

Corrigendum

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There was an error in the legend to Fig. 3. The published version reads:

Parameter functions for three gleaning echolocation call sequences of an individual *M. septentrionalis*. (A) Attack on non-arctiid moth; (B) attack on muted *C. tenera*; (C) attack on intact *C. tenera*. See Fig. 1 for further details.

The correct version should read:

Fig. 3. Parameter functions for three aerial hawking echolocation call sequences of an individual *M. septentrionalis*. (A) Attack on non-arctiid moth; (B) attack on muted *C. tenera*; (C) attack on intact *C. tenera*. See Fig. 1 for further details.

The authors apologise for this mistake and any inconvenience caused to readers.

The adaptive function of tiger moth clicks against echolocating bats: an experimental and synthetic approach

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Summary

We studied the efficiency and effects of the multiple sensory cues of tiger moths on echolocating bats. We used the northern long-eared bat, *Myotis septentrionalis*, a purported moth specialist that takes surface-bound prey (gleaning) and airborne prey (aerial hawking), and the dogbane tiger moth, *Cycnia tenera*, an eared species unpalatable to bats that possesses conspicuous colouration and sound-producing organs (tymbals). This is the first study to investigate the interaction of tiger moths and wild-caught bats under conditions mimicking those found in nature and to demand the use of both aerial hawking and gleaning strategies by bats. Further, it is the first to report spectrograms of the sounds produced by tiger moths while under aerial attack by echolocating bats. During both aerial hawking and gleaning trials, all muted *C. tenera* and perched intact *C. tenera* were attacked by *M. septentrionalis*, indicating that *M. septentrionalis* did not discriminate *C. tenera* from palatable moths based on potential echoic and/or non-auditory cues. Intact *C. tenera* were attacked significantly less often than muted *C. tenera*

during aerial hawking attacks: tymbal clicks were therefore an effective deterrent in an aerial hawking context. During gleaning attacks, intact and muted *C. tenera* were always attacked and suffered similar mortality rates, suggesting that while handling prey this bat uses primarily chemical signals. Our results also show that *C. tenera* temporally matches the onset of click production to the ‘approach phase’ echolocation calls produced by aerial hawking attacking bats and that clicks themselves influence the echolocation behaviour of attacking bats. In the context of past research, these findings support the hypotheses that the clicks of arctiid moths are both an active defence (through echolocation disruption) and a reliable indicator of chemical defence against aerial-hawking bats. We suggest these signals are specialized for an aerial context.

Key words: aposematism, echolocation, Chiroptera, Arctiidae, coevolution, *Myotis septentrionalis*, *Cycnia tenera*.

Introduction

The evolutionary arms race between insectivorous echolocating bats and moths has long fascinated biologists (Roeder, 1967; Fullard, 1998; Miller and Surlykke, 2001; Jones and Rydell, 2003; Waters, 2003). The primary purpose of the moth’s simple ear – to detect bat echolocation calls – has made this a particularly useful model for study (Fullard, 1988; Waters, 2003). The ears of moths have evolved as a direct result of selective pressure by bats; they are broadly tuned to the frequency ranges of sympatric insectivorous bat communities and inform the central nervous system to initiate erratic flight behaviours and/or stop flying (Fullard, 1988; Hoy et al., 1989). As part of the acoustic startle response, some species of tiger moths (family Arctiidae) produce clicks using thoracic tymbals that appear to deter attacks from nearby bats (Dunning and Roeder, 1965; Hirstov and Conner, 2005a). Many arctiid species contain sequestered or synthesized defensive chemicals (Rothschild et al., 1970; Weller et al., 1999; Nishida, 2002) unpalatable to a variety of predators,

including bats (Dunning, 1968; Coutts et al., 1973; Goss, 1979; Boppré, 1990; Hristov and Conner, 2005b).

The clicks of arctiid moths have been proposed to function as acoustic aposematic signals (Blest et al., 1963; Dunning and Roeder, 1965; Dunning, 1968; Hristov and Conner, 2005a) and as signals that interfere with information processing facilitating escape, by startling the bat (deimatism) and/or jamming echolocation (Bates and Fenton, 1990; Fullard et al., 1979, 1994; Miller, 1991; Masters and Raver, 1996; Tougaard et al., 1998, 2004). These functional hypotheses are not mutually exclusive although they are often portrayed as such (e.g. Surlykke and Miller, 1985; Fullard et al., 1994; Waters, 2003; Hristov and Miller, 2005a). Until recently (Hristov and Conner, 2005a), all laboratory studies had used (1) synthetic bat echolocation calls and stationary moths, (2) synthetic arctiid clicks and stationary bats or (3) free-flying bats capturing mealworms while synthetic clicks were broadcast >1 m away from the prey trajectory (see Waters, 2003 and

Hristov and Conner, 2005a for a review). In field studies (e.g. Dunning et al., 1992; Acharya and Fenton, 1992), predation on intact and muted arctiid moths has been compared, but the sounds intact moths presumably produce were not monitored and the numbers of bats sampled could not be accurately determined.

The two dominant foraging strategies used by echolocating predatory bats are substrate gleaning (taking prey from surfaces) and aerial hawking (taking airborne prey) (Bell, 1982; Norberg and Rayner, 1987; Arlettaz et al., 2001). In contrast to hawking, during substrate gleaning attacks bats attempt to capture stationary or slow-moving prey from the ground, foliage or tree trunks and bats should, arguably, have more opportunity to assess potential non-auditory prey cues. To our knowledge, no study has investigated the efficacy of arctiid clicks as defence against the gleaning attacks of bats.

