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THE ROLE OF ARCTIID MOTH CLICKS
IN DETERRING BAT PREDATION.

by

Michael G. Stoneman, B.Sc.

A thesis submitted to the
Faculty of Graduate Studies and Research
in partial fulfillment of the requirements
for the degree of Master of Science.

Department of Biology, Carleton University

Ottawa, Canada

April, 1986

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ABSTRACT

Trains of high frequency clicks are produced by some species of moths during evasive manoeuvres triggered by approaching bats. Three hypotheses have been suggested to explain the mechanism of action of this anti-predator defence. Clicks have been suggested to function as aposematic warnings of unpalatability, false echoes to interfere with echolocation, and protean displays to startle the bat. Moth clicks, when presented randomly to captive bats (Megaderma lyra (Megadermatidae) and Macrotus californicus (Phyllostomidae)) as they closed with a target, disrupted the bats' attack whether the bat was orienting by echolocation or by vision. This rules out interference with echolocation as the sole function of the clicks. The persistence of the disruption despite a lack of negative reinforcement suggests that aposematism is not the sole mechanism. The clicks protect the arctiid moths by startling the bat during the final phase of its attack.

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INTRODUCTION

All carnivores are faced with the problem of obtaining food by capturing and killing other animals. As the prey animal has a vested interest in not being eaten, many defenses have evolved to give animals an advantage in avoiding predators. Cryptic colouration, hard shells and sharp spines, chemical agents and social behaviour are a few of the many types of defensive strategies used by animals to avoid being eaten. Not surprisingly, the evolution of prey defences are paralleled by the evolution of predatory counter-defences. Insectivorous bats and their insect prey provide an interesting example of such a predator-prey system.

Many species of insectivorous bats use echolocation to locate prey (Griffin, 1958). As echolocation is an active means of orientation there is the potential for prey to detect hunting bats (Fenton, 1984). Many insects detect the echolocation calls of hunting bats, eg., Roeder (1967) found that many species of moths in the families Noctuidae, Ctenuchidae, Geometridae, and Arctiidae have ears which detect sounds in the frequency range of bat echolocation calls. The behavioural responses of these moths to bat calls give them substantial protection against bat predation (Roeder and Tjebat, 1961). The initial response of a flying insect to a distant bat is to turn and fly in

the opposite direction. Because the insect can detect the bat at a greater range than the bat can detect the insect, this response may carry the insect away from the approaching bat. The response to a bat at close range is sudden, erratic changes in flight speed and direction, often finishing with a full speed dive to the ground. Similar responses have been shown in Green Lacewings (Neuroptera) (Miller and Olesen, 1979), crickets (Orthoptera) (Moiseff et al, 1978), and praying mantises (Orthoptera) (Yager and Hoy, 1986).

Some arctiid moths also produce sounds (see Figure 1) as part of their bat evasion response. These sounds are produced by buckling modified metathoracic episternites, causing a series of grooves (microtymbals) in the cuticle to pop in and out, producing a series of high frequency clicks (Blest et al, 1963; Fenton and Roeder, 1974). The clicks of arctiids have been labelled as defensive but the actual mechanism by which arctiids are protected is open to debate. Three hypotheses have been proposed to explain the function of the clicks: aposematism, jamming and startle.

Dunning and Roeder (1965) showed that Myotis lucifugus trained to catch mealworms thrown in the air avoided the mealworms if moth sounds were presented as the bat closed with the target. Dunning (1968) showed that arctiids placed in small cages with M. lucifugus had a higher chance of survival if they clicked than if they

remained silent. Because many arctiids are unpalatable to predators, the clicks were identified as part of an aposematic display intended to warn experienced predators (Blest, 1964; Dunning, 1968).

Fullard, Fenton, and Simmons (1979) considered the similarity between the power spectra and time-frequency structures of moth clicks and terminal phase echolocation calls of a number of Eptesicus fuscus and suggested that the arctiid clicks jam the bats' echolocation by interfering with information processing.

Humphries and Driver (1970) suggested that the moth clicks are startle displays (deimatic of Edmunds, 1974) analogous to the sudden colour changes in fish and the underwing flashes of many Lepidoptera.

