# JAMMING BAT ECHOLOCATION: THE DOGBANE TIGER MOTH *CYCNIA TENERA* TIMES ITS CLICKS TO THE TERMINAL ATTACK CALLS OF THE BIG BROWN BAT *EPTESICUS FUSCUS*

JAMES H. FULLARD

*Department of Zoology, Erindale College, University of Toronto, Mississauga, Ontario, Canada L5L 1C6*

JAMES A. SIMMONS AND PRESTOR A. SAILLANT

*Department of Neuroscience, Brown University, Providence, RI 02912, USA*

## Summary

Certain tiger moths emit high-frequency clicks to an attacking bat, causing it to break off its pursuit. The sounds may either orient the bat by providing it with information that it uses to make an attack decision (aposematism) or they may disorient the bat by interrupting the normal flow of echo information required to complete a successful capture (startle, jamming). At what point during a bat's attack does an arctiid emit its clicks? If the sounds are aposematic, the moth should emit them early in the attack echolocation sequence in order to allow the bat time to understand their meaning. If, however, the sounds disrupt the bat's echo-processing behaviour, one would expect them to be emitted later in the attack to maximize their confusion effects. To test this, we exposed dogbane tiger moths (*Cycnia tenera*) to a recording of the echolocation sequence emitted by a big brown bat (*Eptesicus fuscus*) as it attacked a stationary target. Our results demonstrate that, at normal echolocation intensities, *C. tenera* does not respond to approach calls but waits until the terminal phase of the attack before emitting its clicks. This timing is evident whether the moth is stationary or flying and is largely independent of the intensity of the echolocation calls. These results support the hypothesis of a jamming effect (e.g. 'phantom echoes') and suggest that, to determine experimentally the effects of arctiid clicks on bats, it is important that the bats be tested under conditions that simulate the natural context in which this defence operates.

## Introduction

Many moths avoid hunting bats by listening for their echolocation calls and taking evasive manoeuvres to escape predation (Roeder, 1967). Besides these flight defences, certain tiger moths (Arctiidae) emit high-frequency clicks, causing an attacking bat to break off its pursuit (Dunning and Roeder, 1965). The clicks are generated by a pair of

thoracic tymbals and, although something is known about the acoustic features of the sounds and the mechanisms of sound production (Blest *et al.* 1963; Dunning, 1968; Fullard and Fenton, 1977; Fullard, 1982, 1984, 1992; Fullard and Heller, 1990), why the clicks cause the bat to end its attack is the subject of debate. Presently, there are three (not necessarily mutually exclusive) proposed mechanisms: (1) aposematism, the sounds remind the bat of the moth's noxious qualities (e.g. bad taste) (Dunning and Roeder, 1965); (2) jamming, the sounds confuse the bat by generating phantom echoes (Fullard *et al.* 1979); and (3) startle, the sounds simply surprise the bat (Edmunds, 1974; Bates and Fenton, 1990). A simple way of categorising these mechanisms is that they either orient the bat by providing it with information that it uses to make an attack decision (aposematism) or that they disorient the bat by interrupting the normal flow of echo information required to complete a successful capture (jamming, startle).

The challenge of understanding how arctiid sounds operate against bats arises from the difficulty of observing these animals in natural situations. The rapid flight of bats coupled with the rapid attenuation (to the observer) of the moth sounds because of their high frequencies (Lawrence and Simmons, 1982) makes it presently impossible to quantify how the two participants in this encounter perform their actions. As a result, experiments that attempt to simulate this encounter have used artificial designs to infer the natural function of the clicks. Some of these experiments have exposed live bats to moth clicks to test whether their decision-making abilities are hindered in the presence of the moth sounds (Dunning and Roeder, 1965; Surlykke and Miller, 1985; Stoneman and Fenton, 1988; Bates and Fenton, 1990; Miller, 1991). They generally concluded that disorientation is not an important effect. The other approach has been to expose arctiids to bat-like sounds and, by determining the sounds to which the moth is most sensitive, extrapolating to their effects on the bat (Fullard and Fenton, 1977; Fullard, 1979, 1982, 1984, 1992). Most of these experiments have favoured a disorientation effect.

At what point during a bat's attack does an arctiid emit its clicks? If the sounds are aposematic, the moth should emit them as early as possible in the bat's attack echolocation sequence to allow the bat enough time to react to them. If, however, the sounds disorient the bat, they should be emitted later in the attack to maximize their confusion effects by denying the bat enough time to adjust. As an indirect means of estimating the distance from an approaching bat that an arctiid responds, researchers have measured the behavioural thresholds of tiger moths to artificial bat sounds but have arrived at considerably different values (2–3 m, Surlykke and Miller, 1985; 0.5–1 m, Fullard, 1984). The behavioural thresholds obtained from most of these experiments are, however, based upon acoustic stimuli (e.g. 5–10 ms, constant-frequency sound bursts) that do not accurately simulate the details of the natural echolocation sequence of an attacking bat. Arctiids will emit their sounds in response to a variety of sounds (e.g. hand slaps, key jingles) that bear little resemblance to bat echolocation calls. Microchiropteran bats, as they close upon a target, change their echolocation pulse design depending upon the acoustic environment in which they hunt (Simmons *et al.* 1979). Bats begin their pursuit of prey while in the search mode, emitting pulses with long durations and inter-pulse intervals. Once they have detected a potential prey item, they decrease their pulse duration, shorten the time between pulses and change the intensities of the pulses as they

proceed from the search phase to the capture of the target through the approach, track and terminal phases of the echolocation attack sequence (Kick and Simmons, 1984). To determine more empirically the natural response of an arctiid to the approach of a hunting bat, we have used a recording of the attack sequence of echolocation calls emitted by the big brown bat (*Eptesicus fuscus* Beauvois) as a playback to the dogbane tiger moth (*Cycnia tenera* Hübner).