The northern long-eared bat, *Myotis septentrionalis*, and the sympatric dogbane tiger moth, *Cynia tenera*, are good models for investigating the influence of foraging strategy and signal design on bat–tiger-moth interactions. Brack and Whitaker (2001) found that four wild populations of *M. septentrionalis* fed predominantly on Lepidoptera. Ecomorphology, flight behaviour and echolocation call design demonstrate that *M. septentrionalis* is well adapted for both aerial hawking and gleaning prey (Ratcliffe and Dawson, 2003). Preferred foraging habitat and the presence of non-volant arthropods in their diet suggests that *M. septentrionalis* gleans in the wild (Brack and Whitaker, 2001), while open field and over-water recordings of *M. septentrionalis* echolocation attack sequences indicate aerial hawking (Miller and Treat, 1993; M. B. Fenton, personal communication). *C. tenera* is active day and night (Fullard and Napoleone, 2001) and has both conspicuous colouration and sound-producing tymbals (Fullard and Fenton, 1977). This species sequesters and/or synthesizes a number of defensive chemical compounds (Cohen and Brower, 1983; Weller et al., 1999; Nishida, 2002; Hristov and Conner, 2005b); captive *M. septentrionalis* do not eat *C. tenera* when presented together with non-arctiid moths (J.M.R. and J.H.F., unpublished data).

Our purpose was to determine which of *C. tenera*'s putative multiple sensory warning signals would be effective deterrents against *M. septentrionalis* during aerial hawking and gleaning attacks. We predicted that during all attacks *M. septentrionalis* would not use visual or other non-acoustic signals prior to contact with *C. tenera* due to the relatively reduced size of the visual and olfactory systems in myotid bats (Bhatnagar, 1975). We did not expect *C. tenera* to produce sounds in response to a gleaning attack because the ears of *C. tenera* are less sensitive to sympatric bat echolocation calls than those of catocaline (family Noctuidae) moths (Fullard and Dawson, 1999), to which the gleaning attacks of *M. septentrionalis* are inaudible (Faure et al., 1993). Therefore, we predicted that gleaning *M. septentrionalis* would attack and contact both muted and intact *C. tenera*. We predicted that during aerial hawking attacks the bats would use acoustic cues when available, aborting attacks on intact *C. tenera* in response to the moth's clicks. We

expected that attacks on muted *C. tenera* would result in contact with the moth. We also expected that *C. tenera* would be unpalatable to the bats and that during gleaning and hawking trials intact and muted *C. tenera* would be rejected rather than consumed.

In spite of the >40 years that scientists have investigated the acoustic interactions between arctiid moths and bats, there has never been a documented recording of the sounds emitted by these animals during an actual attack. Based on reported click emission rates to a big brown bat (*Eptesicus fuscus*) aerial hawking attack echolocation call sequence (Fullard et al., 1994) and the critical time window for degrading echolocation ranging ability (Miller, 1991), we predicted that (1) the clicks of *C. tenera* would affect the echolocation behaviour of *M. septentrionalis*, as revealed by increased time between calls, and (2) at least some click modulation cycles would coincide with echolocation calls in our recordings and thus provide indirect support for the jamming hypothesis (Miller, 1991; Tougaard et al., 1998, 2004). The existence of studies that support both jamming and aposematism implies that an 'either/or' approach to the function of arctiid clicks is incorrect and so we propose a synthesis of the role that these unique sounds play in the defence of these insects.

Materials and methods

Animals and study site

All experiments were conducted at the Queen's University Biological Station (hereafter QUBS) near Chaffey's Lock, Ontario, Canada (43°34'N, 79°15'W) during June and July 2004. Twelve adult male northern long-eared bats *Myotis septentrionalis* Trouessart, were captured at several night roosts (abandoned mica mines) in modified harp traps (Tuttle, 1974) and housed in wooden boxes (70×30×30 cm) with water for drinking until testing began. Individual bats were kept in captivity for 2–6 nights. Bats were fed nightly during the experimental procedure (see below) and were additionally given water and mealworms, *Tenebrio molitor*, by hand. During experiments, moths were presented individually and were the only prey items available. Bats were kept separately, in individual cloth bags, during experiments.

Dogbane tiger moths *Cynia tenera* Hübner, were reared from eggs collected from wild specimens captured at QUBS during the summer of 2003, raised to pupae on milkweed and dogbane (*Apocynum androsaemifolium* and *A. cannabinum*, respectively) and stored in constant temperature rooms at 4°C with a 12 h:12 h light:dark photoperiod for approximately 7–8 months at the University of Toronto at Mississauga. Pupae were then transferred to constant temperature rooms at 25°C with a 16 h:8 h light:dark photoperiod at QUBS, and adults emerged 2–3 weeks later. Adults were allowed to mature for 24–72 h. Of 113 individuals successfully reared, 37 were used as prey. Eleven more *C. tenera* were caught as adults from nearby fields (day) and light traps (night) during the summer of 2004.

