat activity than those flying in the summer (late June to September) (Fullard, 1977a). The presence of peripherally functional, similarly tuned ears on these moths raises the obvious question: what is the source of selection for the maintenance of these ears as defensive organs? The apparent discrepancy may be due to one or more of several possibilities: 1) the ears of spring arctiids are not bat-specific but are being used to detect ultrasound from other sources, 2) the ears are in a state of degradation and are not functional beyond the peripheral level, 3) the ears are peripherally and behaviourally functional and the levels of bat activity are sufficient to provide a selection force for maintaining them.

The possibility exists that the ears of moths are not necessarily bat-directed. The sudden flight of

Catocala spp. (Noctuidae) in response to the rustling sounds of leaf litter (i.e. an approaching predator) is an example of a non-chiropteran directed use of tympanal organs but is not observed in arctiid moths. Arctiids, many of which are visually aposomatic, would be selected to remain sluggish upon the approach of a predator so as to furnish a conditioning experience for that predator (Edmunds, 1974). In this instance, ears would be superfluous for an animal which is selected to be sedentary to begin with. There is little evidence to suggest that moths acoustically communicate with each other but this may be only a reflection of the scant research in this area. Certainly the tymbal organs of arctiids (Fullard and Fenton, 1977) and the wing slaps of noctuids (Kay, 1969; Agee, 1971) indicate that moths are capable of producing high frequency sounds and Roeder and Treat (1957) demonstrated that the wing-beat sounds of the noctuid, Prodenia eridania, could be detected by the tympanum of a conspecific but there is, as yet, no evidence to suggest that these are intraspecifically communicative sounds. Arctiid sounds lack the stereotypy associated with intra-specific

signals (Fullard, 1977b) and the heavy use of pheromones by moths strongly suggests that conspecifically produced sound is not important to these insects. Whatever secondary functions moth ears possess, the evidence is overwhelming that they function primarily as bat-detectors.

It is considerably more difficult to test, whether or not a sensory organ is functional beyond the peripheral level. Even an investigation of the tympanal response within a spring moth's CNS may not conclusively prove that the ears are behaviourally functional. Certain observations, however, do suggest that the ears of spring arctiids are fully functional. The responses of the spring arctiids tested (Fullard, 1976; Fullard and Fenton, 1977) indicate that these moths will alter their flight behaviour under the influence of ultrasonic stimulation and the low incidence of neurologically deaf specimens (<5%) encountered suggests selection against such handicaps. Under conditions of low selection pressure, one might expect to witness more examples of deaf or impaired

moths. More important, however, is the similarity of tuning curves exhibited by spring species, both inter and intra-specifically. The observation that different moths possess similar audiograms suggests that they possess similar ears tuned to common frequencies (i.e. sympatric bats). Should these ears not be functional, we would expect to observe a much wider range of sensitivity and frequency curves.

The remaining hypothesis is that spring arctiids possess fully functional ears selectively maintained to detect the cries of bats in the area. This, however, conflicts with the phenology of another form of defense behaviour in arctiids: sound production. I have argued (Fullard, 1977a) that for arctiid moths, sound production does not appear in the defensive repertoire of the family until approximately early to mid-June corresponding to the sharp rise in summer levels of flying bats as monitored in the same area. Five arctiid species that emerge, as adults, in May and disappear before mid-June do not produce sound and one of these species, Phragmatobia assimilans, possesses a tymbal

organ that appears to retain a vestigial microtymbal band (Fullard, 1977a) Even if we disregard the other species on the basis that they are present until later in the season and would require ears for the increased bat levels encountered then, we are still confounded with the silence of P. assimilans, a species only present as adults in early to mid-May. Range maps for the genus Phragmatobia (Donahue and Newman, 1966) suggest that it is limited to north of New England and would be experiencing similar levels of predation throughout its range.

What is poorly understood in this problem is the feeding patterns exhibited by insectivorous bats during the spring prior to partuition. Although there are full-sized colonies in the area at this time (personal observation), only during the first half of June does the incidence of bat activity increase to measurable levels near the feeding site monitored. What are the activity and feeding patterns of these bats during May? Belwood and Fenton (1976) and Anthony and Kunz (1977) demonstrated an increase in the percentage of moth

scales in the feces of female Myotis lucifugus during lactation (June-July), coinciding to the emergence of sound-producing arctiids caught in the same area. This may indicate that although dipterans still comprise the largest proportion of their diet, female M. lucifugus may shift their preferred prey size to meet the increased energy demands placed on them by lactation. Larger insects, such as beetles and moths, flying during this time may be exposed to an increased level of predation from these females. The higher levels of scales present in feces samples could also indicate a geographical shift in feeding. Females appear to spend less time feeding over water and more time over dry land close to the nursery colony during lactation (R. M. R. Barclay, personal communication; T. M. Harrison, unpublished data) and may, as a result, prey more heavily on moths and other inland insects.

Increased predation pressures could result in a twofold complication for tympanate moths. First, the higher levels of bat activity would result in a higher probability of encountering a foraging bat and second,

the shift in feeding to land may result in a higher likelihood of being surprised by a bat in the acoustic clutter of a forest. Since sound-production is a close-encounter form of defense (Dunning, 1968; Fullard, 1976) arctiids emerging during low bat levels would be less likely to require these defenses. Phragmatobia assimilians, emerging in early May, might still require the acoustic input of distant bats to gauge what habitats and general areas to avoid, but would not require sound-production defense to ward off close-quarter bat attacks. Much of the behaviour of hungry bats in the spring requires clarification before these speculations can be resolved.

Behavioural Auditory Analyses

The data presented in this study suggest a behavioural translation of the neural relationships previously described (Roeder, 1970; present study). Since sound production and flight cessation are behavioural events, attention must be paid to the context in which they function in the moth. Noctuids

employ a graded series of actions intended to avoid the attacks of hunting bats (Roeder, 1962). These actions are based on the position and intensity of the signals of the bats as they are monitored by the moth's tympanic organ (Roeder, 1967). Distant bats emit relatively low intensity cries that elicit a negative phonotactic response in flying moths. As the bat closes, its cries become more intense (to the moth) and the moth's flight adopts a highly erratic, non-directional nature intended to dodge the attacking bat. As a final resort, the moth often dives or drops to the ground under conditions of auditory saturation (i.e. imminent attack). Arctiids perform a similar array of evasive maneuvers (Roeder, 1974b; Goldman and Henson, 1977). Sound production, an additional facet of defense behaviour appears at some point during evasive flight (erratic flight movements) preceeding total flight cessation. Therefore, the audiograms (Figures 22, 23, 24) are not representative of the baseline level of auditory sensitivity but rather the result of behaviourally expressed intensity discrimination by the moth's CNS. The differences in thresholds for the two

criteria reflect the differences in bat-moth distances when the particular response is elicited. Sound production or flight cessation would be either unnecessary or potentially hazardous to moths (e.g. in flight over water) if performed in response to distant bats.

