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Tiger moth responses to a simulated bat attack: timing and duty cycle

J. R. Barber* and W. E. Conner
Department of Biology, Wake Forest University, 226 Winston Hall, Winston-Salem, NC 27109, USA
*Author for correspondence (e-mail: barbjr2@wfu.edu)

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Summary

Many night-flying insects perform complex, aerobatic escape maneuvers when echolocating bats initiate attack. Tiger moths couple this kinematic defense with an acoustic reply to a bat's biosonar-guided assault. The jamming hypothesis for the function of these moth sounds assumes that tiger moth clicks presented at high densities, temporally locked to the terminal phase of the bat attack will produce the greatest jamming efficacy. Concomitantly, this hypothesis argues that moths warning bats of bad tasting chemicals sequestered in their tissues should call early to give the bat time to process the meaning of the warning signal and that moths calling at low duty cycles are more likely to employ such an aposematic strategy. We report here the first investigation of a tiger moth assemblage's response to playback of a bat echolocation attack sequence. This assemblage of arctiid moths first answered the echolocation attack sequence 960±547 ms (mean ± s.d.) from the end of the bat attack. The assemblage reached a half-maximum response shortly after the first response, at 763±479 ms from the end of the terminal buzz. Tiger moth response reached a maximum at 475±344 ms from the end of the sequence; during the approach phase, well before the onset of the terminal buzz. In short, much of tiger moth response to bat attack occurs outside of the jamming hypotheses' predictions. Furthermore, no relationship exists between the duty cycle of a tiger moth's call (and thus the call's probability of jamming the bat) and its temporal response to bat attack. These data call into doubt the assumptions behind the jamming hypothesis as currently stated but do not directly test the functionality of arctiid sounds in disrupting echolocation in bat-moth aerial battles.

Key words: Arctiidae, tiger moth, echolocation, aposematism, jamming, startle, predator, prey.

Introduction

Decades of anecdotal and experimental evidence have revealed that tiger moths (Lepidoptera: Arctiidae) are attacked less and survive bat attack more often than similarly sized eared moths in the night sky (Dunning, 1968; Acharya and Fenton, 1992; Dunning et al., 1992; Dunning and Krüger, 1995). Their survival advantage appears to rest with a pair of metathoracic sound-producing structures, the tymbals, allowing these moths to respond with high-frequency clicks when pursued by the biosonar-guided attacks of bats (Fig. 1). Muscles attached to these modified sclerites actively buckle the tymbals inward producing a train of clicks (Fullard and Heller, 1990). The number of clicks produced per buckling is correlated with the number of striations (microtymbals) on a narrow band along the antero-ventral surface of the tymbals (Blest et al., 1963). A second burst of clicks is produced as the tymbal passively pops outward.

Fifty years of research have produced three functional hypotheses for the sounds produced by arctiids in response to bat attack. (1) Bats may be startled by the clicks. Laboratory work has shown that the behavioral response decays in the first few pairings of arctiid clicks with a food reward in naïve big brown bats (Bates and Fenton, 1990; Miller, 1991; Hristov and Conner, 2005a). Startle, therefore, seems unlikely to be a powerful evolutionary driving force, except perhaps where arctiids are rare (Hristov and Conner, 2005a), although it is difficult to rule out startle as bat/arctiid encounter rates in nature are unknown (Ratcliffe and Fullard, 2005). (2) Active jamming of biosonar has been offered as an explanation for arctiid clicks in two very different forms. Blest et al. originally proposed that clicks may act as acoustic camouflage (Blest et al., 1963). This idea was championed by others (Fullard et al., 1979), who showed that tiger moth clicks' power spectra, frequency-time structures and intensity closely match echoes returning to the bat from the moth's body and thus may create the illusion of multiple targets. In 1994, Fullard et al. refined the phantom-echo hypothesis to include the timing of *Cycnia tenera*'s response to bat attack (Fullard et al., 1994). This arctiid responded at the end of an echolocation attack, when cross-correlation analysis revealed the closest match with the terminal phase cries of the played back *Eptesicus fuscus* attack. A second version of the jamming hypothesis asserts that the