Recently, Surlykke and Miller (1985) used discrimination experiments to test the jamming hypothesis with two species of arctiids and captive Pipistrellus pipistrellus. They concluded that arctiid clicks are aposematic signals. For three reasons, their results are not convincing. Firstly, they trained the bats to sit on a platform and echolocate stationary targets, an unnatural scenario for an aerial insectivore like P. pipistrellus. Secondly, the moth clicks were presented to the bats for such lengthy periods that the bats habituated to the clicks. Thirdly, the bats were allowed unlimited time to make a choice, whereas a bat in a natural situation would

have only a very short time to make a decision. For these reasons, I have attempted to conduct a more valid test of the jamming hypothesis.

The purpose of my study was to assess the effect of arctiid clicks on the behaviour of hunting bats and to evaluate the jamming hypothesis. To do this, I used captive Megaderma lyra (Megadermatidae), and Macrotus californicus (Phyllostomidae), two species which can locate prey by echolocation (in darkness) or by vision (in light) (Fiedler, 1979; Bell, 1983; Audet, pers. comm.). An important advantage of using these two species is that they often glean prey from the ground so my experiments involved "natural" hunting scenarios with flying bats and stationary prey.

If the clicks function solely to interfere with echolocation, they should have no effect on either M. lyra or M. californicus when they are orienting by vision because these bats will ignore contradictory information from echolocation. When orienting by echolocation, both species should be disrupted by the moth clicks.

The startle hypothesis predicts that the bats would be disrupted equally in light and in dark. Acoustic startle is a reflex which is independent of echolocation so the bats should be affected whether orienting by echolocation or visually.

If clicks are aposematic, bats which have experienced unpalatable arctiids and learned to associate the sound with the taste would avoid the clicks in light and in dark. Bats with no prior experience should not be affected by the sounds in either light or dark.

MATERIALS AND METHODS

i. Housing and maintenance of animals

Three Megaderma lyra were obtained from Prof. Dr. G. Neuweiler, West Germany. These bats had been in captivity for at least eight months prior to the beginning of the experiments. Seven Macrotus californicus were collected by Dr. G.P. Bell in the Sonoran desert of California. Two of these bats had been in captivity at Carleton University for at least 2 years while the rest had been in captivity at UCLA for approximately two months before being transferred to Carleton University where they were held for another month before the experiments began. The M. lyra were housed in a flyway 2 m high, 3 m long and 1 m wide. The M. californicus were housed in a flyway 2 m high, and 2.5 m X 2.5 m. On days when no experiments were performed, mealworms were supplied in a dish on the cage floor. M. lyra were given 25 mealworms each and M. californicus were given 7 each. Fresh water was always available in dishes on the floor. Approximately once a week, each M. lyra was given one freshly sacrificed laboratory mouse.

ii. Experimental chamber

The experiments were conducted in a flyway 2 m high, 3 m long, and 1 m wide. Bats were introduced to the chamber for testing one at a time and were allowed to recover for about 10 min before the testing began. The bats were trained to hang at the end of the cage farthest from the

door, fly to a dish at the near end of the cage to pick up a mealworm, and return to the far end. The feeding dish was placed on a platform which concealed a high frequency speaker (Panasonic EAS-10TH4008) for presenting the moth sounds and a microphone connected to a bat detector (QMC S200) for monitoring echolocation calls. The bottom of the dish was made of fiberglass window screen to allow the passage of sounds from the speaker which was underneath. Figure 2 shows a schematic of the arrangement of equipment in the experimental chamber.

111. Preparation of moth sounds

I captured three species of arctiid moths at ultraviolet lights in the villages of Manotick and Chaffey's Locks, 20 km. and 150 km., respectively, south of Ottawa. Using a QMC PSM1 electrostatic microphone and a Racal Store 40 tape recorder operated at 76 cm./sec., I recorded the clicks produced by Euchaetias egle, Purrharctia isabella, and Hypoprepria fucosa. In addition, a tape of Cynhia tenera sounds was obtained from Dr. J.H. Fullard at University of Toronto. The recorded sounds were transferred to an Ampex PR500 2 track tape recorder modified to play endless tape loops. I prepared four tape loops, one for each species, with moth sounds on one channel and nothing on the other channel. Each loop was about one and a half seconds long and was made from a section of the original tape with abundant click trains.