The high degree of inter-individual variation may reveal something of the relative success of individual moths in evading the approach of hungry bats. Several factors, not examined in this study, (eg. sex, age, parasitism) may affect the tuning characteristics of various moths. As the tuning of an individual becomes more mismatched to the spectral peaks of the bats for which it must detect, those bats will appear (acoustically) farther and farther away. Thus, a moth whose particular tuning is substantially altered may react to the approach of an echolocating bat in a behaviourally delayed (and possibly fatal) fashion. Differing auditory abilities may explain Roeder and Treat's (1961) observation of widely differential response characteristics of free-flying moths in field

conditions.

The variability present in the intensities required to elicit flight cessation may be an indication of the greater degree of unpredictability in the moth under conditions of very intense acoustic stimulation. This variability may reflect Roeder's (1967) observation that unpredictability at this crucial phase in the moth's behaviour might well confuse the bat as well as the observer and, therefore, be adaptive.

As with many behavioural observations there were difficulties in eliciting certain of the defense behaviours under experimental conditions. Tympanic nerve recordings from other species were usually 75-80 % successful and sound production trials could be completed with about 50% of the C. tenera tested. Eliciting behavioural responses from specimens in stationary flight, however, met with considerably less success with the moths. That behaviour becomes more unpredictable at higher neuronal functions was discussed by Roeder (1975) who maintained that

otherwise predictable and strongly selected for behaviour patterns (eg. avoidance flight in moths) became more "evitable" as the specimen was moved farther from natural conditions. Certainly, the experimental design involved in studying flight alteration in C. tenera is an unnatural one but there should be, by Roeder's (1975) argument, little difference in evitability between sound production and flight cessation responses. The contention that behavioural variability has a selective advantage might better explain the different levels of success encountered between the two criteria. If sound production serves a role as an acoustic deterrent by interfering with the echo perception of the closing bat (Fullard et al., 1979), selection would favour moths that used the defense consistently since a failure to emit sound would not impart any advantage to the moth. Flight cessation, on the other hand, might benefit more from an increased variability since bats may be partially conditioned, from previous encounters, for the evasive flight of moth prey. By exhibiting a high variability in flight patterns, moths may benefit by

not conditioning bats when to expect them to cease flight. That Hypoprepia fucosa could not be induced to resume stationary flight may reveal something of interspecific differences in response to bat cries. H. fucosa apparently exhibits a longer recovery period to intense stimuli and would therefore, be more inclined to remain on the ground after initially ceasing flight. This reaction might be expected in a lithosiinid, a subfamily of arctiids which generally spends much of its adult life on the ground (Forbes, 1960).

The relative simplicity of the arctiid's auditory apparatus and the stereotypy of its intra-individual responses are inviting mechanisms for the study of the relationships between sensory-derived neural input and discrimination-modified motor output. Electrophysiological and morphological studies (Roeder, 1966b; 1969; Roeder and Fenton, 1973; Paul, 1973; 1974) have demonstrated a number of ganglionic interneurons in various noctuids reaching as far forward as the protocerebrum. A study of the simple behavioural responses of arctiids based of afferent neural activity

should help to elucidate the discriminatory functions of these interneurons and the role they play in modifying the behaviour of tympanate moths.

CONCLUSIONS

CONCLUSIONS

1. Heretofore unreported, peripherally functional tympanic organs exist in species from the following families: Thyateridae, Thaumetopoeidae, Agaristidae and Thyretidae. Preliminary analyses indicate that the innervation of these species are the same as those previously reported for North American moths from the same superfamilies.

2. Different sizes of arctiid species in south-eastern Ontario possess similar sized tympanal membranes. This is thought to be a morphological response based on tuning resonance characteristics of the tympanum to those frequencies most predominant in the echolocation/hunting cries of sympatric bats.

3. Tympanate moths tested in south-eastern Ontario exhibit a close frequency match to the echolocation cries of their chiropteran predators. In west Africa, higher populations and diversities present in bat faunas are apparently reflected in the wider ranges of

best frequencies exhibited by the moths there.

4. Ivorian moths are significantly more sensitive over the entire frequency range tested and, in particular, at high frequencies, than their Ontario counterparts.

5. For Ivorian moths, acoustic sensitivity at low frequencies increases with the number of sense cells associated with the tympanal organ.

6. Five species of Arctiidae that emerge, as adults in early May to June possess neurologically and, apparently, behaviourally functional tympanal organs. It is hypothesized that moths which exist at times of low bat activity (i. e. predation potential) have retained functional ears so as to determine the presence of distant bats but do not possess the close-encounter defenses of sound-production due to these low predation potentials.

7. Predicted distances at which given bat signals are detected, computed from auditory threshold values,

agree with observed distances, where measurements were possible. These computations predict that as the spectral peak of a bat's echolocation cry becomes more mismatched to the peak sensitivity of a given moth, the distance at which that moth will first detect the bat decreases logarithmically. A similar effect is experienced by lowering the initial intensity of the emitted bat cry. An increase in the relative humidity has the theoretical effect of increasing the detection distances at lower frequencies and decreasing them at higher ones.

8. The notodontid moth, Desmeocraera graminosa, exhibited a differential ability to detect the echolocation cries of four different species of sympatric, insectivorous bats. By emitting cries of low intensity or very high frequency, the bats Nycteris macrotis and Hipposideros ruber, respectively, were able to reduce their detection distances to within 2 m. Nycteris macrotis appears to have compensated for its own reduced perception by adopting an extremely agile flight ability.

9. The possibility exists that certain species (especially of the Hipposideridae) are employing echolocation signals of atypical design to exploit the acoustic relationships that tympanate moths have with the majority of their echolocating predators. These acoustic countermeasures may be responsible, in part, for the heavy predation on lepidoptera by some of these bats.