## Materials and methods

### Animals

To guard against colony-induced abnormalities (Richerson and Cameron, 1974; Pallas and Hoy, 1986; Cardone and Fullard, 1988), *C. tenera* were reared in the field from eggs collected from wild specimens captured at the Queen's University Biological Station in Chaffeys Locks, Ontario, Canada, raised to pupae on local plants (*Apocynum androsaemifolium* and *A. cannabinum*) and stored in constant-temperature rooms at 4 °C with a 12 h:12 h light:dark photoperiod for 5 months. Pupae were transferred to 16 h:8 h light:dark rooms at 25 °C and adults emerged 2–3 weeks later. Adults were allowed to mature for 24–48 h and then tested during the nocturnal part of their circadian cycle.

### Playback procedures

Individual moths (males and females) were fastened to the head of a dissecting pin with a drop of molten Cenco Softseal Tackiwax and put into a Faraday cage lined with sound-attenuating foam. The moth was suspended 20 cm from a Technics EAS10TH400B speaker positioned to simulate the approach of a bat from a dorsal angle of approximately 45 °. All moths were placed with the speaker on their right side. Moths were positioned under red light and left in complete darkness for 20 min before playbacks began.

Playbacks consisted of a tape recording of an *Eptesicus fuscus* made in the laboratories at Brown University, Providence, Rhode Island, USA. We used the calls of *E. fuscus* because this species feeds on moths (Black, 1972) and is sympatric with *C. tenera*. In our field site (south-eastern Ontario), *C. tenera* is not a common arctiid (Ward *et al.* 1974) but exists syntemporally with *E. fuscus* in the summer months of June and July (Fullard, 1977*a*). The recordings used in the playbacks were made from wild bats captured in house attics in Rhode Island and Massachusetts. Bats were trained to capture meal worms tethered to the end of a string while in flight and emitting entire attack echolocation sequences in a sound-absorbing foam lined room (4.3 m×2.7 m×10.5 m). Once bats could capture mealworms, they were trained to fly along a prescribed path around a post and towards a stationary target. The bats therefore express the flight and echolocation behaviour of a bat in an attack sequence approximately 15 m from a target. After the bats had been trained to attack a mealworm, a Knowles electret microphone, type ET1759 (0.8 cm×0.5 cm×0.2 cm), was substituted for the mealworm on alternate trials and recordings of the subsequent attack on the microphone were made onto a Lockheed Electronics Store 4D tape recorder, after being bandpass-filtered between 10 and 100 kHz (Rockland, model 442). These recordings were digitized and low-pass filtered at 6 dB per octave to partially correct for the microphone's frequency bias. With these settings, the

Knowles microphone is flat (±2 dB) from 10 to 30 kHz with a 6 dB per octave roll-off from 30 to 85 kHz. One of these recordings was used as the stimulus playback to the moths.

The recording was played from a RACAL Store 4D tape recorder at 30 inches s$^{-1}$ and amplified with a Epitek 1210 amplifier. Playback intensities were adjusted so that the highest amplitude signal in the playback equalled the following intensities (dB re SPL as measured with a pure 25 kHz tone played back at identical amplitudes, Stapells *et al.* 1982): 82 dB, 88 dB, 94 dB, 100 dB and 104 dB. According to the recorded amplitudes, 94 dB represents the actual intensity emitted by the bat at the time of recording. The playback was presented to the moth at randomly chosen intensities at 2 min intervals. A Larson-Davis type 2520 1/4 inch microphone preamplified by a type 2200C power supply was positioned 3–4 cm from the moth's ventrum to record the moth's clicks while minimizing reflection from the echolocation playback signals. The echolocation playback signals and moth clicks were recorded onto a second RACAL tape recorder running at 30 inches s$^{-1}$.

## Results

Thirty-two moths were run in the playback trials, of which 19 phonoresponded (produced clicks) to the stimulus tape playback when delivered at 104 dB. Of these 19 moths, 15 responded to 100 dB and eight to 94 dB. No moths responded to 88 or 82 dB playbacks (cf. Fullard, 1984). Fig. 1 describes the acoustic response of one moth to a 94 dB playback. The echolocation attack sequence lasts for approximately 1.1 s and consists of 44 calls in three phases, defined by their inter-pulse intervals (Kick and Simmons, 1984): approach (calls 1–9), track (calls 10–15) and terminal (calls 15–43). The initial calls in this recording never lasted longer than 3 ms, values similar to search call durations reported from other laboratory studies (Griffin, 1974). Since the search calls of wild *E. fuscus* average 10.6 ms (range 3.4–19.7 ms) in open flight environments (Obrist, 1989), we have identified the initial calls in our playbacks as approach. Calls increase in amplitude throughout the approach and track phase as the bat approaches the microphone. At the beginning of the terminal phase, the amplitudes of the calls become constant and then diminish as the bat responds to the echoes returning from the target (Kick and Simmons, 1984). Fig. 1 also shows the moth's click phonoresponse commencing at the bat's twelfth echolocation call (track phase), reaching its highest emission rate during the terminal phase and persisting past the last call in the sequence. The clicks are emitted as trains called modulation cycles (Blest *et al.* 1963, Fig. 1, MC) that consist of two components: (1) the active modulation half-cycle (Fig. 1, AMHC), caused by the collapse of the tymbal surface under the force of the tymbal musculature and (2) the passive modulation half-cycle (Fig. 1, PMHC) emitted as the tymbal surface returns to its resting position.