The tymbals (modified metathoracic episterna) of 24 of the

48 *C. tenera* used as prey in experiments were ablated under a dissecting microscope using an insect pin. For ablation, moths were first cooled for 10 min in a refrigerator and then held by their wings using flat tweezers. Before and after tymbal ablation, moths were stroked gently with a small brush over a Holgate ultrasonic heterodyne detector tuned to 50 kHz, representing the peak frequencies of the clicks (Fullard and Dawson, 1999), to ensure moths had been completely muted. Intact moths that did not respond to tactile stimulation (7) and moths that were improperly ablated (18) were not used. We also tested for sound production in all 48 *C. tenera* used in this study immediately before and after each moth interacted with a bat (except in one instance when the moth was not recovered).

All other moths used in this study were captured nightly from light traps (mercury vapour incandescent and ultraviolet fluorescent) positioned around QUBS. Moths were identified to family using criteria in Ward et al. (1974), Covell (1984) and Riotte (1992). Some of the moth species used for experiments (families Arctiidae, Noctuidae, Notodontidae, Lymantriidae and Geometridae) had ears while others (family Lasiocampidae) were earless (Fullard and Napoleone, 2001). All moths used, including *C. tenera*, had a body length of 1.5–2.5 cm and, for gleaning trials, were kept at ~5–10°C until presented to the bats.

Flight room and experimental design

Experiments one and two were run in a large, screened (ceiling and roof) flight room (9.14×3.66×3.66 m, length × width × height; see fig. 1 in Ratcliffe and Dawson, 2003) built in a small glade within a mixed temperate forest (canopy intact), mimicking a cluttered habitat where the only light available was that from the moon and stars. Experiments were run two weeks after the emergence of adult *C. tenera* in the wild (Ward et al., 1974; J.M.R., personal observation). Bats were observed using an infrared-sensitive night vision scope with a built-in infrared LED light source (Night Owl Explorer NOCX3; JNL Trading Company, Aurora, IL, USA). We released individual *M. septentrionalis* into the flight room and presented each bat with 10 live moths positioned on substrate or tethered (described below) to simulate foraging conditions, demanding substrate gleaning or aerial hawking, respectively. One trial entailed one presentation of a single moth followed by an attempt at capture (Ratcliffe and Dawson, 2003). To control for possible ordering effects within and between subjects, moths were presented to each bat in pseudo-randomized order such that *C. tenera* of the same sound-producing class (intact or muted) were never presented one after another and such that no more than two *C. tenera* were presented in unbroken sequence. For each successive trial, moths were placed at different positions on the trellis for gleaning trials and at slightly different heights and distances from the long walls of the flight room when tethered. Bats were hand-fed three mealworms before being introduced to the flight room to ensure they were ready to eat while at the same time not starving. After having hunted in the flight room, bats were fed to satiation and released at point of capture.

High-frequency sound recording

Call sequences emitted during foraging trials were recorded using two D 980 Ultrasound Detectors (Pettersson Elektronik AB, Uppsala, Sweden) using the high-frequency output. The D 980 (hereafter ‘the microphone’) output was passed through a F2000 Control/Filter Unit (Pettersson Elektronik AB) with gain set to ‘low’ before input to a computer (Dell Notebook C800, Pentium III 800 MHz processor, 512 MB RAM) using a DAQCard-6062E (National Instruments, Austin, TX, USA) as interface. Data were stored as .wav files using BatSound Pro v. 3.30 (Pettersson Elektronik AB) software in high-speed sampling mode (500 kHz sampling frequency, circular buffer, 10-second storage time, 150 kHz external anti-aliasing filter).

Experiment one: gleaning trials

Six *M. septentrionalis*, 24 *C. tenera* (12 intact, 12 muted) and 36 non-arctiid moths served as subjects in experiment one. These animals did not serve as subjects in experiment two. *Myotis septentrionalis* were introduced individually into the flight room and presented with a moth on substrate. The gleaning substrate was a trellis (1×1.5 m, width × height) covered with matt black canvas to maximize contrast between *C. tenera* and background. During trials (10 trials per bat), the bat was allowed to fly and perch freely in the room. At the beginning of the trial, the moth was not placed into position until the bat was either perched at one end of the room or was flying at one end of the room away from the moth’s ultimate position. Between trials, we varied the position of the moth at one of five almost equidistant screen windows fashioned into the canvas (each 3 cm², ~30 cm apart). A microphone was positioned 10 cm behind this screen window. For *M. septentrionalis*, fluttering sounds are necessary for the detection of perched moths (Ratcliffe and Dawson, 2003). Therefore, we held a second moth between the microphone and the trellis such that one fluttered against the screening. Moths used as lures included arctiid moths.

Experiment two: aerial hawking trials

An additional six *M. septentrionalis*, 24 *C. tenera* (12 intact, 12 muted) and 36 non-arctiid moths served as subjects in experiment two. *M. septentrionalis* were introduced individually into the flight room and presented with a live moth that was tethered (for details and diagram of set-up, see Ratcliffe and Dawson, 2003). Most moths, but never *C. tenera*, were tethered approximately in the centre of the flight room (within 1 m to the right and left of centre) to the end of a 0.2 mm-diameter black cotton thread, 1–2 m long, by passing a threaded sewing needle through the anterior portion of the abdomen. The thread, which was unknotted, extended on average 1 cm below the moth’s body. All *C. tenera* and eight of the non-arctiid moths were attached to this same thread using a drop of beeswax on the centre of the dorsal thorax rather than by passing a needle through their abdomen.