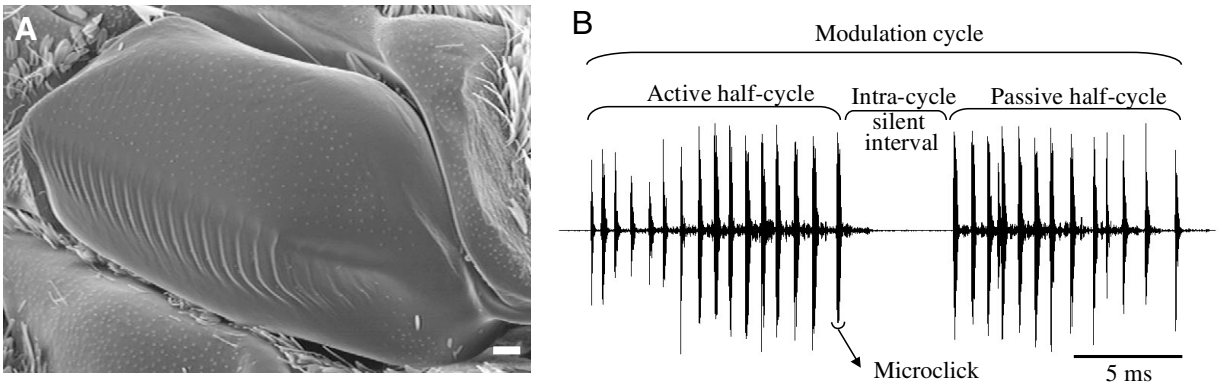

Fig. 1. (A) Scanning electron micrograph of the metathoracic tymbal of *Bertholdia femida.* Scale bar, 100 μm. (B) Oscillogram of one complete modulation cycle of *B. femida* with both tymbals intact. The active modulation half-cycle is produced as muscles buckle the structure inward. After a brief intra-cycle silent interval the structure returns to its resting state producing the passive modulation half-cycle.

clicks are not perceived as phantom objects but directly interfere with neuronal processing of returning echoes. The interference hypothesis was put forth by Miller (Miller, 1991), who trained sitting bats in a range discrimination task to determine if a test echo was at the same distance as a reference echo presented either with or without recorded arctiid clicks. He found a marked decrease in performance if the clicks arrived within ~1.5 ms before the return of an echo. Two subsequent studies (Masters and Raver, 1996; Tougaard et al., 2004) found similar detriments in ranging performance within this temporal window, although the degradation of ranging accuracy was significantly less intense. Interestingly, other workers (Simmons et al., 1989; Møhl and Surlykke, 1989) have defined a comparable ranging perturbation window of 1–2 ms when investigating clutter interference. Also in support of the interference hypothesis, Tougaard et al. (Tougaard et al., 1998) recorded responses of single units in the lateral lemniscus of big brown bats to frequency modulated sweeps in the presence of arctiid clicks and further confirmed that the moth sounds suppress neuronal responses and created ambiguity in latency coding only when the clicks fell within a 2–3 ms window preceding the test signal. (3) An acoustic aposematism or warning function for the sounds was originally proposed to explain the avoidance of catapulted mealworm prey when arctiid clicks were played to hunting wild bats (Dunning and Roeder, 1965). Examinations of bats in captivity or hunting around streetlights presented with arctiids that could or could not produce sound showed that only those moths offering an acoustic signal were avoided by their bat predators (Dunning, 1968; Eckrich and Boppré, 1990; Acharya and Fenton, 1992). Evidence for acoustic aposematism also comes from laboratory conditioning studies with synthetic arctiid clicks and noxious food rewards (Bates and Fenton, 1990; Surlykke and Miller, 1985).

Recently, Hristov and Conner were able to investigate the role of learning in bat–tiger moth aerial interactions (Hristov and Conner, 2005a). They pitted flying, naïve big brown bats against four groups of arctiids varying in a pair of characters: presence or lack of a chemical defense and ability or inability to produce sound. The learning profiles of capture success over 7 days were consistent only with an acoustic aposematism function for the clicks. The bats failed to learn to avoid chemically protected moths unless those moths also provided an acoustic warning. Moths that produced sound, but did not back it up with defensive chemistry, were initially captured in 75% of trials and by day 6, 100% of these moths were captured. Thus, it seems that the two sound-producing arctiids tested, *Cycnia tenera* and *Euchaetes egle*, are not capable of jamming big brown bats under these laboratory conditions.