I determined the power spectra of the moth clicks, the tape noise, and the terminal echolocation calls of the two bat species, using a Princeton Applied Research Model 4513 Fast Fourier Transformation spectrum analyser. The power spectra are given in Figures 3 and 4.

iv. Presentation of moth sounds

Output from one channel of the tape recorder at a time was fed into an ultrasonic amplifier (Simmons et al, 1979) which contained a switching circuit triggered by an external input. A "softswitch" circuit in the amplifier ensured that the amplifier turned on without any clicks or pops. The trigger input came from a set of infrared light beams (Science Technology Workshop, Carleton University) oriented perpendicular to the bats flight path about 0.5 m in front of the target. When the bat flew through the beams on it's way to the target, the amplifier switched on and sent the signals from the tape recorder to the speaker located underneath the target. The output of the amplifier was regulated so that the intensity of the moth clicks at a height of 2 cm above the dish was equal to the intensity at 2 cm from a live moth, approximately 70 dB sound pressure level (SPL) root mean square (rms) re 2×10^{-5} N/m² (Fullard and Fenton, 1977). The amplifier remained on until a reset button was pressed, which I did after the bat had flown back to the roosting end of the cage.

v. Data collection

One trial was considered to be one flight from the rear of the cage to the front and back. A trial was scored as "completed" when the bat landed on the dish and at least tried to take a mealworm. Sometimes, especially when the mealworms were almost gone, a bat would land and attempt unsuccessfully to find a mealworm. I treated these as completed trials even though the bat did not obtain a mealworm. The other possible outcome of a trial was a "balk", when the bat turned back, after flying within 0.5 m. of the target, without landing or attempting to take a mealworm.

Trials were conducted until each bat had eaten all of the mealworms or until it stopped coming to the dish. When a bat stopped feeding even though a couple of mealworms remained in the dish, the trial was stopped after 10 minutes of inactivity. Each M. californicus was given 7 mealworms in each set of trials while each M. lyra received 25.

Each trial involved one of three possible treatments: 1) a baseline with the amplifier turned off (no sound), 2) a control with the amplifier operating on the light trigger but receiving input from the blank channel of the tape recorder (equipment generated noise ie. tape hiss, amplifier switching noises), or 3) a treatment with the amplifier operating on the light trigger and receiving

input from the recorded channel (moth noises). The treatments were assigned in the following proportions; 60% baseline: 20% equipment noises: 20% moth noises. I used a random digit table (Rohlf and Sokal, 1981) to create a sequence of treatments. The starting point within the sequence was varied for each set of trials. I used Cygnia tenera as the main species of moth tested and I conducted a few trials with each of the other species to test if the bats reacted differently to various species of moths.

Trials were run in either normal room lighting, with two fluorescent light fixtures illuminating the near end of the cage, or in as close to "total darkness" as possible. The light intensity was not measured but with the lights off, it was certainly below the threshold at which the bats switch to vision because echolocation calls could be heard through the headphones of a bat detector and seen on an oscilloscope. With the lights on, echolocation calls were heard in less than 20% of the trials. With the lights on, the trials were scored visually by watching through a small opening in the opaque plastic covering the front of the cage. In the dark, a Javelin night vision scope was used to watch the bats. An array of infrared light emitting diodes lit up the cage to make watching through the scope easier. Infrared light is not visible to the naked eye so the bats were still operating in darkness.

RESULTS

The experiment involved a total of 8414 trials; 5071 baseline, 1674 control, and 1669 experimental. For each trial, I tabulated the bats' response as either "complete" meaning the bat at least attempted to take a mealworm, or as a "balk". Data were summed over individuals and days and maintained separately for the two species.

In approximately 90% of the trials in darkness, echolocation calls were detected as the bat approached the target. In trials with the lights on, echolocation calls were heard in less than 20% of the approaches.

In baseline trials, the bats typically flew directly to the dish, hovered very briefly at a height of about 20 cm and then dropped onto the platform. After nosing around in the dish to find a mealworm, the bat seized a mealworm in its mouth and flew back to the far end of the cage to eat it.

In trials involving the presentation of equipment sounds, the bats reacted to the onset of the sound by reducing their flight speed and hovering longer and at a greater height above the dish. Sometimes the bat balked when presented with the control sounds.

Almost all trials involving moth clicks resulted in the bat balking as soon as the sound began. As the bats approached the dish, their heads were directed toward the dish. As soon as the clicks began, the bats' heads snapped

up and the bats executed a quick pirouette and flew back to the far end of the cage.