TABLES

TABLE 1

Auditory Organs in the Lepidoptera

Location	Families	Acoustic Cells	Reference
(Tympanal)			
Metathorax	Notodontidae	1	Roeder, 1974b
	Thyretidae	1*	present study
	Thaumetopoeidae	1*	present study
	Noctuidae	2	Roeder, 1967
	Arctiidae	2	Roeder, 1974b; present study
	Lymantriidae	unknown	Haskell, 1961
	Agaristidae	2*	present study
Abdomen	Geometridae	4	Roeder, 1974a
	Pyralidae	4	Agee, 1969b
	Drepanidae	unknown	Haskell, 1961
	Thyateridae	unknown	present study
	Cymatophoridae	unknown	Sick, 1935

	Uraniidae	unknown	Sick, 1935
	Epiplemlidae	unknown	Sick, 1935
	Axiidae	unknown	Forbes, 1936
	Cossidae	unknown	Kiriakoff, 1956
(Non-tympanal)			
Pilifers	Sphingidae	.	
	(Choerocampinae)	1	Roeder, 1974b
Wing Joint	Nymphalidae	unknown	Swihart, 1967

* Tentative Assessment

TABLE 2

Audiogram Characteristics of Moth Species Tested in
QUBS and Lamto with samples sizes of three or greater.

species	N	best frequency (kHz)	threshold (dB)					
			frequency (kHz)					
			10	20	40	60	80	100
<hr/>								
(QUBS)								
<u>Spilosoma</u>								
<u>virginica</u>	3	15-40	74	51	49	73	73	78
 <u>S.</u>								
<u>congrua</u>	6	15-40	81	52	52	73	69	84
 <u>Halysidota</u>								
<u>caryae</u>	5	20-40	78	56	55	69	69	73
 (Lamto)								
 <u>Desmeocraera</u>								
<u>graminosa</u>	10	40	85	59	44	54	50	58

Balacra

<u>inflammata</u>	4	45-95	96	91	75	72	65	73
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Rhodogastria

<u>vitrea</u>	3	30	72	57	40	50	48	62
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Caryatis

<u>phileta</u>	4	25-40	91	65	52	67	65	74
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Estigmene

<u>unilinea</u>	4	30	82	62	49	61	56	71
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Spilosoma

<u>penicillata</u>	6	25-40	75	48	43	57	54	68
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Geolyces

<u>convexaria</u>	5	30	66	49	47	62	61	70
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Colocleora

<u>potaenia</u>	5	25	64	48	49	59	64	76
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Miantochora

<u>venerata</u>	4	30	66	49	45	62	64	75
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Miantochora

<u>interrupta</u>	5	25-30	61	48	44	59	64	78
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Megadepana

<u>cinerea</u>	5	25-30	68	45	47	62	71	85
----------------	---	-------	----	----	----	----	----	----

Anaphe

<u>ambrizia</u>	6	40	88	74	59	70	67	75
-----------------	---	----	----	----	----	----	----	----

TABLE 3

Comparisons of Auditory Characteristics of Moths

From QUBS and Lamto (mean $\pm$ s.d.).

	QUBS	Lamto	t(s) *
Best Frequency (kHz)	30.4 $\pm$ 10.8 (45)	37.8 $\pm$ 13.8 (83)	2.19**
Sensitivity (N/m ² ·kHz)			
5-25 kHz	2.5 $\pm$ 0.4 (24)	2.3 $\pm$ 0.7 (81)	0.76 (NS)
30-50 kHz	3.0 $\pm$ 0.2 (24)	3.0 $\pm$ 0.3 (82)	0.38 (NS)
55-80 kHz	2.5 $\pm$ 0.6 (24)	3.0 $\pm$ 0.3 (82)	5.05***
85-110 kHz	2.8 $\pm$ 0.8 (23)	3.6 $\pm$ 0.8 (82)	4.74***

5-110 kHz	10.8 $\pm$ 1.25	11.8 $\pm$ 1.6	4.03***
	(23)	(82)	

* Wilcoxon two-sample test (Sokal and Rohlf, 1969)

** $p < .05$

*** $p < .001$

TABLE 4

Auditory Sensitivities of Ivorian Moths
as a Function of the Number of Acoustic Sense
Cells Servicing the Tympanum.*

A cell number	Frequency Ranges (kHz)			
	low	low-mid	high-mid	high
	(5-25)	(30-50)	(55-80)	(85-110)
1	1.46 $\pm$.72 (5)	2.97 $\pm$.19 (5)	2.89 $\pm$.2 (5)	3.44 $\pm$.81 (5)
2	2.54 $\pm$.26 (10)	3.12 $\pm$.02 (10)	3.09 $\pm$.05 (10)	4.15 $\pm$.2 (10)
4	2.88 $\pm$.06 (5)	3.13 $\pm$.01 (5)	3.05 $\pm$.02 (5)	3.37 $\pm$.66 (5)

*Number of A cells for tympana extrapolated from North American studies (Roeder, 1974b).

TABLE 5

Comparison of Acoustic Sensitivity of Ivorian
Moths as a Function of the Number of A cells
Servicing the Tympanum.

Frequency	A cell Number Comparison*		
Range	1 x 2	1 x 4	2 x 4
(kHz)			
<hr/>			
5-25	3.125***	4.319***	3.480**
30-50	1.674	1.790	0.852
55-80	1.905	1.529	1.671
85-110	1.633	0.486	2.516

*t-ratio (Fisher-Behren's test).

** $p < .05$

*** $p < .02$

TABLE 6

Response Characteristics of Desmeocraera graminosa
to the Echolocation Signals of Sympatric Bats.
(Predicted and Observed).

bat species	number of signals detected *	detection distance (m)	
		observed	predicted (MDD**)
<hr/>			
<u>Pipistrellus</u>			
<u>nanus</u>	305	>3	6.3 (1)
<u>Nycteris</u>			
<u>macrotis</u>	64	0.2	0.4 (2)
<u>Hipposideros</u>			
<u>ruber</u>	135	1.5	0.1 (3)
<u>Rhinolophus</u>			
<u>landeri</u>	371	>3	2.4 (4)

* As monitored by the tympanic nerve in 180 seconds of exposure to the flying bat.