Fig. 2 summarizes the playback results for all the moths tested. The click density (the numbers of clicks emitted for every 40 ms of the playback) were counted and displayed as frequency histograms for each of the three playback intensities that elicited responses from the moths. At 104 dB, the highest average click density occurs 831.5 ms from the
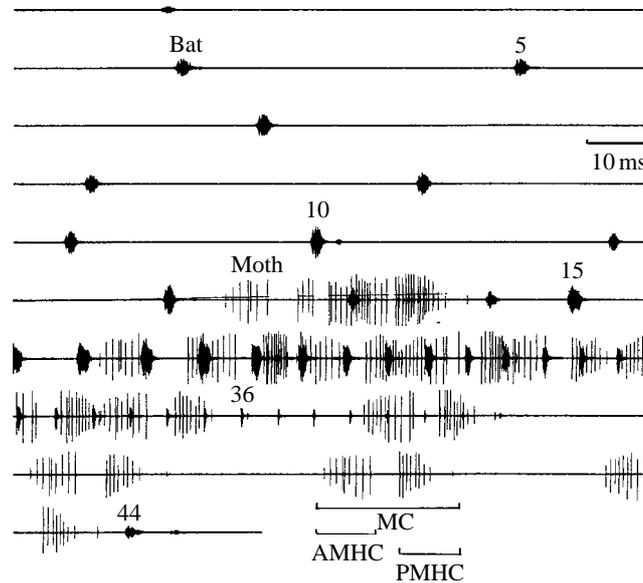
Fig. 1. Oscillogram of the playback attack echolocation sequence of *Eptesicus fuscus* at 94 dB with the clicking response of a stationary *Cycnia tenera*. The sounds of the speaker (bat) and of the moth (moth) were tape recorded and are displayed in the figure. The numbers above the individual bat calls refer to the number of the call in the sequence. The components of the phonoresponse of *C. tenera* are also displayed in the trace (MC, modulation cycle; AMHC, active modulation half-cycle; PMHC, passive modulation half-cycle).

start of the recording, during the terminal phase of the attack sequence. At this point, *C. tenera* moths emit a mean of 26.7 clicks per 40 ms (667.5 clicks s$^{-1}$). At lower playback intensities, the mean click density is lower [100 dB, 14.0 clicks per 40 ms (350 s$^{-1}$); 94 dB, 6.0 clicks per 40 ms (150 s$^{-1}$)] and the response occurs later in the attack sequence (100 dB, 905.4 ms; 94 dB,: 957.8 ms), but always within the terminal phase. At no time did any moths click in response to early approach phase echolocation calls. The timing displayed in Fig. 2 is not an artefact of the particular sampling period chosen (40 ms) as demonstrated by the results from one moth also sampled at 20, 10 and 5 ms (Fig. 3).

Since the moths used in these trials were stationary, playbacks were conducted with specimens induced to fly by gently blowing on their heads. Most moths in these trials did not continue flying throughout the playback [the normal reaction of arctiids when attacked by bats is probably first to fly erratically (Agee, 1969) and then to cease flying (Fullard, 1979) (but see Dunning *et al.* 1992)]. The results from two moths that did sustain flight throughout the playback are displayed in Fig. 4 and suggest that flight does not change the point at which clicks are issued. Whether *C. tenera* is flying or not, it times its clicks to the terminal phase of the attack sequence of *E. fuscus*.

To examine the relationship between the moth clicks and the echolocation calls at the time when the moth emits its sounds, the temporal characteristics of the 44 calls in the echolocation sequence were compared with the acoustic variables of all of the moth clicks
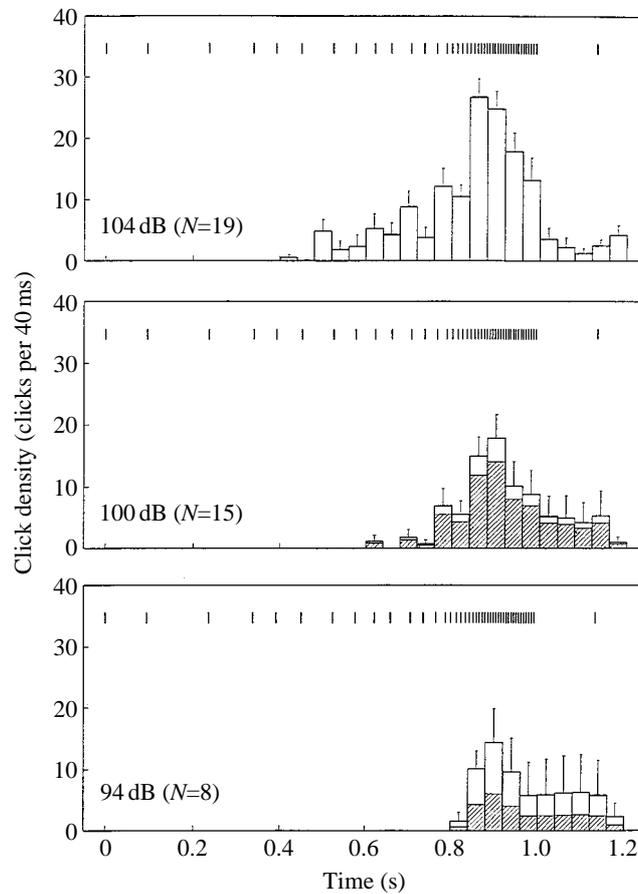
Fig. 2. Results of the playback experiments to stationary *Cycnia tenera* indicate that it phonoresponds to a bat as it is in the terminal phase of its attack sequence. For each playback intensity (104, 100 or 94 dB), the bat's individual calls are indicated by vertical lines commencing from time zero (the start of the playback). The moth clicks were counted and are displayed as click density (number of clicks per 40 ms) using the same time scale. For playback intensities of 100 and 94 dB, the results of the moth response are shown for those that responded (open bars, sample sizes in parentheses) as well as for all of the moths tested (*N*=19) (hatched bars). Values are means; standard error bars are shown only for moths that responded.