The two different species behaved in much the same manner in the experiments, the only difference being that the M. californicus were somewhat more shy than the M. lyra. The M. californicus usually took longer to start feeding after being moved to the experimental cage and took longer to resume feeding after any disturbance. (eg. the experimenter sneezing) Within each species, the individuals showed no difference in responses. None of the bats ever became habituated to the moth clicks.

The data were compiled as the proportions of balks under each set of conditions. Proportions were used for ease of interpretation but the raw data were used for statistical testing. Tables 1 and 2 show the results of the trials for Megaderma lyra and Macrotus californicus, respectively. Figure 5 gives a graphical representation of the same data, showing only the results of C. tenera presentations.

I used Chi-square contingency tables to test for effects of experimental conditions and light level on the response of the bats. I examined the numbers of balks and total numbers of trials and compared between light and dark under each set of experimental conditions. Under a null hypothesis of no difference between the ratios of balks to completed trials in light and in darkness, there were no

significant differences, with chi-square values ranging between 0.08 and 3.50 giving probabilities between 0.9 and 0.1. Similarly, I tested for effects of experimental conditions by comparing the baseline to the control and to the experimental results, and comparing the control to the experimental. Under a null hypothesis of no difference between the ratios of balks to completed trials between experimental conditions, the differences were all highly significant, with chi-square values between 170 and 1000 for probabilities of much less than 0.001.

My results unambiguously show that the clicks of the moths interrupted the attacks of bats significantly more effectively than equipment noise. Furthermore, both species of bats, whether hunting by vision (in light) or by echolocation (in darkness) were equally disrupted.

DISCUSSION

Bats are thought to derive much of the useful information in echoes by timing the delay between an outgoing call and its returning echo. Suga and O'Neill (1979) found that neurons in the auditory cortex fire maximally when exposed to two sounds with a characteristic delay. The first sound is the outgoing call and the second is the returning echo. The best delays of these neurons vary in a systematic way along the axis of the cortex, providing a map of best delays from short to long delays, corresponding to near and far distances. Muscles in the inner ear dampen the direct input of echolocation calls to the cochlea (Schuller, 1979) but enough direct stimulation occurs to effectively "prime" the cortex by starting a timer (Suga and Scoville, 1973). When an echo is detected by the bat, the region of the cortex which is stimulated corresponds to the distance of the target from the bat.

The jamming hypothesis suggests that the clicks of the arctiids are initially interpreted as returning echoes by the bats' auditory system (Fullard et al, 1979) which could give rise to a number of effects. The arrival of echoes at an unexpected time could interfere with the distance perception of the bat. The sudden flurry of clicks by the moth could also be interpreted as the sudden appearance of a cluster of objects in the vicinity of the moth. The third

possibility is that the clicks simply disrupt the echolocation processing by acting as nonsense input.

The startle hypothesis differs from the jamming hypothesis by postulating a more general function for the clicks. Rather than interfering with just echolocation, startle responses interrupt the animal's whole-mental process. Edmunds (1974) describes deimatic or startle reactions as a conflict in drives. The predator is simultaneously driven to attack and to flee. This conflict in drives causes the predator to hesitate briefly, allowing the prey animal an extra bit of time to escape.

Psychological and neurological studies have shown that mammals have a startle reflex which causes a stereotyped response to sudden, unexpected acoustic and visual stimuli (Davis, 1984). The reflex has a very short latency (as short as 14ms.) and sweeps down the body at the speed of neural conduction. In mammals ranging from cats and rats to orangutans, grizzly bears and humans, the reflex involves a clenching of the jaw muscles, retraction and dorsiflexion of the neck and flexion of the limbs. The startle hypothesis suggests that the arctiid clicks function by triggering the bats' startle reflex, causing the bat to hesitate and buying the moth a little more time to escape.

Aposematism differs from the other two hypotheses in that it is a learned response. Some arctiids have toxic

chemical defences (Bisset et al, 1959) which make them unpalatable to at least some bats (Dunning, 1968). Bats which attempt to eat these moths usually reject them and they could learn to associate the clicks of the moths with the distasteful result of attacking the moth. Under this hypothesis, the palatable moths which click are Batesian mimics of the unpalatable ones.