However, as described above, there is indirect evidence that with the correct timing, bats can be jammed. Given tiger moths' (*Cycnia tenera*) response time for producing clicks: 25–35 ms (Fullard, 1982); 80–150 ms (Fullard, 1992), it would be impossible for arctiids to hear the bat's first biosonar cry and then place clicks before the returning echo. It would also be virtually impossible for the moths to predict when the next biosonar pulse would be issued by the bat and place clicks before that echo due to the constantly changing pulse repetition rate of an echolocation attack. Therefore, the arctiid's only feasible strategy is to make as many clicks per unit time as possible, maximizing the chances that some clicks will fall within the narrow jamming window (*sensu* Tougaard et al., 1998). There are three ways in which a tiger moth could accomplish this goal: they could increase the number of microtymbals on each tymbal organ; they could increase the rate at which they activate the tymbal, and they could increase the degree of asynchrony between the tymbals on either side of the moth. All would result in more clicks per unit time. There are over 11 000 species of tiger moths (Watson and Goodyear, 1986) and it is uncertain whether the arctiid clicks emitted routinely fall within the narrow time window for effective jamming.

It is also uncertain when arctiids respond during a bat echolocation attack. Only one member of an incredibly specious family has been assayed and the natural distribution of both operational click emission rates and temporal response profiles bears strongly on the efficacy of the jamming

hypothesis as currently presented, in either form. If phantom-echo jamming is a viable strategy, the moths should click maximally at the end of the attack when the moth sounds most closely resemble the returning terminal stage echoes and when confusion from multiple-targets would produce the greatest angular errors (Fullard et al., 1979; Fullard et al., 1994). In support of the interference version of the jamming hypothesis, Tougaard et al. argue that tiger moths attempting to jam biosonar should respond at the end of the echolocation attack, where the probability will be highest for microclicks to fall within the narrow interference window (Tougaard et al., 1998; Tougaard et al., 2004). Both hypotheses also predict that higher click rates should be more strongly associated with a late response, creating greater confusion in the phantom-echo hypothesis and increasing the probability of information corruption in the interference hypothesis. In fact, when integrating their work with Miller's (Miller, 1991), Fullard et al. concede that the 'allowable window of interference is short' (Fullard et al., 1994), indicating that for phantom echoes to be created moth clicks must also fall within Miller's jamming window of 1–2 ms, supporting the prediction that higher duty cycle arctiid calls are more likely to create phantom echoes.

Concomitantly, both of these hypotheses affirm that tiger moths with simple, low click rate calls, should call early to give the bat time to process the meaning of the warning signal (aposematism) as these calls are inadequate to produce confusion (phantom-echo hypothesis) (Fullard et al., 1994) or disrupt echo processing (interference hypothesis) (Miller, 1991; Tougaard et al., 1998; Tougaard et al., 2004)]. Here we present evidence from an assemblage of tropical tiger moth species as they respond to a recorded bat echolocation attack sequence. Regardless of call structure, from simple two-click sequences to crescendos of overlapping click trains, the moths respond similarly to bat attack, with maximal response of the assemblage occurring near the end of the approach phase.

Materials and methods

Field site and animal collection

Arctiids were collected at ultraviolet lights from July 3–20, 2003 at Tinalandia Lodge, 8 km east of Santo Domingo de los Colorados in western Ecuador. The area is principally composed of secondary tropical forest with some sugar cane and fruit agriculture. The lights were placed at an elevation of approximately 800 m overlooking the Rio Toachi valley. Arctiids were visually identified, collected and temporarily stored from 20:00 h to 05:00 h in 28 ml plastic cups. A reference collection of pinned specimens was deposited at the Pontificia Universidad Católica del Ecuador in Quito, Ecuador. The collection was later matched to archived specimens at the Smithsonian National Museum of Natural History using digital pictures of their dorsal and ventral surfaces.

Moths from 130 species (550 individuals) were assayed for sound production. The sounds produced by 350 individuals (36 species) are included in this analysis. All species included produced two or more usable sound records. Additional species (with only one sound record) and their general response categories are listed in the Appendix. Sound records of *Cycnia tenera* (Huebner) are included as a reference point but were not used in our analyses of the tropical assemblage. The *C. tenera* tested were collected from wild populations in Forsyth Co. NC, USA.

Sound recording and stimulation procedures

All recordings were made with a Pettersson Electronics D940 bat detector (±21 dB 20-80 kHz) and were digitized (sample rate: 250 kHz) using a National Instruments (Austin, TX, USA) 6062E PCMCIA A/D sound card and laptop computer. Sounds were analyzed using BatSound Pro v. 3.3 (Pettersson Electronic, Uppsala, Sweden).