(*N*=1288) (Fig. 5). Fig. 5A illustrates the decrease of the bat's call period (measured as the time from each pulse to the preceding pulse) from 100 ms to approximately 10 ms during the approach and track phase. The terminal phase is characterised by a sudden reduction in inter-pulse interval to 4 ms (the 'terminal buzz'), where it remains for the terminal phase. *Cycnia tenera* phonoresponds in the bat's terminal phase with clicks of intervals ranging from 0.001 to 128.75 ms (mean 1.86 ms). Fig. 5B compares the durations of the bat calls to those of the moth clicks. The bat maintains a steady pulse duration of 2–4 ms (mean 2.74 ms) until approximately one-third of the time into its terminal phase, when it steadily reduces its pulse duration to a minimum of 0.32 ms. The
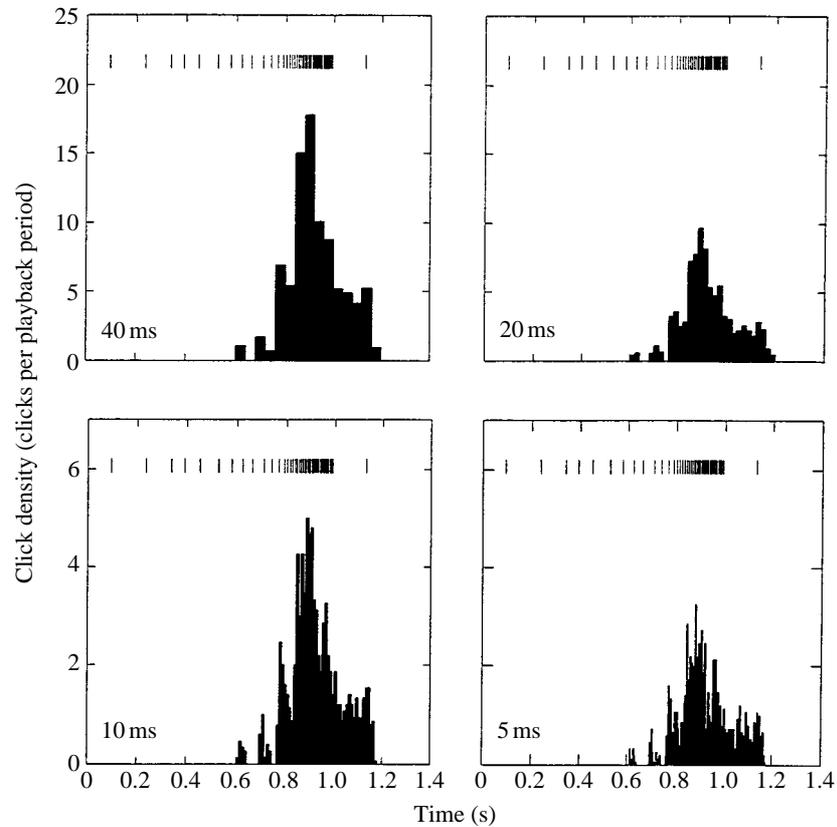
Fig. 3. The timing of the moth's response is not an artefact of the sampling period used to measure click density. For responses to the 100 dB playback intensity, four different periods were chosen using the same time scale as that of the playback recording. For further details, see Fig. 2.

moth emits clicks with a relatively consistent duration ranging from 0.002 to 0.275 ms (mean 0.102 ms) throughout the terminal phase of the bat's attack sequence.

Fig. 6 describes the acoustic structure of two bat calls within the attack sequence and three moth clicks. Both the duration and frequency structure of the calls change between the bat's approach and terminal phases and there is considerable acoustic variation among the clicks. These variations can result in a wide diversity of call/click cross-correlation functions (CCFs), with peak values ranging from less than 0.1 to over 0.3 (examples are shown in Fig. 6C). The lowest CCFs observed were between clicks and early approach phase calls and the highest were between clicks and terminal calls.

## Discussion

Debate continues about the defensive effects of arctiid clicks on bats, and we stress that our study deals with only two species, *C. tenera* and *E. fuscus*, and that our conclusions may not apply to other arctiids and bats. Nevertheless, our results demonstrate that
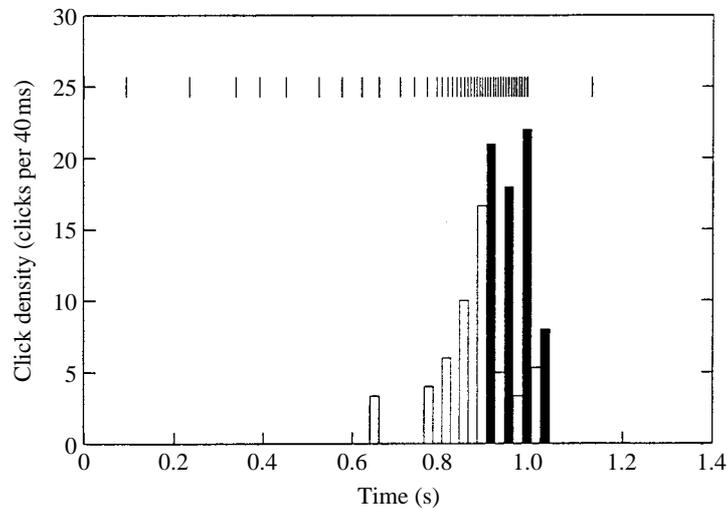
Fig. 4. The phonoresponses of two *Cycnia tenera* in tethered flight (CT23, open bars, and CT31, filled bars). Although the total number of clicks is reduced, their timing (within the terminal phase) is similar to that observed for stationary moths.