**** Maximum Detection Distance (Appendix II).**

- 1- using signal of 80 kHz, 100 dB.
- 2- using signal of 80 kHz, 70 dB.
- 3- using signal of 110 kHz (highest attainable), 75 dB.
- 4- using signal of 100 kHz, 90 dB.

TABLE 7

Acoustic Parameters of the Echolocation Cries
of Bats Sympatric with Moths Tested at
QUBS and Lamto (mean $\pm$ s.d.).

species	duration (msec) 1	maximal spectral peak (kHz) 2	intensity (dB)	directionality
<hr/>				
<u>Myotis</u>				
<u>lucifugus</u>	2.5 $\pm$ 1.2	44.96	109*	low
<u>Eptesicus</u>				
<u>fuscus</u>	1.0-2.5**			
	10-15*	28.32	107-114**	low
<u>Pipistrellus</u>				
<u>nanus</u>	1.2 $\pm$ 0.3	81.92	96***	low
<u>Nycteris</u>				
<u>macrotis</u>	0.6 $\pm$ 0.2	86.88	58***	marked
<u>Hipposideros</u>				
<u>ruber</u>	6.3 $\pm$ 0.1	139.36	75***	marked

Rhinolophus

<u>landeri</u>	25.0 <u>±</u> 1.0	100.96	80***	marked
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1- from Fenton and Fullard (in press)

2- Machine Averaged FFT Spectra (Figures 26 and 28).

* Griffin (1958)

** Simmons (1971)

*** Measured from pure tones at equal voltage amplitude to that recorded from signals collected in the laboratory at Lamto.

FIGURES

Figure 1

Camera lucida drawing illustrating the non-auditory body sclerites that were measured on tympanate moths as a function of thoracic size (volume).

a- lateral thoracic view:

MW - mesothoracic meron width

CL - coxa (III) length

td - thoracic depth

b- dorsal thoracic view:

SL - scutum length

tl - thoracic length

tw - thoracic width

c- anterior cranial view

CW - clypeus width

a

b

c

1 mm

Figure 2

The tympanum of Halysidota caryae illustrating
the measurement taken as an indicator of tympanal
size.

Tm- tympanal membrane

SA- sensillum attachment site

Ra- radius

Ep- epaulette

Cj- conjunctivum

Th- tympanal hood

Figure 3

Block diagram of playback procedures for neurological (A) and behavioural (B) analyses of auditory sensitivity.

A:

Neurological Analysis Set-up

- 1- specimen mounted on plasticine block
- 2- microscope base
- 3- microscope supporting stand (microscope absent)
- 4- microelectrodes and micromanipulators
 - a- recording electrode
 - b- ground (reference) electrode
- 5- microelectrode pre-amplifier (DC powered)
- 6- audio speaker for nerve activity monitoring
- 7- dual-trace oscilloscope
- 8- two-channel tape recorder
 - channel one- nerve activity
 - channel two- stimulus
- 9- signal generator
- 10- ultrasonic stimulus amplifier
- 11- stimulus speakers
 - a- low frequency (5 kHz to 40 kHz)
 - b- high frequency (45 kHz to 110 kHz)

- 12- grounded Faraday cage
- 13- sound-attenuating foam

Low frequency stimulus playback indicated by (-----)

High frequency stimulus playback indicated by (-----)

B:

Behavioural Analysis Set-up

- 1- specimen mounted on pin-head by wax drop
- 2- retort stand
- 3- high-frequency microphone and pre-amplifier
- 4- measuring amplifier
- 5- dual-trace oscilloscope
- 6- signal generator
- 7- amplifier
- 8- high frequency speaker (20 kHz to 100 kHz)
- 9- low-noise fan
- 10- wind current shield
- 11- sound-attenuating foam and backing

A

B

Figure 4

The audiogram analyses studied for comparisons
between moths captured at QUBS and LAMTO.

A- best frequency (kHz)

B- low frequency sensitivity (5-25 kHz)

(bars represent areas taken as
audiogram area)

C- low mid-frequency sensitivity (30-50 kHz)

D- high mid-frequency sensitivity (55-75 kHz)

E- high frequency sensitivity (80-110 kHz)

(Total sensitivity = B+C+D+E)

F- Q10 value (tuning)

Sensitivity was measured as audiogrammic area below
arbitrary SPL of 0.63 N/m^2 (90 dB re. $20 \mu\text{Pa}$).

Figure 5

Response of Cycnia tenera to a 10 msec.

70 kHz stimulus pulse (80 dB).

(Figure courtesy of Dr. J. A. Simmons)

Figure 6

The relationship between the size of auditory and non-auditory sclerites to the body sizes (thoracic volume) of eighteen species of Arctiidae surveyed at QUBS.

The values graphed are averages and are plotted as the proportionate increase from that of the smallest moth measured.

The species and sample sizes (n) measured in order of increasing size are: Holomelina aurantica (5), Lycomorpha pholus (4), Hypoprepia fucosa (10), Cycnia tenera (10), Hyphantria cunea (10), Haploa lecontei (3), Euchaetias oregonensis (4), Haploa contigua (1), Euchaetias egle (10), Spilosoma prima (4), Spilosoma congrua (10), Phragmatobia assimilis (10), Spilosoma virginica (10), Halysidota caryae (10), Apantesis nais (9), Halysidota tessellaris (10), Pyrrharctia isabella (10), Callarctia virgo (8).

(non-auditory sclerites: MW- mesothoracic meron width, SL- scutum length, CL- coxa (III) length, CW- clypeus width; (inter-optic distance); auditory sclerite: TR- tympanum radius).

Figure 7

Oscillograms of (a) spontaneous tympanic nerve activity and (b) A1 and A2 cell response to intense (95 dB), 55 kHz stimulus (bar) in Pyrharctia isabella.

A1- A1 cell spike,

A2- A2 cell spike

B- B cell spike

rec.- recovery period

a

.1 sec

b

4 sec

Figure 8

PST (Post-stimulus time) histograms of A1 cell
response in Pyrrharctia isabella to
continuous pure tone of 55 kHz at
given intensities.

Figure 9
Tympanic nerve response
of Pyrrharctia isabella
to 55 kHz pulsed stimuli.

40msec

Figure 10

Tympanic response of Pyrrharctia isabella to tonal
bursts (55 kHz; 85 dB) of varying duration.