Moths flew vigorously within the limits of the thread and frequently changed direction and altitude. During trials (10 trials per bat), the bat was allowed to fly and perch freely

in the room. At the beginning of the trial, the moth was tethered but not placed into position until the bat was either perched at one end of the room or was flying at one end of the room away from the moth's ultimate position. The moth was then hoisted into position, allowing the bat to discover and interact with it. Based on a previous study (Ratcliffe and Dawson, 2003), we predicted that *M. septentrionalis* would typically initiate its aerial attacks from the back of the room and fly towards our position at the front of the room. Accordingly, we positioned one microphone approximately 1 m in front of and 50 cm below the tail of the tether's resting position and another microphone 50 cm to the side of and 50 cm below the tail of the tether, near to the closest wall.

For both gleaning and aerial-hawking trials, bats typically attacked moths well within 30 s of being made available. However, bats would sometimes roost for several minutes after a trial. When this happened, we would leave the flight room for approximately 20 min; upon returning we found the bats once again ready to hunt. For gleaning trials, the maximum distance from the bat (if at the back wall) to the moth was approximately 8 m; for aerial hawking trials, this distance was never more than 5 m.

Sound analysis

Using BatSound Pro v. 3.30, we high-pass filtered .wav files at 12 kHz (filter type, Butterworth; filter order, 8). We analyzed one echolocation call sequence (from first visually discernible search phase call through to calls emitted after completing or aborting attack) for each moth class for each foraging condition for each bat; sequences were selected on the basis of the quality of the sound recordings (i.e. high signal-to-noise ratio). We measured onset and duration of echolocation calls and tymbal click cycles using the oscillograms (while referencing the spectrograms for aberrations). For gleaning trials, we also measured time elapsed from last call emitted (or recorded) to the bat's initial contact with substrate from spectrograms and oscillograms (the bat hitting the trellis produced sound more intense than either fluttering moth wings or an echolocation call). We used these data to calculate period and duty cycle of echolocation sequences and the timing of tymbal clicks with respect to period and duty cycle.

Statistical analysis

For both gleaning and aerial hawking trial data, we ran approximate randomization tests (Noreen, 1989; 1000 shuffles per test) to identify potential relationships between three moth classes (intact *C. tenera*, muted *C. tenera* and non-arctiid moth) and three attack classes (aborted attack; moth attacked but left undamaged; moth attacked and mortally injured/killed). Approximate randomization tests were conducted using a custom program (written in Visual Basic). This distribution-free analysis, aside from being free of the assumptions of conventional statistics (e.g. data need not constitute a random sample), is more powerful than the chi-squared test because unexpected departures from the null

model can be distinguished from expected departures, and it does not assume that such departures are normally distributed (Noreen, 1989). A positive test statistic refers to the number of cases (e.g. moth class/condition class) that deviated from expectations under the null hypothesis (equal distribution of moth classes among condition classes) in the direction expected under the alternative hypothesis: the larger the value of the test statistic the stronger the evidence for this departure (Noreen, 1989). The *P* value then refers to the percentage of shuffles for which the test statistic for the shuffled data was as large or larger than the original test statistic (Noreen, 1989).

For echolocation sequences of aerial attacks on intact *C. tenera*, we ran a repeated-measures ANOVA using SPSS/PC 12 to compare call period for the two calls preceding the first *C. tenera* click, the call period during which the first click was recorded and the subsequent call period (where clicks were never detected). We also determined whether the first complete tymbal modulation cycle coincided with an echolocation call and whether subsequent modulation cycles coincided with echolocation calls before the bat aborted or completed its attack (i.e. contacted the moth). Calls produced with greater than 50 ms between calls are designated as 'search phase' calls; calls with less than 50 ms but more than 10 ms between them are designated as 'approach phase' calls; calls with less than 10 ms between them are designated as 'buzz phase' calls (Griffin et al., 1960).

Results

Experiment one: gleaning trials

Within an hour of being introduced to the flight room, each of the six bats caught moths by gleaning; two hovered approximately 30 cm in front of the moth before contact with the trellis (three of six attacks for one bat; two of six attacks for the other). All landed directly on the available moth in 53 of 60 trials and within 5 cm of the moth in the remaining seven trials. Gleaning *M. septentrionalis* attacked all intact *C. tenera*, muted *C. tenera* and non-arctiid moths. These results show that *M. septentrionalis* did not differentiate palatable non-arctiid moths from *C. tenera* based on echoic or visual cues.

The bats ate all 36 non-arctiid moths (i.e. mortally injured/killed). Eleven of the 12 muted *C. tenera* were rejected: seven were mortally injured/killed, four were undamaged. Although we never observed any bat eating *C. tenera*, we were unable to locate one muted moth after the attack (this moth was scored as mortally injured/killed). All of the 12 intact *C. tenera* were rejected: five were mortally injured, seven were undamaged. The bats killed significantly fewer *C. tenera* than non-arctiid moths ($N=60$; test statistic=32.6, $P<0.001$), but intact *C. tenera* did not have significantly lower mortality rates than muted *C. tenera* ($N=24$; test statistic=3.6, $P=0.20$). These results show that *M. septentrionalis* differentiated *C. tenera* from non-arctiid moths based on chemical cues. See Table 1 for percentage breakdown of these results.