Surlykke and Miller (1985) attempted to test the jamming hypothesis using Pipistrellus pipistrellus which they trained to discriminate distances. The bats were trained to sit on a platform, echolocate two targets, and crawl toward the nearer of the two targets. Arctiid clicks were then played from the nearer, the farther or both targets to test the bats ability to discriminate distances in the presence of moth clicks. The bats' distance discrimination abilities were unaffected by the clicks, and the bats could be trained to associate the clicks with a distasteful chemical, so Surlykke and Miller concluded that the clicks are aposematic in function. There are several serious problems with this conclusion, not the least of which is the unnatural scenario which they used.

Pipistrellus pipistrellus is an aerial insectivore which only feeds on flying insects so making them sit on platforms and echolocate stationary targets is not very realistic. In a natural encounter, a bat is travelling about 5 m/sec (Aldridge, pers. com.) so it has very little

time to react to the moth's sounds. By allowing the bat to take as long as necessary to choose a target, Surlykke and Miller removed much of the relevance from their test. In addition, they didn't adequately consider the startle hypothesis. In fact, when they first presented moth clicks to the bats, the bats were so startled that they flew off the platform. By repeatedly placing the bats back on the platform and playing the sounds, Surlykke was able to habituate the bats to the clicks. She then concludes that a startle function is unlikely because it would only work if the clicks were infrequently encountered. For these reasons, I find Surlykke and Miller's conclusions questionable and I have attempted to conduct a more valid test of the jamming hypothesis.

My results clearly show that the bats are disturbed by the moth clicks in both light and dark conditions. In the few cases where the bats did not use echolocation in darkness, they were presumably using spatial memory to fly to the expected location of the target (Gaudet, 1983; Neuweiler and Mohres, 1967). In the rest of the trials in darkness, the bats were orienting by echolocation. In light conditions, the bats were orienting by vision (Bell and Fenton, 1986) but were still disrupted in their attacks by the moth clicks. This indicates that jamming can't be the sole function of the moth clicks. The auditory system of the bat is optimized to collect, amplify and analyse

echolocation calls so even if the bat is not echolocating, those are the type of sounds that it is best equipped to hear. Therefore, if a moth was to evolve a sound directed at bats, it would converge on the most effective sound, namely something which resembled an echolocation call.

If I assume that all of the bats had previous experience with clicking, distasteful arctiids, then my results are consistent with both the startle and aposematic hypotheses. However, there are some points that make the aposematic hypothesis unlikely. Firstly, the moth clicks were never paired with any unpleasant stimuli so there was no reason for the bats to learn an aversion to the clicks. The bats had been in captivity for periods ranging from 2 months to 2 years before the experiments began, during which time the bats had no exposure to moths. It seems unlikely that all of the bats would retain a previously learned aversion for that length of time without any negative reinforcement. On 27 occasions, a bat did not balk when presented with moth clicks and obtained a mealworm, which it ate with no ill effects. Under these circumstances, the bat could have learned that the clicks were not an indicator of distastefulness, and should then have learned to ignore the clicks. Since none of the bats ever learned to ignore the clicks, I conclude that the bats were disrupted by the clicks for some reason other than a learned aversion.

Edmunds (1974) defines aposematism as a primary defence, a strategy which involves deterring a predator before an attack takes place. For this reason, most aposematic displays are conspicuous and continually displayed. Startle displays are defined as secondary defences, invoked only when an attack is imminent. Many Lepidoptera have brightly coloured underwings which are normally hidden and suddenly exposed to attacking diurnal predators when the butterfly or moth is disturbed. The short duration of a predator's startle reaction requires that the prey wait until the predator is very near before presenting a startle display.

The sounds of arctiid moths appear to be secondary defences because they are produced when the bat is very close (about 0.5m). If a moth was attempting to identify itself to an experienced predator, it would make sense to click at a greater distance to provide a greater margin of error. By producing a startling sound about 0.1 sec before the bat would catch it, the moth takes advantage of the bat's brief hesitation. This hesitation, in conjunction with the moth's erratic evasive manoeuvres, gives the moth an advantage over the bat. This strategy is only viable if the clicking arctiids are rare enough that the bats can't habituate to the sounds.

One point that comes out of this is the importance of time in predator-prey encounters. The reaction time of a

predator to capture a prey item is often limited, especially for flying, echolocating bats when even a very brief hesitation could allow the prey to escape. For this reason, mechanisms like startle displays can be effective predator deterrent strategies.

FUTURE RESEARCH

In order to retain their effectiveness, startle displays have to be rare because startle reactions habituate with frequent exposure. One of the obvious extensions of my work would be to determine how common clicking arctiids could be and still be effective.