*C. tenera* emits its clicks in response to an attacking *E. fuscus* when this bat is in the terminal phase of its echolocation sequence and support the theory that the sounds have a jamming function. These results further suggest that the clicks of *C. tenera* do not operate as aposematic signals against the aerial attacks of bats. Typically, aposematic animals either display their warning advertisements continually (primary defence) or alert their potential predators as soon as they are discovered (secondary defence) (Edmunds, 1974). The ears of *C. tenera* can detect pulsed 30 kHz sounds at intensities of 55–65 dB (E. Budziak, unpublished data), indicating that this species will first detect an approaching bat when it is still in its search phase and could produce its sounds earlier than the terminal phase. The observation that *C. tenera* does not phonorespond until late into the bat's attack [as predicted by the behavioural thresholds in Fullard (1984)] suggests that the function of the clicks is not to orient the bat by means of an aposematic message. While we recognize that our results cannot prove that aposematism does not operate against flying bats, we feel that our study allows us to re-interpret the conclusions of others that have discounted the role of jamming as a natural function for the clicks. We also stress that, in our discussion, we limit the definition of jamming to the creation of false (phantom) echoes of sufficient quality to create the perception of objects in the path of an attacking bat.

Fullard *et al.* (1979) suggested that the similarity between the clicks of *C. tenera* and *E. fuscus* indicated the moth's sounds would be perceived as phantom echoes by the attacking bat. The present study demonstrates that this jamming effect will only be evident during the last 200–400 ms of the bat's attack, in its terminal phase. It is reasonable to predict that, if arctiid clicks act as phantom echoes, the clicks should resemble the acoustic structure of bat calls. A comparison of the clicks of *C. tenera* with the terminal calls of *E. fuscus* (Fig. 5) suggests that, even at the terminal phase, the duration of the moth sound is too short to mimic a bat's call effectively. The auditory
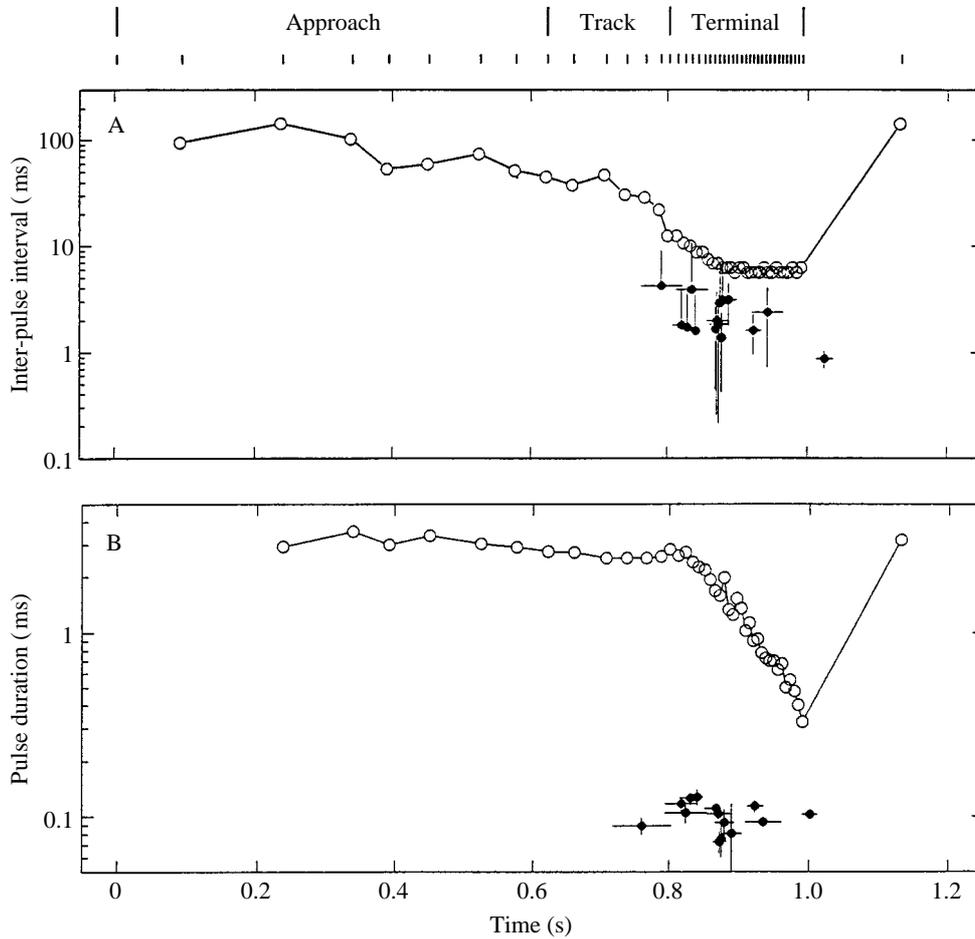
Fig. 5. A comparison of the temporal characteristics of each of the pulses of the echolocation sequence (open circles) (played at 100 dB) with those of the moth clicks (filled circles). The moth clicks from each individual tested are plotted as the average (± 99 % confidence interval) time they are emitted and the average (± 99 % confidence interval) temporal characteristic displayed. Above the graphs are the individual pulses with the echolocation phases as defined by Kick and Simmons (1984).

integration time for *E. fuscus* (200–400 $\mu$s, Simmons *et al.* 1989; 2 ms, Møhl and Surlykke, 1992), however, is longer than the duration of the clicks, and we suggest that each of the moth's clicks, when processed by the bat's auditory system, will be stretched by a ringing effect lasting at least as long as the integration time of the ear, thus amplifying the effective duration of each of the clicks. Since *C. tenera* emits trains of rapidly repeated clicks, the effect of the integration time of the bat's ear should be to cause each click to run into the one following it, resulting in severe interference with the perceptive processes used by the bat that depend upon spectral information.