Table 1. Percentage of moths for each class not contacted (aborted attack), contacted/undamaged (attacked but left undamaged) or contacted/killed (attacked and killed/mortally wounded) during gleaning and hawking attacks

Trial	Attack class	Intact <i>C. tenera</i> (%)	Muted <i>C. tenera</i> (%)	Non-arctiid (%)
Gleaning	Not contacted	0	0	0
	Contacted/undamaged	58.3	33.3	0
	Contacted/killed	41.7	66.7	100
Hawking	Not contacted	66.7	8.3	0
	Contacted/undamaged	25	66.7	0
	Contacted/killed	8.3	25	100

Sound analysis

All intact *C. tenera* produced sounds detected by our microphone when handled by the bats; none produced sounds prior to contact with the bats (Fig. 1).

Experiment two: aerial hawking trials

Within an hour of being introduced to the flight room, all six bats caught moths by aerial hawking. Four of 12 intact *C. tenera*, 11 of 12 muted *C. tenera* and all 36 non-arctiid moths were attacked by *M. septentrionalis*. Two of the bats attacked intact *C. tenera* during their first presentation of an intact *C. tenera*; two other bats during their second presentation of an intact *C. tenera*. The bats always ate non-arctiid moths. These results show that *M. septentrionalis* did not differentiate palatable non-arctiid moths from *C. tenera* based on echoic or

visual cues and that the clicks of *C. tenera* are a salient deterrent against attack.

The bats never ate *C. tenera* (muted or intact), and three of the four intact moths and eight of the 11 muted moths were alive and presumably reproductively viable (i.e. wings and body intact, still able to fly and produce clicks) after the bats' attacks. The remaining four *C. tenera* had crushed body parts and/or were missing wings (or were simply dead). The bats killed significantly fewer *C. tenera* than non-arctiid moths ($N=60$; test statistic=51.2, $P<0.001$). The bats made contact with significantly fewer intact *C. tenera* than muted *C. tenera* ($N=24$; test statistic=11.6, $P<0.003$), but for those contacted, intact *C. tenera* did not have significantly lower mortality rates than muted *C. tenera* ($N=15$; test statistic=0.6, $P=0.77$). These results suggest that after capture, the chemical defences, but not the tymbal clicks, of *C. tenera* are at least partially effective against bats. See Table 1 for percentage breakdown of these results.

Sound analysis

We were confident, based on the position of the moth with respect to the microphones, that we would have detected most, if not all, of the clicks produced by the intact *C. tenera* for at least one of the two trials recorded for each bat. Visual inspection of spectrograms and oscillograms supported this impression. For these six trials, intact *C. tenera* never produced clicks until the bats had switched from producing search phase calls (call period >50 ms) to approach phase calls (mean call period, 31.6 ms; range, 6–43.3 ms; Figs 2–5).

Clicking behaviour in the intact dogbane tiger moths that were attacked (four of six trials analysed) and hit by *M. septentrionalis* commenced on average 532.8 ms

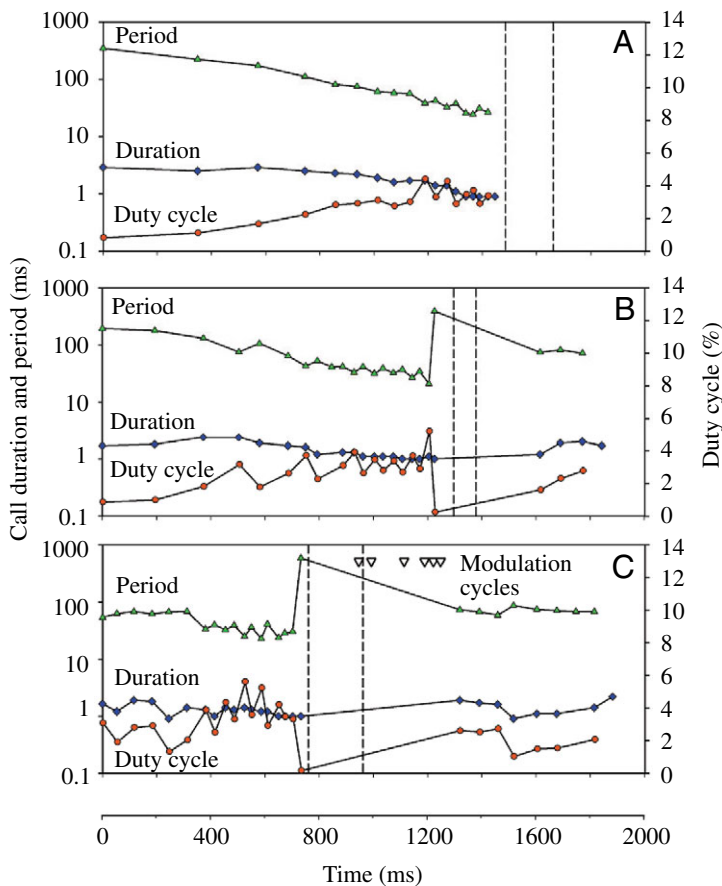


Fig. 1. Parameter functions for three gleaning echolocation call sequences of an individual *M. septentrionalis*. (A) Attack on non-arctiid moth; (B) attack on muted *C. tenera*; (C) attack on intact *C. tenera*. Duration = call duration. Duty cycle = duration/period. Modulation cycle (open triangles) indicates the onset of the first click of each tymbal modulation cycle. Broken lines represent the bat's initial contact with the trellis and the bat taking off from the trellis (estimated from spectrograms). In A, the bat did not produce calls detected by our microphone from just prior to contact with the trellis, as expected, or as it flew away, perhaps due to the moth in its mouth.