It is still possible that moth clicks could interfere with echolocation in some circumstances. One way to test the effect of echo-like sounds on a bat using echolocation would be to play the bat's own terminal phase calls as the bat was closing with a target.

It would also be possible to habituate bats to the clicks and then test their ability to orient while flying in the presence of moth clicks. This would eliminate the effects of startle reactions and determine if the clicks had any effect on echolocation.

Testing the effects of moth clicks on bats which use constant frequency calls would indicate whether the clicks have to mimic echoes to be effective. The frequency modulation and wide bandwidth of the moth clicks make them quite different from the calls of constant frequency bats so mimicry is unlikely.

Naive bats would presumably have no knowledge of arctiids and so would make ideal subjects for a study to separate the roles of startle and aposematism.

CONCLUSIONS

1) Clicks produced by four species of Arctiid moths (Cynia tenera, Hypoprepria fucosa, Purrharctia isabella, and Euchaetias egle) interrupted the attacks of Megaderma lyra and Macroctus californicus significantly more than equipment noise.

2) The clicks were equally effective in light, where the bats orient by vision, and in darkness, where the bats orient by echolocation, indicating that the clicks do not act solely to jam echolocation.

REFERENCES

- Bell, G.P. 1985 The sensory basis of prey location by the California leaf-nosed bat Macrotus californicus (Chiroptera: Phyllostomidae). Behav. Ecol. Sociobiol. 16:343-347
- Bell, G.P. and Fenton, M.B. 1986 Visual acuity, sensitivity and binocularity in a gleaning insectivorous bat, Macrotus californicus (Chiroptera: Phyllostomidae). Anim. Behav., In press
- Blest, A.D. 1964 Protective display and sound production in some New World arctiid and ctenuchid moths. Zoologica (NY) 49:161-181
- Blest, A.D., Collett, T.S. & Pye, J.D. 1963 The generation of ultrasonic signals by a New World arctiid moth. Proc. R. Soc. London Ser. B. 158:196-207
- Davis, M. 1984 The mammalian startle response. In. Neural mechanisms of startle behavior. R.C. Eaton ed. Plenum Press New York
- Dunning, D.C. 1968 Warning sounds of moths. 2. Tierpsychol. 25:129-138
- Dunning, D.C. & Roeder, K.D. 1965 Moth sounds and the insect-catching behavior of bats. Science 147(3653):173-174

- Edmunds, M. 1974 Defence in animals. Longmans, Essex
- Fenton, M.B. 1984 Echolocation: Implications for ecology and evolution of bats. Quart. Rev. Biol. 59:33-53
- Fenton, M.B. & Roeder, K.D. 1974 The microtymbals of some Arctiidae. J Lepidopt Soc 28(3):205-211
- Fiedler, J. 1979 Prey catching with and without echolocation in the Indian False Vampire (Megaderma lyra). Behav. Ecol. Sociobiol. 6:155-160
- Fullard, J.H. & Fenton, M.B. 1977 Acoustic and behavioural analyses of the sounds produced by some species of Nearctic Arctiidae (Lepidoptera). Can J Zool 55:1213-1224
- Fullard, J.H., Fenton, M.B. & Simmons J.A. 1979 Jamming bat echolocation: the clicks of arctiid moths. Can J Zool 57:647-649
- Gaudet, C.L. 1983 Behavioural basis of foraging flexibility in three species of insectivorous bats; an experimental study using captive Antrozous pallidus, Eptesicus fuscus and Myotis lucifugus. Msc Thesis, Carleton University, Ottawa
- Griffin, D.R. 1958 Listening in the dark. Yale Univ Press, New Haven

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

Miller, L.A. & Olesen, J. 1979 Avoidance behavior in green lacewings I. Behavior of free flying green lacewings to hunting bats and ultrasound. *J Comp Physiol* 131:113-120

Moiseff, A., Pollack, G.S. & Hoy, R.R. 1978 Steering responses of flying crickets to sound and ultrasound: Mate attraction and predator avoidance. *Proc. Nat. Acad. Sci. U.S.A.*, 75:4052-4056

Neuweiller, G. & Mohres, F.P. 1967 The role of spatial memory in the orientation of bats, pp.129-140. IN *Animal sonar systems Vol. 1* (R.G. Busnel, ed.), Jouy-en-Jonas, France.