Figure 11
Tympanic nerve activity from the two species
of overwintering moths,
Scoliopteryx libatrix (a) and Triphosa haesitata (b).
A1- A1 cell
A2- A2 cell
B- B cell
Stimulus (bar) in (a) - key jingle
Stimulus (bar) in (b) - 55 kHz, 80 dB pulsed pure tone

a

b

400 msec

20 msec

Figure 12

Tympanic nerve activity of the thyaterid moth,

Euthyatira pudens.

Stimulus (bar) - 55 kHz, 85 dB pulsed pure tone

40 msec

Figure 13

Tympanic nerve response of spring arctiids from
Chaffey's Locks. Single spikes in all records
from B cell.

- a) Phragmatobia assimilis
- b) Spilosoma virginica
- c) Spilosoma prima
- d) Spilosoma congrua
- e) Hyphantria cunea
- f) Halysidota caryae

Stimulus (bar) - 55 kHz, 10 msec, 85 dB pulsed pure tone

a

d

b

e

c

f

20msec

Figures 14a-1

Histograms of neurological auditory comparisons between North American (Chaffey's Locks) and Ivorian (Côte d'Ivoire) species.

a,b) Best frequency.

c,d) Total sensitivity (5 kHz to 110 kHz).

e,f) Low frequency sensitivity (5 kHz to 25 kHz).

g,h) Low mid-frequency sensitivity (30 kHz to 50 kHz).

i,j) High mid-frequency sensitivity (55 kHz to 75 kHz).

k,l) High frequency sensitivity (80 kHz to 110 kHz).

e

CHAFEEY'S LOCKS

f

COTE D'IVOIRE

g

CHAFFEY'S LOCKS

% relative frequency

80

40

0

h

COTE D'IVOIRE

80

40

0

0 0.4 0.8 1.2 1.6 2.0 2.4 2.8 3.2

sensitivity ($\text{N/m}^2 \cdot \text{kHz}$)

Figure 15

Comparison of sensitivities at low (a),
low mid- (b), high mid- (c) and high (d)
frequency ranges for Ivorian moths with
one, two or four A cells servicing the
tympanum.

(Neurological A cell data extrapolated from
Roeder, 1974b)

Figure 16

Computed Q10 values for North American (□) and Ivorian (■) species with sample sizes 5 or more. Values are taken from species averages (Table 2).

Figure 17

Tympanic nerve response of Pyrrharctia isabella to the echolocation signals of Myotis lucifugus.

- a) Response (top trace) to cruising bat (note slight echo in bottom trace)
- b) Response to double pulses (possibly close echoes)
- c) Response to feeding buzz (note contracted time scale)

a

b

c

40msec

Figure 18

Responses of Desmeocraera graminosa to the echolocation
signals of the insectivorous bats:

- a) Pipistrellus nanus
- b) Rhinolophus landeri
- c) Hipposideros ruber
- d) Nycteris macrotis

40 msec

a

b

40 msec

Figure 19

Extreme signal directionality as shown by tympanic nerve response of Desmeocraera graminosa to echolocation cries of a) Hipposideros ruber and b) Rhinolophus landeri. In both cases, the ultrasonic microphone (bottom trace) was positioned 20 cm from the ear preparation and oriented in the same direction.

Figure 20

Audiograms for the specimens of Desmeocraera graminosa
used in bat exposure trials.

Figure 21

Tympanic nerve response of Desmeocraera graminosa to the echolocation signals of low frequency hunting bats (possibly molossids) over the Bandama River in Côte d'Ivoire.

a

b

20 msec

Figure 22

Auditory threshold curves for six individual specimens of Cycnia tenera using sound production as behavioural criterion. Means are joined by straight line, vertical lines represent ranges.

dB (re 2×10^{-5} N/m²)

kHz

Figure 23
Auditory threshold curves for four Cycnia tenera,
using flight cessation as behavioural criterion.

Figure 24

Audiogram of Hypoprepia fucosa using
sound production as behavioural criterion.
Data are from four specimens, means joined
by lines, vertical lines represent ranges.

Figure 25

Echolocation signals of North American insectivorous
bats and their FFT analyses.

- a) FFT of Myotis lucifugus cries with evidence
of second harmonic.
- b) FFT of single cry from M. lucifugus without evidence
of second harmonic.
- c) FFT of single cry from Eptesicus fuscus.
- d) Time-amplitude trace of two M. lucifugus cries.
- e) Time-amplitude trace of single E. fuscus cry.

Figure 26

Machine averaged FFT spectra of (a) Myotis lucifugus
and (b) Eptesicus fuscus echolocation signals.

(m- tape machine induced noise)

Figure 27

Echolocation signals of African insectivorous bats
used in exposure trials with Desmeocraera graminosa

(left) FFT spectra of single cry.

(right) Time-amplitude trace of Cry

a) Pipistrellus nanus

b) Nycteris macrotis

c) Hipposideros ruber

d) Rhinolophus landeri

(Hann Weighting used in analysis of R. landeri signal)

Figure 28

Machine averaged echolocation signals of African insectivorous bats used in exposure trials with Desmeocraera graminosa (sample size = number of echolocation signals averaged).

- a) Pipistrellus nanus
- b) Nycteris macrotis
- c) Hipposideros ruber
- d) Rhinolophus landeri

(Note linearized dB scale for N. macrotis;

m- machine induced noise)

Figure 29

Period meter analysis of foraging bats in the field at (a) QUBS and (b) Lamto. Signals from flying bats were monitored from an oscilloscope screen and recorded as number of bat passes/minute.

Figure 30

A representation of the maximum distances at which tympanate moths detect the echolocation signals of bats based on auditory threshold values (Appendix II).

- a) Scalmicauda bisecta (Notodontidae), one of the most sensitive moths studied in Côte d'Ivoire. Values are for 20 % R.H., initial bat intensities given on graph.
- b) Balacra inflammata (Thyretidae), the least sensitive Ivorian moth studied (20% R.H.)
- c) Rhodogastria vitrea (Arctiidae), for initial bat intensity of 110 dB at 20% R.H. (●—●) and 100% R.H. (○---○).
- d) Same moth for initial bat intensity of 70 dB.

frequency (kHz)

Figure 31

Effects of humidity on the maximum detection distances
of some species (North American and Ivorian) tested.