As another method of comparing moth and bat sounds, Miller (1983) presented cross-correlation functions (CCFs) of the clicks of the European arctiid *Arctia caja* to the 'pre-
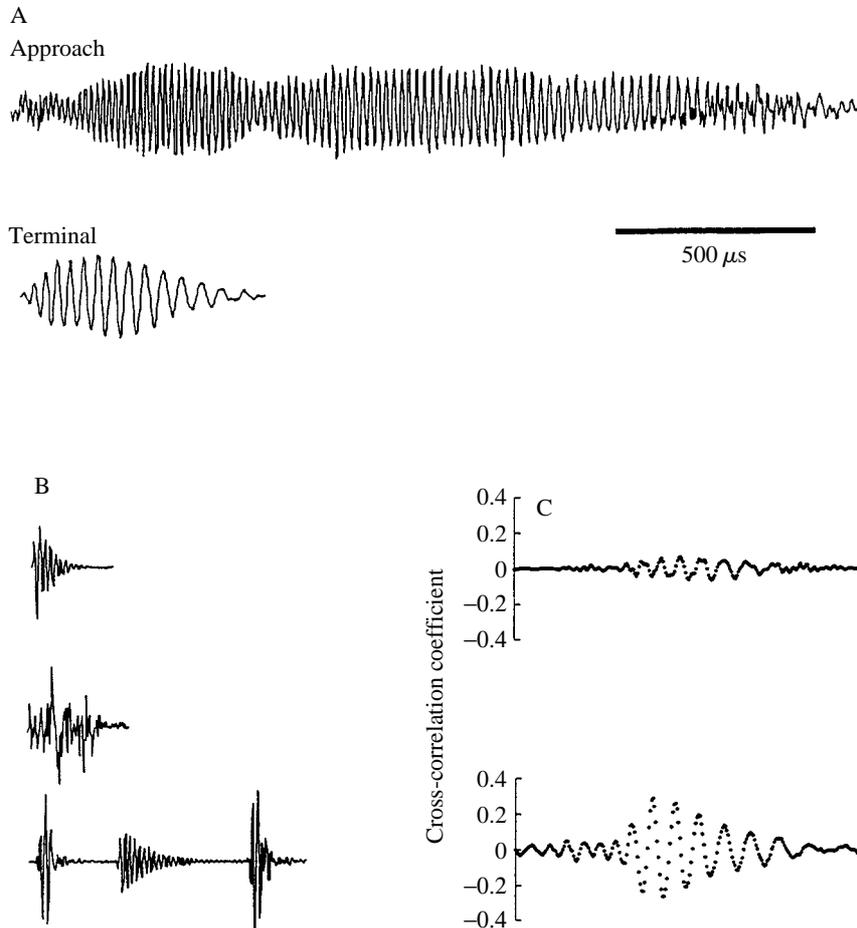
A

Approach



Terminal

500 μs



Fig. 6. (A) Two calls from the bat's attack sequence differ in their durations and frequency structures. (B) A selection of randomly chosen clicks from three *Cycnia tenera* also indicate that variation exists in their acoustic structure both within and between individuals. (C) These call/click variations can result in cross-correlation functions (CCFs) of differing maximum values (the top CCF is between a click and an approach call while the bottom is between a click and a terminal call).

buzz' (the actual phase was not specified) calls of *Eptesicus serotinus* and concluded that the low CCF values indicated that phantom echoes could not be a role for arctiid clicks. In the light of the present study, the relevance of the CCFs reported by Miller (1983) depends upon the phase of the attack sequence of *E. serotinus* during which *A. caja* emits its clicks. Fig. 6 indicates that a variety of CCFs can be obtained, depending upon which click is correlated with which call. Our results, however, suggest that the only CCFs that are relevant (at least for interactions between *C. tenera* and *E. fuscus*) are those *between clicks and terminal phase calls*. Other arctiids may produce their clicks earlier in a bat's attack (Surlykke and Miller, 1985), but these predictions have not been tested using complete echolocation sequences. Surlykke and Miller (1985) cross-correlated search and terminal

calls of the bat *Pipistrellus pipistrellus* against a single synthetic click of *Phragmatobia fuliginosa* and also used low CCF values to argue against a phantom echo effect, since the cross correlations between moth clicks and bat calls are lower than the autocorrelation of the bat's call itself. The decorrelation (i.e. acoustic dissimilarity) of the moth clicks reported by these authors could, however, be overcome by the high amplitude of the moth's click, as perceived by the bat *in its terminal phase*. Surlykke and Miller's (1985) conclusions were based on the assumption that moth clicks are emitted when a bat is farther away (i.e. during the approach phase) than our study suggests. We suggest that a critical point in these cross-correlation arguments is that the relevant CCF in the bat/arctiid comparisons is not that between the moth click and the bat call but that between the click and the call's *echo*. Since moths are three-dimensional objects with bodies and wings covering 1–2 cm in space, the echoes of a bat's call will return to the bat extended over 100–120 $\mu$s, arriving as a series of replicas of the bat's emitted call. A moth click, when received by a bat in its terminal phase, should result in an auditory cross correlation that will simulate the echo of the bat's call. Echoes are complex phenomena, and we suggest that simple CCFs between bat calls and moth clicks will not demonstrate the degree to which a bat might be fooled into believing that the clicks represent actual objects.

A more empirical critique of the jamming hypothesis arises from the results of Surlykke and Miller (1985) and Miller (1991), who exposed bats to artificial arctiid clicks while observing their echo discrimination performances and concluded that, because the bats in these experiments were not sufficiently confused by moth sounds, jamming was not their natural function. These experiments used *non-flying* bats that were either not emitting terminal calls or were emitting them unrelated to the natural timing of the moth's clicks (which was undetermined). These bats were mostly using search and approach calls and were not under the stress associated with flying in cluttered environments, and we suggest that there is little similarity between a stationary bat in a searching mode and a flying one in the terminal phase of its attack mode when it reaches speeds up to 10 m s$^{-1}$ (Norberg, 1987). Any *unexpected* event (e.g. the sudden appearance of phantom echoes) occurring during this phase will momentarily interrupt the bat's information processing and should evoke a break-off flight reflex, such as those reported in wild bats exposed to arctiid clicks (Dunning *et al.* 1992). The bats used by Surlykke and Miller (1985) and Miller (1991) were trained, resting animals in controlled, familiar surroundings. They were neither surprised by the moth sounds in these experiments nor received any penalties for making wrong decisions, as would be the case for free-flying animals. Also, the moth sounds used in the experiments of Surlykke and Miller (1985) and Miller (1991) were synthesized re-recordings of 1–5 of the same clicks from one moth. *Cycnia tenera* produces up to 700 clicks s$^{-1}$ with acoustic variability both within and between individuals (Fullard, 1977*b*; Fig. 6); it is possible that this variety and number of clicks increases its chances of acoustically matching at least some of them to the bat's calls during its terminal phase. Since the unpredictability of the clicks is removed in the experiments of Surlykke and Miller (1985) and Miller (1991), these studies are more correctly interpreted as tests of the effects of masking rather than of jamming sounds on bat discrimination performance, and the resolution of the sitting bats in their experiments reflects observations using flying bats (Griffin, 1974).