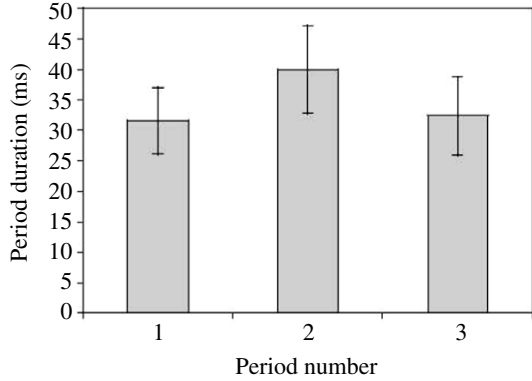


Fig. 2. During aerial-hawking attacks on intact *C. tenera*, the call period (ms) for two echolocation calls immediately preceding the first click (period 1) and the period for two echolocation calls immediately after the first click (period 3) were shorter in duration than the period for two calls between which the first click fell (period 2). Period represents the time from the beginning of call x to the beginning of call $x+1$. Values are means \pm S.E.M.

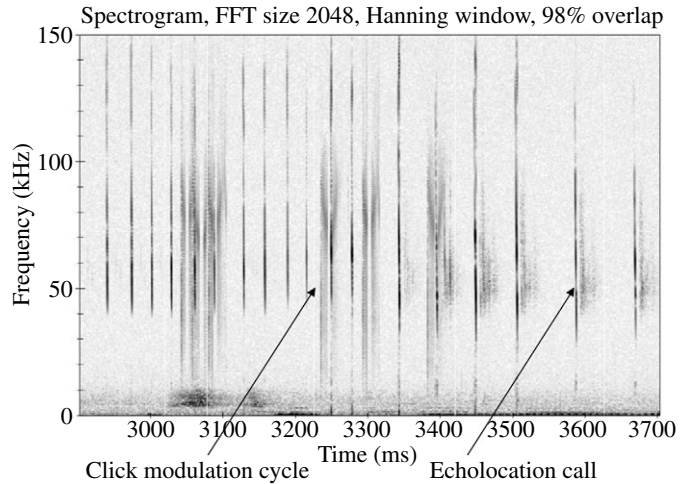


Fig. 4. Spectrogram of *M. septentrionalis* during aborted aerial-hawking attack on tethered intact *C. tenera*.

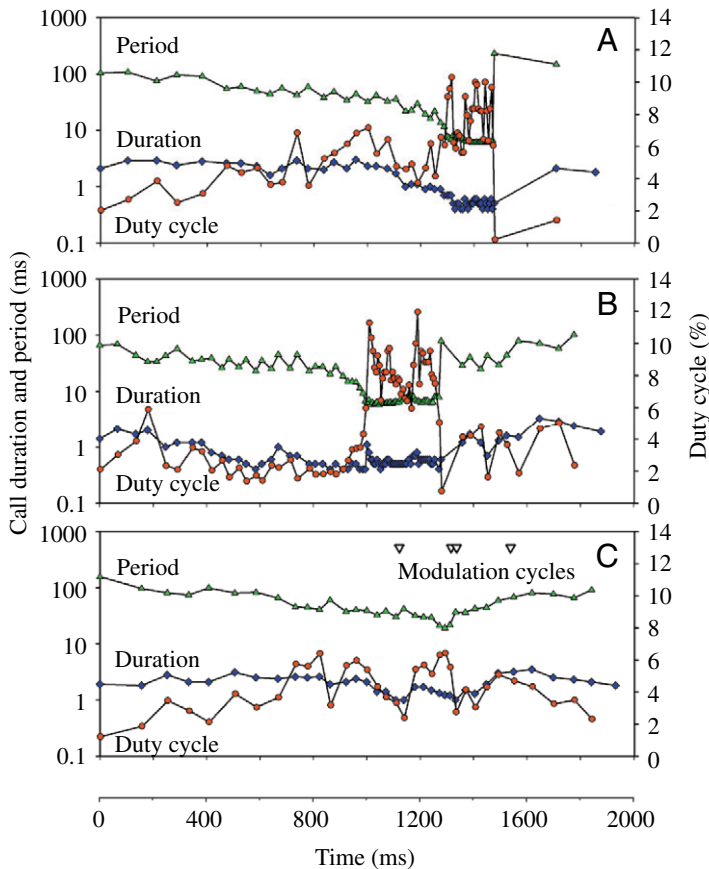


Fig. 3. Parameter functions for three gleaning echolocation call sequences of an individual *M. septentrionalis*. (A) Attack on non-arctiid moth; (B) attack on muted *C. tenera*; (C) attack on intact *C. tenera*. See Fig. 1 for further details.

(range 68.4–944 ms) before the bat contacted the moth [values calculated by adding 25 ms to the time elapsed between the first click and the last buzz call (pause between last call and contact estimated using data from Wilson and Moss, 2004 for *M. septentrionalis*); Fig. 5].

The bats paused significantly longer between calls at the onset of the first click: the call period immediately before and following the period in which the first click fell was significantly lower (repeated-measures ANOVA; $N=6$, $F=8.87$, $P=0.006$; Fig. 2). The first tymbal modulation cycle produced overlapped with an echolocation call in only one of six attacks, but at least one complete tymbal modulation cycle (and as many as three) overlapped with echolocation calls produced during attack for five of six trials analyzed.