- a) Desmeocraera graminosa; initial bat SPL, 110 dB,
R.H.: 20% (———), 100% (-----).
- b) Gorua apicata; initial bat SPL, 110 dB,
90 dB, 70 dB; R.H.: 20% (———), 100% (-----).
- c) Halysidota caryae; initial bat SPL, 110 dB; R.H.:
20% (———), 100% (-----).

APPENDICES

APPENDIX I

Auditory System Dissection and Recording Techniques

The methods that were used to expose the moth auditory system were modified from those described by Roeder and his colleagues (Roeder, 1964; 1966a; Roeder and Treat, 1957) Two attitudes of surgical approach were used in these studies, both of which are particularly compatible for field set-up and involve a minimum of microdissection techniques.

Parasagittal Approach (Noctuoidea, Notodontoidea)

The unanesthetized moth is decapitated and dealeated, its legs and posterior one-half of its abdomen removed and is placed on a block of plasticine. The thorax is braced with pieces of plasticine and is bisected along an approximately parasagittal plane by means of a single stroke with a double-edged razor blade. The cleavage should be one continuous, slightly sawing motion so as to minimize internal tissue damage. The two halves of the thorax are separated and examined

to determine the half containing the thoracic ganglion.

The metathoracic ganglion is located, slightly lifted and cleared of tracheal and muscle tissue. This procedure should be done with extreme caution to avoid stretching the associated nerve trunks leading into the ganglion from the contralateral side. Portions of the longitudinal flight musculature inserting on the dorsal mesophragma may be removed by severing the posterior tip of the phragma and removing it with the muscle. Again, this should be executed with extreme caution to avoid damaging the proximal nerve tissue.

Once the mesothoracic ganglion has been isolated and exposed, the main metathoracic nerve trunk (IIIN1, Nüesch, 1957) is lifted gently away and the tympanic nerve can be seen as the first posteriorly directed nerve of moderate size. Care should be taken to distinguish the tympanic nerve as one connecting to the nerve trunk and not one of the associated nerves running alongside the ganglion. In living preparations the translucent nerve may be difficult to see and I recommend prior dissections with methylene blue stained

specimens. The proximity of the ganglion, the tympanic nerve's moderate size and its posterior direction should serve as cues for its identification. Depending on the species of moth under investigation the tympanic nerve may lie directly over a V formed by the branching of the large metathoracic tracheal vessel as it enters the thoracic cavity. In some cases, this vessel may obscure the nerve, especially if the preparation is not flooded with saline. Flooding with insect saline will facilitate the isolation of the tympanic nerve as it floats in the fluid. Once the tympanic nerve is located, it may be suspended by the hooked end of the microelectrode and lifted from the thoracic fluid. Care should be taken in the tension brought to bear on the nerve owing to its proximity to the tympanic air sac.

Generally, the parasagittal approach is recommended only for the initial familiarization of the nervous geography of the thoracic cavity. Its chief drawbacks include the destruction of one half of the auditory system and the reduced accessibility to the tympanic nerve due to the obstruction of the metathoracic ganglion (although this can be partially relieved by

removal of the ganglion).

Dorsal Approach (Noctuoidea, Notodontoidea)

Of the two dissections described here, the dorsal is the preferred due to its increased accessibility to the auditory nervous system and the increased working area allowed in the preparation.

The moth's head and legs are removed and the wings spread forward as far as possible to fully expose the tympanic membrane. The wings are then fastened, dorsum up, onto a block of plasticine with small paper staples. A third staple is placed across the abdomen to prevent movement during the dissection. The dorsum of the thorax is brushed completely free of scales and hair, particularly near the wing joints. With the edge of a micro-scalpel the post-notal ridge is slit down the centre to above the articular wing sclerites. Using iridectomy scissors, an incision is made dorsal to the wing joints and continued around the thoracic terga. The cut should be a shallow one to avoid severing nerve branches below the cuticle. The exoskeletal tergum is

then removed in one piece leaving the longitudinal flight musculature in place. Using iridectomy scissors, sever the bridge between the post-notal wing processes and the post notum on both sides of the thorax. This can be accomplished by inserting the scissors directly downwards and snipping the posterior notal wing process. Once the process has been severed, grasp the mesophragma with micro-forceps and gently lift it away from its pocket in the anterior half of the abdomen. As the phragma is drawn forward, begin to sever the dorso-ventral flight musculature as close to the thoracic walls as possible. Once the phragma and attached musculature is lifted forward, lay the mass over the prothorax and use the partially amputated flight musculature as a site for the reference electrode.

Place a drop of insect saline on the thoracic ganglia and clear away the associated tracheal vessels and alimentary tract before isolating the tympanic nerve. With the cavity flooded with saline, locate the tympanic nerve as it passes over the tracheal branch V. In this approach the tympanic nerve will possess a

good deal less tension and will tolerate a moderate amount of force as it is lifted from the saline by the microelectrode.

(Geometroidea, Drepanoidea)

For moths in these superfamilies, I recommend a slightly different approach since the tympanic organs lie in the abdomen rather than the thorax. The dorsal approach is used and the thoracic cavity exposed as previously described. Using the iridectomy scissors make two lines of incision down the abdominal dorsum to the second segment. Join these two incisions and remove the dorsal segments. This will expose the abdominal ventral cord connectives and the tympanic nerve which runs alongside these connectives as they pass over the thoracic-abdominal junction. Lift the tympanic nerve from the saline behind the point at which the tympanic nerve joins the ventral nerve cord. Once the tympanic nerve is isolated, sever the abdominal connectives to reduce efferent neural activity.

Recording

Recording procedures are the same for both dissection techniques. Using micromanipulators, position the reference electrode in some inert tissue (the partially dissected thoracic flight musculature serves as a good reference site) and suspend the intact tympanic nerve from the hook microelectrode. Suitable microelectrodes can be made from electrolytically tapered thin strands of stainless steel or silver wire with the ends bent into minute hooks to facilitate snaring of the tympanic nerve. When the tympanic nerve has been isolated and lifted from the saline solution, break the fluid shunt between the draped nerve ends using a piece of absorbant tissue (Kimwipe) twisted into a point. Once the saline is removed from the nerve relax it back into the thoracic fluid until only a small portion of the nerve is free of the saline. This will lengthen the life of the preparation and reduce damage from tension on the nerve.