Miller (1991) questions the jamming hypothesis from his observations that a synthesized moth click produces an interference effect with *E. fuscus* only if the clicks appear 1.0–1.5 ms before the bat's echo, presumably too narrow a window for the natural function of the sounds to include jamming [Møhl and Surlykke (1989) observed a similar window of 2 ms and discounted a masking function for the same reasons]. In Miller's (1991) experiments, the extreme deterioration of the bat's ranging performance at these critical times (up to 4000 %) strongly demonstrates that a moth click produces an event along the bat's perceived delay axis that resembles the event caused by a real echo. Although the allowable window of interference is short, the fact that this interference occurs means the bat is assigning to the click a delay value and *perceiving it as an object* (i.e. the clicks act as phantom echoes). Whether arctiids emit enough clicks to enter this critical window depends upon which species is being considered. The phonoresponse of *C. tenera*, consisting of many clicks emitted during the bat's terminal phase (Fig. 1), would seem to satisfy this requirement. We suggest that Møhl and Surlykke's (1989) and Miller's (1991) results, when viewed in the context of how the clicks are normally delivered (at least for *C. tenera*), actually support the theory of jamming.

We recognize that the most convincing test of the defensive effects of moth clicks will be to observe a bat's behaviour when exposed to them. However, for these experiments to be meaningful, certain 'real-world' conditions should be satisfied. First, the bats must normally use a terminal buzz as part of their attack sequence, thus eliminating surface-gleaning bats that normally do not alert sitting prey to their approach (Faure *et al.* 1993). Second, the bats must be trained to find a target while flying (preferably in the presence of randomly moving physical clutter, such as branches, to provide for realistic penalties for wrong or risky decisions; Manville, 1963). Third, the bats must be exposed to a full array of arctiid click trains to preclude the chance that the bat compensates for the unpredictable acoustic effects of the sounds. Fourth, the clicks must be timed to the appropriate sequence of the bat's attack in which they are emitted by the moth (in the case of *C. tenera*, the terminal phase).

### *What do arctiid clicks do against bats?*

There is, finally, the (perhaps unsatisfying) realisation that no single function may explain the defensive effects of arctiid clicks on the attacks of bats (Fullard, 1987; Bates and Fenton, 1990; Miller, 1991; Dunning *et al.* 1992). Since arctiids must contend with predators other than bats, their sounds should not be expected to satisfy all the expected criteria required for a purely anti-bat role. The sounds of *C. tenera* may be aposematic against terrestrial predators (e.g. shrews), but may not play such a role against aerially hunting bats. The theory of jamming has largely been discounted in the literature, but our results indicate that this may be the clicks' primary function against flying bats. *Cycnia tenera* may represent the jamming end of a continuum of evolved functions that the sounds are capable of possessing. By debating specific functions for the sounds in different species of tiger moth, we may be losing sight of the possibility that this fascinating defence is a rapidly evolving one operating against a mosaic of predators. We further suggest that no experiment has yet tested the jamming theory's actual prediction, the *sudden and momentary* disruption of information processing by the interference of

phantom echoes at a time when reflexive defensive procedures in the bat would cause it to break off its pursuit (i.e. during the terminal phase). Since this interference would prevent an attacking bat from predicting the position of a moving moth, it is a protean display (Humphries and Driver, 1970; Driver and Humphries, 1988), complementing the erratic movements of the arctiid. We suggest that, when tested with bats in the natural context in which the interaction evolved (for *C. tenera*, flying bats using terminal phases), the effects of arctiid clicks may shed light on the bat's auditory processing during this little-understood facet of its hunting behaviour.

## References

AGEE, H. R. (1969). Response of flying bollworm moths and other tympanate moths to pulsed ultrasound. *Ann. ent. Soc. Am.* **62**, 801–807.

BATES, D. L. AND FENTON, M. B. (1990). Aposematism or startle? Predators learn their responses to the defenses of prey. *Can. J. Zool.* **68**, 49–52.

BLACK, H. L. (1972). Differential exploitation of moths by the bats *Eptesicus fuscus* and *Lasiurus cinereus*. *J. Mammal.* **55**, 138–157.

BLEST, A. D., COLLETT, T. S. AND PYE, J. D. (1963). The generation of ultrasonic signals by a New World arctiid moth. *Proc. R. Soc. Lond. B* **158**, 196–207.

CARDONE, B. AND FULLARD, J. H. (1988). Auditory characteristics and sexual dimorphism in the gypsy moth. *Physiol. Ent.* **13**, 9–14.

DRIVER, P. M. AND HUMPHRIES, D. A. (1988). *Protean Behaviour.* Oxford: Clarendon Press.

DUNNING, D. C. (1968). Warning sounds of moths. *Z. Tierpsychol.* **25**, 129–138.

DUNNING, D. C., ACHYARA, L., MERRIMAN, C. B. AND DAL FERRO, L. (1992). Interactions between bats and arctiid moths. *Can. J. Zool.* **70**, 2218–2223.

DUNNING, D. C. AND ROEDER, K. D. (1965). Moth sounds and the insect-catching behavior of bats. *Science* **147**, 173–174.