Discussion

We found that *M. septentrionalis* attacked clicking *C. tenera* significantly less than muted *C. tenera* during aerial hawking attacks. During both aerial hawking and gleaning attacks, we found no evidence that *M. septentrionalis* used echolocation to distinguish palatable from unpalatable prey, reflecting the findings of others (gleaning attacks – Marimuthu and Neuweiler, 1987, Ryan and Tuttle, 1983; aerial hawking attacks – Barclay and Brigham, 1994). Similarly, during both gleaning and aerial hawking attacks, *M. septentrionalis* showed no observed response to the visually conspicuous wings (white and yellow) of *C. tenera*. This may be due to a sensory constraint: *M. septentrionalis*, like its congener *M. lucifugus*, presumably has scotopic vision with poor resolving power (Bhatnagar, 1975; Suthers, 1966; Suthers and Wallis, 1970). During gleaning attacks, intact *C. tenera* did not produce clicks until handled by bats and did not enjoy lower mortality rates than muted *C. tenera*.

The conspicuous colouration of *C. tenera* therefore appears to have evolved as an aposematic signal for visual predators (e.g. insectivorous birds) while the predominantly ultrasonic clicks act as defensive signals against primarily auditory predators (e.g. insectivorous bats). Our results suggest, however, that although chemical signals did not deter bats' attacks, they caused the bats to release dogbane moths once caught.

Gleaning

As predicted, during gleaning attacks *C. tenera* did not produce clicks in response to echolocation call sequences of *M. septentrionalis* but did produce clicks upon tactile stimulation (i.e. handling by bat). The short-duration, low-intensity, broad-bandwidth, high-frequency calls used by gleaning *M. septentrionalis* (Faure et al., 1993; Ratcliffe and Dawson, 2003) are inaudible to the ears of the most sensitive sympatric noctuid moths (Faure et al., 1993) and would therefore be unheard by the less-sensitive ears of *C. tenera* (Fullard and Dawson, 1999). We suggest that calls with these features serve at least two adaptive functions: (1) to discriminate prey from background clutter, by reducing call-echo overlap (Schnitzler and Kalko, 2001), reducing self deafening (Fenton et al., 1995) and increasing resolution (Ratcliffe and Dawson, 2003; Siemers and Schnitzler, 2004), and (2) for undetected approach leading to capture of eared prey from substrate (Faure et al., 1993; Fenton and Ratcliffe, 2004; present study). Gleaning attacks may be an insurmountable problem for moths and, perhaps, most substrate-bound prey, palatable or not (Faure et al., 1993).

Aerial hawking

As predicted, intact, sound-producing *C. tenera* were attacked significantly less than muted *C. tenera*, supporting the hypothesis that clicks serve a defensive function against aerial hawking bats not served by other sensory cues. Our results support earlier reports that *C. tenera* clicks in response to

echolocation calls at intensities greater than those required for detection at the sensory level (Fullard, 1979; Fullard and Dawson, 1999). For echolocation calls within *C. tenera*'s range of frequency sensitivity, we suggest that thresholds for call intensity at the moth's ear (Fullard, 1984; Fullard and Dawson, 1999) and call period (mean, 31.6 ms; range, 6–43.3 ms; present study) must both be crossed to elicit defensive clicking behaviour. This is corroborated by data from gleaning trials: pulse rate had exceeded required threshold but call intensity at the moth's ear had presumably not (Faure et al., 1993; Fig. 1). During aerial hawking attacks, our results indicate that *C. tenera* first produces clicks in response to close-range approach-phase calls of actual attacking bats: bats that are a very real threat to the moth.

Based on observed changes in call emission, wing gait and flight speed, Wilson and Moss (2004) suggest that aerial hawking *M. septentrionalis* generate a motor plan for prey capture approximately 400 ms before contact with prey. Wilson and Moss (2004) also found an approximately 25-ms pause between the last buzz call and contact with prey. In the context of these results and our own, *C. tenera* appears to click at approximately the same moment as the bat decides to attack it. Therefore, clicks are not produced until approximately the same time as an attack has been initiated, a characteristic atypical of most aposematic signals, which are continuously displayed (e.g. brightly coloured and contrasting wings of monarch butterflies, the persistent buzz of the wings of wasps and bees; Edmunds, 1974; Ruxton et al., 2005). However, from the perspective of the predator, non-continuous prey-generated cues can be timed to act as deimatic and/or aposematic signals so long as there is still time available for the attack to be aborted (Edmunds, 1974; Endler, 1991).

C. tenera clicks are within the same frequency spectrum as the ultrasonic echolocation calls of sympatric bats (Fullard and Fenton, 1977) and should be easily detected by bats against almost non-existent background noise at these frequencies (estimated from spectrograms). The change in echolocation call emission upon the onset of the clicks indicates that the bats did notice these sounds. While overlap between call and click was not necessary to influence call emission rate (i.e. first clicks produced overlapped with an echolocation call in only one of six attacks), for five of the six aerial attack sequences analyzed, one complete tymbal modulation cycle, and as many as three, overlapped with echolocation calls. Given that, within a modulation cycle, clicks are produced, on average, once every 1.3 ms (14 clicks cycle⁻¹; mean cycle length, 18 ms; Fullard and Fenton, 1977; present study), clicks would have fallen within the window required for degrading accuracy in echolocation range discrimination (Miller, 1991; Masters and Raver, 1996; Tougaard et al., 1998, 2004) at least once during five of the six attacks analyzed. Therefore, our results suggest that the clicks of *C. tenera* may indeed interfere with bat echolocation and result in target-ranging miscalculations in the wild. Further, even without synchronization, clicks might degrade attack accuracy simply by forcing the bats to process two streams of information concurrently (Barber et al., 2003).