Individual moths were assayed for their responses to tactile and ultrasonic stimulation either the night they were captured or early the next morning. The moths were tested by restraining the wings above the abdomen in forceps and suspending the moths inside a 50 cm×20 cm×20 cm anechoic foam-lined aluminum-screened cage. Previous work has shown that arctiids respond similarly whether restrained or in tethered flight (Fullard et al., 1994) (J.R.B. and W.E.C., unpublished data). The tests were conducted in darkness and experiments were not started until the moths remained silent for at least 1 min in the recording chamber. The order of stimulus type (ultrasound or tactile) was randomized.

Each moth was queried for response to a played back bat echolocation attack sequence of a big brown bat (*Eptesicus fuscus* Beauvois). The 2100 ms sequence used was of a trained bat attacking a tethered moth in an anechoic foam lined room (5.8 m×4.0 m×3.0 m) at Wake Forest University in Winston-Salem NC, USA. The attack was recorded with the microphone 10 cm from the position of the moth. While *E. fuscus* is not found in Ecuador, *E. furinalis* and other bats with similar echolocation calls are known to occur in the area (Albuja-V., 1999; Rydell et al., 2002). As moths are unable to discriminate frequency (Roeder, 1967), the temporal and amplitude dimensions of the attack are the most salient parameters and follow a similar profile across many species of bats that emit frequency-modulated cries (Schnitzler and Kalko, 2001). Thus, we believe the attack sequence we used accurately represents an aerial echolocation attack by a frequency-modulated bat (but see Kroodsma et al., 2001).

The echolocation attack sequence used consisted of 52 calls in three phases. Big brown bats do not emit a search phase in our laboratory but the approach and buzz stages are very similar to field recordings (see Surlykke and Moss, 2000). Our sequence began with 28 approach phase calls. The first two interpulse intervals were 98 ms, slowly decreasing to 38 ms just before the onset of the buzz. Individual biosonar pulse durations were initially 4–5 ms and decreased to 3 ms at the onset of the buzz. Buzz I was distinctly marked by the first combined decrease in minimum frequency and duration of the biosonar pulses (Surlykke and Moss, 2000). This phase consisted of 7 calls with an average interpulse interval of

18.1 ms and pulse duration of 2.5 ms. The final buzz II phase was distinguished by a sudden decrease in interpulse interval to 5–6 ms. The 17 calls in this phase had an average duration of 0.8 ms. Calls increase in intensity throughout the approach and buzz I phases and at the onset of buzz II intensity slowly decreases. Moths can detect bats at distances ca. 10 times greater than the predators can detect moths (Surlykke et al., 1999; Norman and Jones, 2000) and although a typical *E. fuscus* bat attack in the field usually lasts little more than 1 s (Surlykke and Moss, 2000), many in our laboratory last up to twice as long and given the variation in echolocation behavior across bat species we chose to playback a 2.1 s sequence to allow arctiid moths a broader time scale in which to respond.

For playback experiments the moths faced away from the speaker (Radioshack Supertweeter 40-1310B; ±15 dB from 20–50 kHz; Fort Worth, TX, USA) with the tip of the abdomen 5 cm from the speakers center, maximizing stimulation of the moth's rear-facing ears (Scoble, 1995). The microphone or bat detector recording the moth's sound was placed perpendicular to the body of the moth and 5 cm from the left tymbal, ensuring a high quality sound recording of the moth. This set-up allowed recordings of both the ipsilateral and contralateral tymbal sounds. The peak equivalent sound pressure level of the playback was 100 dB at 40 kHz as measured by a B&K ¼″ microphone (grid off) at 5 cm.

Each moth was stimulated tactilely by hand using three subjective categories of touch previously defined (Fullard and Fenton, 1977): (1) light: picking up or lightly touching the moth with the index finger (2) moderate: prodding with the index finger or shaking the moth and (3) heavy: squeezing the moth between the thumb and index finger or flicking the moth with the index finger. The response for each individual was scored as the first category of stimulation that produced a reply. A tactile stimulation score, or tactile threshold was calculated for each species by averaging the category values of the individual responders. As in the playback experiments the microphone was placed 5 cm from the left tymbal.