Roeder, K.D. 1967 *Nerve cells and insect behavior*, rev edn. Harvard Univ Press, Cambridge

Roeder, K.D. & Treat, A.E. 1961 The detection and evasion of bats by moths. *Am. Sci.* 49:135-148

Rohlf, F.J. & Sokal, R.R. 1981 *Statistical Tables* 2nd. Ed. W.H. Freeman and Co., San Francisco

Schuller, G. 1979 Vocalisation influences auditory processing in collicular neurons of the CF-FM bat *Rhinolophus ferrumequinum*. *J Comp Physiol* 132:39-46

- Simmons, J.A., Fenton, M.B., Ferguson, W.R., Jutting, M. & Palin, J. 1979 Apparatus for research on animal ultrasonic signals. Life Sci. Misc. Publ. R. Ont. Mus.
- Suga, N. & O'Neill, W.E. 1979 Neural axis representing target range in the auditory cortex of the moustache bat. Science 206:351-353
- Suga, N. & Schlegel, P. 1973 Coding and processing in the auditory systems of FM-signal-producing bats. J Acoust Soc Am 54(1):174-190
- Surlykke, A. & Miller L.A. 1985 The role of arctiid moth clicks on bat echolocation: jamming or warning? J Comp Physiol 156:831-843
- Yager, D.D. & Hoy, R.R. 1986 The cyclopean ear: a new sense for the praying mantis. Science 231(4739):727-729

Table One Results of experiments with Megaderma lura
Results are presented as proportions of balks
under each set of conditions. The numbers in
brackets are the total numbers of trials.

<u>Conditions</u>	<u>Light</u>	<u>Dark</u>
Baseline	0.15 (1561)	0.18 (1182)
Control	0.47 (515)	0.53 (388)
<u>Cygnia tenera</u>	0.97 (449)	0.98 (326)
<u>Hypoprepria fucosa</u>	1.0 (24)	0.96 (25)
<u>Purcharctia isabella</u>	1.0 (25)	1.0 (23)
<u>Euchaetias egle</u>	1.0 (21)	1.0 (29)

Table Two Results of experiments with Macropus
californicus.

<u>Conditions</u>	<u>Light</u>	<u>Dark</u>
Baseline	0.17 (1209)	0.18 (1119)
Control	0.53 (392)	0.54 (379)
<u>Cygnia tenera</u>	0.99 (333)	0.99 (290)
<u>Hypoprepria fucosa</u>	0.96 (23)	1.0 (20)
<u>Purcharctia isabella</u>	1.0 (22)	1.0 (23)
<u>Euchaetias egle</u>	1.0 (18)	1.0 (18)

FIGURE ONE

Train of clicks produced by Cycnia tenera in response to handling. This train shows nine clicks in the active phase of the modulation cycle, and four clicks in the passive, or recovery phase. The active phase is the part of the cycle produced by the contraction of the muscles which cause the microtymbals to pop inwards. This is followed by the relaxation of the muscles, allowing the microtymbals to pop back out

1 ms

FIGURE TWO

Schematic diagram of experimental apparatus. The bats were trained to hang at the end of the cage away from the food dish and fly to the dish and back. The broken line indicates a typical flight path. The dashed line shows the location of the infra-red light beams which activated the amplifier when the bat came within 0.5 m. of the target dish. The night vision scope and infra-red light array used for observation in the darkness are not shown.

FIGURE THREE

Power spectra of sounds played to the bats.

- A) Cucnia tenera
- B) Mypoprepria fucosa
- C) Purrharctia isabella
- D) Euchaetias egle
- E) tape noise

FIGURE FOUR

Power spectra of A) Megaderma lyra and B) Macrotus californicus terminal phase echolocation calls.

FIGURE FIVE

* Percent balks for the two species of bats (Megaderma lyra and Macrotus californicus) in light and in darkness. The baseline trials were with no sounds presented, the controls were with tape noise, and the C. tenera were with the clicks of Cynia tenera presented. The results for the other three species of moths are identical and were omitted from this figure for clarity.

Percent balks in

PERCENT BALKS

100
80
60
40
20

NO. OF TRIALS 1561 1182 515 388 449 326 1209 1119 392 379 333 290

TREATMENT Baseline Control C. tenax Baseline Control C. tenax

SPECIES Megaderma lyca

Macrotus californicus

PLATE ONE

Megaderma lyra approaching the target.

PLATE TWO

Megaderma lyra in flight.

END

FIN

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