Suitable recordings can be obtained from single-ended pre-amplification if the preparation is

housed within a Faraday cage and properly grounded. Since acoustic trials usually require some form of sound-proofing, the Faraday cage can serve as a suitable housing for the buffering material. When recording in areas without a ground lead, drive a sanded metal pole into the earth and ground all electrical equipment to it. Electrical interference generally tends to be the greatest source of noise in the recording and I strongly recommend careful grounding procedures.

Using stainless steel microelectrodes will result in a substantial amount of electrode tip polarization. This can be removed by employing the offset voltage control on the preamplifier.

Signals can be recorded onto a high-speed, direct record instrumentation tape recorder which allows for simultaneous recordings of stimulus and nerve response. This, however, has the disadvantage of biasing against low frequencies (band width for direct record at 30 ips: 200 Hz to 150 kHz) and eliminates the nerve impulse signals at playback speeds of less than 7.5

ips. Use of an FM board (bandwidth at 30 ips: 0.2 Hz to 20 kHz) for nerve recordings and direct record for high frequency stimulus is recommended for maximum signal recording.

Figure 1a

Camera lucida drawing illustrating the surgical approach used in the dorsal attitude to expose the tympanic nerve of moths.

Ab - abdominal connective

AT - alimentary tract

Cn - thoracic connective

DV - dorso-ventral flight musculature

Ptg - pterothoracic ganglion

T - tergum

TAj - thoracic-abdominal junction

TB - tracheal branch

TN - tympanic nerve (Noctuoidea, Notodontoidea)

● - recording site

TN(gn) - tympanic nerve (Geometroidea)

● - recording site

0.8 mm

APPENDIX II

Calculation of Detection Distances Based on Auditory
Threshold Values

Auditory threshold values were used to compute the maximum detection distances (MDD), in meters, that a moth could theoretically achieve given certain environmental and acoustic parameters.

For each stimulus frequency, a moth will exhibit a particular threshold value (TV). Using the initial bat intensity at 10 cm, that is, the SPL (dB) recorded at 10 cm from the bats's mouth, the dB loss (attenuation value, AV) from the initial value to that of the threshold value is:

$$AV = dB(\text{initial}) - TV$$

The attenuation value can be converted to the maximum detection distance given certain biasing factors. These factors are the attenuation rates (dB/m) of pure tones at given frequencies and relative humidities (Table IIa) (Griffin, 1971; Evans and Bass,

1972).

If, for example, a moth's TV at 40 kHz is 75 dB and a hypothetical constant frequency (CF) bat emits its echolocation signal at 40 kHz with a dB(initial) of 95 dB, the MDD will be a function of the derived attenuation value:

$$\begin{aligned} AV &= 95 \text{ dB} - 75 \text{ dB} \\ &= 20 \text{ dB} \end{aligned}$$

Therefore, the maximum attenuation that the bat's signal can undergo and still be detected by the moth is 20 dB.

To determine the MDD of the moth to the hypothetical CF bat, we apply the attenuation rate at 40 kHz for some given relative humidity (20° C). With a AV of 20 dB and a relative humidity of 50 %, the appropriate calculation for deriving the MDD is:

$$\begin{aligned} \text{MDD} &= 0.00114 (AV)^{2.3} \text{ (from Table IIb)} \\ &= 0.00114 (20)^{2.3} \\ &= 1.12 \text{ m.} \end{aligned}$$

The hypothetical CF bat would therefore, be detected at a distance of 1.12 m, a value dependent on the initial bat's intensity and the particular attenuation rate for the given frequency and relative humidity (Table IIa).

Table IIa

Attenuation rates (dB/m) for various frequencies
at different relative humidities.

freq. (kHz)	% Relative Humidity (20°C)								
	20	30	40	50	60	70	80	90	100
5	.1	.05	.05	.05	.02	.02	.02	.02	.02
10	.2	.2	.2	.1	.1	.1	.1	.1	.1
15	.5	.5	.3	.3	.2	.2	.2	.2	.1
20	.5	.5	.5	.5	.5	.3	.3	.3	.2
25	.5	.5	.5	.5	.5	.5	.5	.5	.5
30	.5	1.0	1.0	1.0	1.0	.5	.5	.5	.5
35	.5	1.0	1.0	1.0	1.0	1.0	1.0	.5	.5
40	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
45	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
50	1.0	1.0	2.0	2.0	2.0	2.0	1.0	1.0	1.0
55	1.0	1.0	2.0	2.0	2.0	2.0	2.0	2.0	1.0
60	1.0	1.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0
65	1.0	1.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0
70	1.0	1.0	2.0	2.0	3.0	3.0	3.0	3.0	3.0
75	1.0	2.0	2.0	3.0	3.0	3.0	3.0	3.0	3.0
80	2.0	2.0	2.0	3.0	3.0	3.0	3.0	3.0	3.0

85	2.0	2.0	3.0	3.0	3.0	3.0	3.0	3.0	3.0
90	2.0	2.0	3.0	3.0	3.0	3.0	3.0	3.0	3.0
95	2.0	3.0	3.0	3.0	3.0	3.0	3.0	3.0	3.0
100	2.0	3.0	3.0	3.0	3.0	5.0	5.0	5.0	5.0
105	3.0	3.0	3.0	3.0	5.0	5.0	5.0	5.0	5.0
110	3.0	3.0	3.0	3.0	3.0	5.0	5.0	5.0	5.0

(Values are extrapolated from Evans and Bass (1972) and rounded to the nearest attenuation rate given by Griffin (1971))

Table IIb

Conversion formulae for determining maximum detection distances from attenuation values at given attenuation rates.

Attenuation rate (dB/m)	Conversion Formula
.01	MDD= 0.000000371 (AV)E4.73
.02	MDD= 0.000000708 (AV)E4.54
.05	MDD= 0.00000432 (AV)E4.02
.1	MDD= 0.00000766 (AV)E3.84
.2	MDD= 0.0000403 (AV)E3.35
.3	MDD= 0.00013 (AV)E3.00
.5	MDD= 0.00028 (AV)E2.75
1.0	MDD= 0.00114 (AV)E2.30
2.0	MDD= 0.0015 (AV)E2.13
3.0	MDD= 0.003 (AV)E1.89
5.0	MDD= 0.004 (AV)E1.73

(MDD = maximum detection distance; AV = attenuation value

E - raised to the power of, i.e. (AV)E1.73 = $(AV)^{1.73}$).