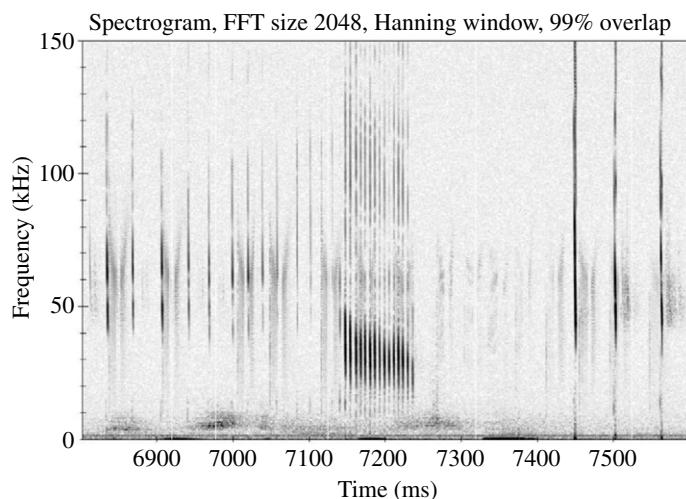


Fig. 5. Spectrogram of *M. septentrionalis* during completed aerial-hawking attack on tethered intact *C. tenera*.

Recently, Hristov and Conner (2005a), using naïve bats in the laboratory, supported an aposematic function for *C. tenera* clicks against aerial hawking attacks by *Eptesicus fuscus* and suggested that the major impetus behind the evolution of arctiid clicks was to serve as a warning of unpalatability. However, Hristov and Conner's results also suggest a non-aposematic function of clicking: 20% of attacks on clicking but not chemically defended tiger moths were repeatedly terminated by naïve bats (i.e. bats that had never experienced a noxious tiger moth) (see figs 1 and 2 in Hristov and Conner, 2005a). Further, although laboratory results suggest that bats habituate to the putatively startling effect of arctiid moth clicks (Miller, 1991; Bates and Fenton, 1990; Hristov and Conner, 2005a), habituation and extinction rate is affected by time elapsed between successive exposures and context, both of which vary dramatically in the wild but tend to be uniform in the laboratory (Shettleworth, 1998). Evidence that habituation occurs under controlled conditions is thus not sufficient to posit that flying, hunting bats habituate to arctiid clicks in the wild. Therefore, under natural conditions we assert that the clicks of the dogbane tiger moth, *C. tenera*, are alone aversive signals to echolocating bats.

Delineating startle, jamming and warning into three distinct characteristics does not accurately describe either the ultimate or proximate functions of these signals. Summers and Clough (2001), using phylogenetically independent contrasts, found that in poison frogs (Dendrobatidae) conspicuousness and toxicity are positively correlated. In *C. tenera*, we hypothesize that a similar parallel process shaped both signal and secondary chemical defence. Furthermore, given the proposed negative qualities of *C. tenera* clicks on echoic information processing (Miller, 1991; Fullard et al., 1979, 1994; Tougaard et al., 1998, 2004) in bats (as a result of affecting echolocation behaviour when first produced and overlapping temporally with calls during most aerial hawking attacks), these signals are not only conspicuous and possibly reliable indicators of further defence (*sensu* Sherratt, 2002; Sherratt and Beatty, 2003) but also especially effective signals of negative consequences in particular (*sensu* Etscorn, 1973).

Synthesis

Warning signals function by informing potential predators that the sender is unprofitable as prey (Servedio, 2000; Summers and Clough, 2001; Sherratt, 2002). During the aerial hawking attacks of insectivorous echolocating bats, tiger moth tymbal clicking is of considerable survival value (i.e. bats abort attacks), while visual and chemical cues are not effective in deterring the predator before contact. During aerial hawking attacks, the clicks of *C. tenera* are effective warning signals (Hristov and Conner, 2005a). However, aposematism is a phenomenon typically defined by an always conspicuous, but harmless cue (warning) and a negative consequence (defence) (Edmunds, 1974; Servedio, 2000; Speed, 2000; Summers and Clough, 2001; Ruxton et al., 2005).

We have demonstrated that *C. tenera* clicks are produced only when attack is imminent or underway and serve as both

defence in and of themselves (as argued above) and as warning of further defence (Hristov and Miller, 2005a). Clicks are, in these respects, more analogous to the bitter and/or sour flavours of plants containing even more toxic compounds (Etscorn, 1973; Chambers, 1990; Cipollini and Levey, 1997; Ratcliffe et al., 2003) than to the bright but benign colours and patterns of defended or mimetic animals (Schuler and Hesse, 1985; Roper and Redston, 1987). We predict that for aerial-hawking echolocating bats, these acoustic signals are more readily associated with unpalatability than visual and/or olfactory signals and, more than this, that dogbane tiger moth clicks are more readily associated with unpalatability than would be equally detectable, but otherwise undistruptive, acoustic signals.

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