EDMUNDS, M. (1974). *Defence in Animals.* New York: Longman.

FAURE, P. A., FULLARD, J. H. AND DAWSON, J. W. (1993). The gleaning attacks of the northern long-eared bat, *Myotis septentrionalis*, are relatively inaudible to moths. *J. exp. Biol.* **178**, 173–189.

FULLARD, J. H. (1977a). Phenology of sound-producing arctiid moths and the activity of insectivorous bats. *Nature* **267**, 42–43.

FULLARD, J. H. (1977b). Variability and absence of sexual dimorphism in the sounds of *Cycnia tenera* Hübner (Lepidoptera: Arctiidae). *J. N.Y. ent. Soc.* **85**, 21–25.

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

FULLARD, J. H. (1982). Cephalic influences on a defensive behaviour in the dogbane tiger moth, *Cycnia tenera. Physiol. Ent.* **7**, 157–162.

FULLARD, J. H. (1984). Listening for bats: pulse repetition rate as a cue for a defensive behavior in *Cycnia tenera* (Lepidoptera: Arctiidae). *J. comp. Physiol.* A **154**, 249–252.

FULLARD, J. H. (1987). Sensory ecology and neuroethology of moths and bats: interactions in a global perspective. In *Recent Advances in the Study of Bats* (ed. M. B. Fenton, P. Racey and J. M. V. Rayner), pp. 244–273. Cambridge: Cambridge University Press.

FULLARD, J. H. (1992). The neuroethology of sound production in tiger moths (Lepidoptera, Arctiidae). I. Rhythmicity and central control. *J. comp. Physiol.* A **170**, 575–588.

FULLARD, J. H. AND 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. AND SIMMONS, J. A. (1979). Jamming bat echolocation: the clicks of arctiid moths. *Can. J. Zool.* **57**, 647–649.

FULLARD, J. H. AND HELLER, B. (1990). Functional organization of the arctiid moth tymbal (Insecta, Lepidoptera). *J. Morph.* **204**, 57–65.

GRIFFIN, D. R. (1974). *Listening in the Dark.* New York: Dover Publications.

HUMPHRIES, D. A. AND DRIVER, P. M. (1971). Protean defence by prey animals. *Oecologia* **5**, 285–302.

KICK, S. A. AND SIMMONS, J. A. (1984). Automatic gain control in the bat's sonar receiver and the neuroethology of echolocation. *J. Neurosci.* **4**, 2725–2737.

LAWRENCE, B. D. AND SIMMONS, J. A. (1982). Measurements of atmospheric attenuation at ultrasonic frequencies and the significance for echolocation by bats. *J. acoust. Soc. Am.* **71**, 484–490.

MANVILLE, R. H. (1963). Accidental mortality in bats. *Mammalia* **27**, 361–365.

MILLER, L. A. (1983). How insects detect and avoid bats. In *Neuroethology and Behavioral Physiology* (ed. F. Huber and H. Markl), pp. 251–266. Berlin: Springer-Verlag.

MILLER, L. A. (1991). Arctiid moth clicks can degrade the accuracy of range difference discrimination in echolocating big brown bats. *J. comp. Physiol.* A **168**, 571–579.

MØHL, B. AND SURLYKKE, A. (1989). Detection of sonar signals in the presence of pulses of masking noise by the echolocating bat, *Eptesicus fuscus. J. comp. Physiol.* A **165**, 119–124.

NORBERG, U. M. (1987). Wing form and flight mode in bats. In *Recent Advances in the Study of Bats* (ed. M. B. Fenton, P. Racey and J. M. V. Rayner), pp. 43–56. Cambridge: Cambridge University Press.

OBRIST, M. (1989). Individuelle Variabilität der Echörtung Vergleichende an vier vespertiliniden Fledermüsarten Kanadas. PhD thesis, Kudwig-Maximilians-University, München.

PALLAS, S. L. AND HOY, R. R. (1986). Regeneration of normal afferent input does not eliminate aberrant synaptic connections of an identified auditory interneuron in the cricket, *Teleogryllus oceanicus. J. comp. Neurol.* **248**, 348–359.

RICHERSON, J. V. AND CAMERON, A. (1974). Differences in pheromone release and sexual behavior between laboratory-reared and wild gypsy moth adults. *Env. Ent.* **3**, 475–481.

ROEDER, K. D. (1967). *Nerve Cells and Insect Behavior.* Cambridge, MA: Harvard University Press.

SIMMONS, J. A., FENTON, M. B. AND O'FFARRELL, M. J. (1979). Echolocation and pursuit of prey by bats. *Science* **203**, 16–21.

SIMMONS, J. A., FREEDMAN, E. G., STEVENSON, S. B., CHEN, L. AND WOHLGENANT, T. J. (1989). Clutter interference and the integration time of echoes in the echolocating bat, *Eptesicus fuscus. J. acoust. Soc. Am.* **86**, 1318–1332.

STAPELLS, D. R., PICTON, T. W. AND SMITH, A. D. (1982). Normal hearing thresholds for clicks. *J. acoust. Soc. Am.* **72**, 74–79.

STONEMAN, M. G. AND FENTON, M. B. (1988). Disrupting foraging bats: the clicks of arctiid moths. In *Animal Sonar: Processes and Performance* (ed. P. E. Nachtigall and P. W. B. Moore), pp. 551–566. NATO ASI Series, Series A: Life Sciences, vol. **156**. New York: Plenum Press.

SURLYKKE, A. AND MILLER, L. A. (1985). The influence of arctiid moth clicks on bat echolocation: jamming or warning? *J. comp. Physiol.* A **156**, 831–843.

WARD, P. S., HARMSEN, R. AND HEBERT, P. D. W. (1974). An annotated checklist of the macrolepidoptera of south-eastern Ontario. *J. Res. Lepid.* **13**, 23–42.