APPENDIX III

Conversion formulae for Stimulus Intensity Values

Stimulus intensity was monitored after amplification and recorded from the oscilloscope screen in mV. These values were transformed to dB using the identical playback equipment and measuring sound pressure levels (SPL) with a Brüel and Kjaer 1/4 inch condenser microphone Type 4135 and Measuring Amplifier Type 2606. Extraneous acoustic interference was removed with a Krohn-Hite Model 3202 variable band-width filter. Measurements were taken in a sound-attenuating room (background SPL: 30-40 dB) (courtesy, Dr. J. Kelly, Department of Psychology, Carleton University). Decibel values are referenced to 20 μ Pa.

Conversion formulae for stimulus frequencies, 5kHz to 40 kHz are for KEF T27 speaker with amplification from output amplifier of signal generator; for frequencies 45 kHz to 110 kHz are for 7cm. KÜhl speaker with DC powered ultrasonic amplifier (see Materials and Methods).

Table IIIa
Formulae for converting signal strength in
voltage to SPL (dB).

Stimulus Frequency (kHz)	Conversion Formula
5	$\text{dB} = 29.50 + 8.67 \ln(\text{mV})$
10	$\text{dB} = 31.88 + 8.70 \ln(\text{mV})$
15	$\text{dB} = 29.20 + 8.62 \ln(\text{mV})$
20	$\text{dB} = 33.41 + 8.66 \ln(\text{mV})$
25	$\text{dB} = 34.52 + 8.67 \ln(\text{mV})$
30	$\text{dB} = 37.13 + 8.45 \ln(\text{mV})$
35	$\text{dB} = 36.60 + 8.61 \ln(\text{mV})$
40	$\text{dB} = 23.26 + 8.56 \ln(\text{mV})$
45	$\text{dB} = 9.40 + 7.61 \ln(\text{mV})$
50	$\text{dB} = 9.13 + 8.22 \ln(\text{mV})$
55	$\text{dB} = 9.90 + 8.26 \ln(\text{mV})$
60	$\text{dB} = 12.52 + 8.45 \ln(\text{mV})$
65	$\text{dB} = 12.93 + 8.48 \ln(\text{mV})$
70	$\text{dB} = 12.65 + 8.47 \ln(\text{mV})$
75	$\text{dB} = 12.83 + 8.67 \ln(\text{mV})$
80	$\text{dB} = 13.00 + 8.41 \ln(\text{mV})$

85	$\text{dB}=16.60 + 8.60\ln(\text{mV})$
90	$\text{dB}=14.88 + 8.52\ln(\text{mV})$
95	$\text{dB}=13.08 + 8.26\ln(\text{mV})$
100	$\text{dB}=12.68 + 8.35\ln(\text{mV})$
105	$\text{dB}=13.22 + 8.39\ln(\text{mV})$
110	$\text{dB}=12.44 + 8.33\ln(\text{mV})$

(dB re. 20 μPa , 10 cm.; mV - millivoltage, peak Amplitude)

APPENDIX IV

Averaged neurological auditory threshold curves
for species tested at the Queen's University Biology
Station and the Lamto Research Station.

(n1, n2)

n1 = total sample size collected

n2 = sample size tested for audiogram

Figure VIa; a-o,aa-uu

QUBS (North America)

Noctuoidea

Arctiidae:

- a- Phragmatobia assimilis Walker (11,2)
- b- Spilosoma prima Slosson (3,2)
- c- Spilosoma virginica (Fabricus) (6,3)
- d- Spilosoma congrua (Walker) (15,6)
- e- Callarctia celia (Saunders) (1,1)
- f- Euchaetias oregonensis (Stretch) (1,1)
- g- Estigmene acrea (Drury) (1,1)
- h- Hyphantria cunea (Drury) (1,1)
- i- Halysidota caryae (Harris) (6,5)
- j- Apantesis nais (Drury) (1,1)
- k- Pyrrharctia isabella (Smith)* (8,2)
- l- Hypocrita jacobaeae Linnaeus * (2,2)

Noctuidae:

m- Scoliopteryx libatrix Linneaus ** (10,2)

Drepanoidea

Thyateridae:

n- Euthyatira pudens Guenée (2,1)

Geometroidea

Geometridae:

o- Triphosa haesitata Guenée** (2,2)

LAMTO (W. Africa)

Noctuoidea

Agaristidae:

aa- Mitrophrys sp. near to or = menete Cramer (1,1)

Noctuidae:

bb- Gorua apicata Holland (4,2)

Arctiidae:

cc- Caryatis sp. near to or = phileta Drury (6,4)

dd- Afroarctia sjöstedti Aurivillius (1,1)

ee- Spilosoma penicillata Walker (10,6)

ff- Spilosoma sp. near to or = quadrilineata
Hampson (6,6)

gg- Rhodogastria brunnea Hampson (1,1)

hh- Rhodogastria sp. (2,2)

- ii- Rhodogastria sp. near to or = vitrea Plötz (4,4)
- jj- Estigmene unilinea Rothschild (5,4)

Notodontoidea

Notodontidae:

- kk- Desmeocraera sp. near to or = graminosa
Walker (12,10)
- ll- Arciera grisea Holland (5,5)
- mm- Epicerura pulverulenta Hampson (2,2)
- nn- Scalmicauda bisecta Rothschild (3,3)

Thaumetopoeidae:

- oo- Anaphe ambrizia Holland (7,6)

Thyretidae:

- pp- Balacra inflammata Hampson*** (15,4)

Geometroidea

Geometridae:

- qq- Geolyces convexaria Prout (5,5)
- rr- Colocleora potaenia Prout (5,5)
- ss- Miantochora venerata Mabille (5,5)
- tt- Miantochora interrupta Bastelburger (5,5)
- uu- Megadrepana cinerea Holland (5,5)

* lab-reared specimens

** collected from hibernacula during winter

*** genus presently under revision

a **b**

c **d**

e

f

g

h

i

j

k

l

m

n

o

aa

bb

cc

dd

ee

ff

gg

hh

ii

ji

kk

II

mm

nn

00

pp

qq

rr

ss

tt

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LITERATURE CITED

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