Data analysis

Moth call signal parameters (Fullard and Fenton, 1977) (Fig. 1) were measured using the marking cursor in BatSound Pro v.3.3 (Pettersson Electronics, Uppsala, Sweden). Each parameter value is an average of 3–5 measurements per recorded sequence from 3–5 sequences per individual. Microclick duration was calculated from the active half-modulation cycle (Fig. 1). Responses from tactile trials were used to characterize call parameters to prevent corruption from overlapping bat sounds in the echolocation playback trials.

Temporal parameters were measured from a plot of the voltage *vs* time signals (oscillograms). Frequency parameters were measured from power spectra created with Fast Fourier Transforms (FFT). An FFT size of 1024 and a Hanning window were most commonly used but parameters were optimized depending on the temporal scale analyzed. Each file was digitally highpass filtered at 16 kHz using a 6th order Butterworth filter. This filtering threshold was necessary to eliminate low-frequency echoes from within our recording chamber and insect calling noise from outside the recording room. A power spectrum was produced for each modulation cycle, and the frequency with most energy and a ±15 dB bandwidth in reference to the dominant frequency were measured. Relative intensity values were measured from a power spectrum of the 100 ms segment of maximum response during tactile stimulation. Relative intensity measurements from BatSound were transformed into peak equivalent sound pressure levels (dB pe SPL re. 2×10^{-5} μPa) using a 55 kHz reference tone of known intensity (Stapells et al., 1982). A Bruel and Kjaer 2610 measuring amplifier with a ¼″ B&K microphone (grid off) was used to measure the intensity (rms) of the pure tone. The final intensity values reported were corrected by adding or subtracting 1–15 dB to the relevant peak frequency to account for the non-flat frequency response of the D940 bat detector calibrated against a ¼″ B&K microphone (grid off).

The timing of moth response within the played back echolocation attack sequence was quantified by delineating the oscillogram window to cover 100 ms segments of each file and counting the number of clicks in that time bin. A 25% amplitude threshold was used to determine the presence of a microclick. This criterion assured that the quieter contralateral tymbal sounds were also included in our click density measurements. We were unable to accurately count microclicks that occurred at the same time as a bat pulse and all such microclicks were ignored. Counting duties were split between three individuals (J. Barber, Josh Ray and Jonathan Holley) with 20 files counted by all three workers with a less than 2% inter-observer error.

In order to determine the likelihood that moth clicks would fall within the narrow window necessary for jamming we calculated the maximum duty cycle for each species. The average number of moth clicks in the two 100 ms time bins with the highest number of clicks was multiplied by the average microclick duration for the species to obtain the percentage of acoustic space occupied in that time window, which we refer to as 'max. duty cycle'.

All statistical analyses were performed in SPSS v. 12.0 on log-transformed data. We realize that the use of species as independent units in our statistical analyses may have increased our chance of Type I errors due to shared phylogenetic history (Harvey and Pagel, 1991). But, due to small sample sizes at all taxonomic levels, and the relative uncertainty of tropical arctiid evolutionary relationships, phylogenetic analyses were not performed.

Results

130 species of arctiids were surveyed for sound production, of which 84 species (64.6%) produced ultrasonic clicks. Of these, 40 species (47.6%) responded to tactile stimulation only and three species (3.6%) responded solely to ultrasonic stimulation. The remaining 41 species (48.8%) produced clicks to both ultrasonic and tactile stimulation. We here report on the

acoustic responses of 36 species for which we have data on two or more individuals (Table 1). These species thus comprise the most common sound-producing arctiids found at the Tinalandia Lodge in western Ecuador during the month of July, 2003. We focus on 29 of these species that responded to playback of a bat echolocation attack. The average dominant frequency of these tiger moths was 58.2±17.6 kHz (mean ± s.d.). Additional call characteristics can be found in the Appendix.

We used four different timing measures to assess when this tropical assemblage of arctiids answered bats (Table 1). We analyzed the data by counting number of clicks in 100 ms time bins and our values reflect this scale of analysis. This population of tiger moths first answered the echolocation attack sequence 960±547 ms (mean ± s.d.) from the end of the 2100 ms bat attack. The assemblage reached a half-maximum response shortly after the first response, at 763±479 ms from

Table 1. *Ecuadorian tiger moth assemblages' response to stimulation type, maximum duty cycle of their calls and temporal response profiles to a simulated bat echolocation attack sequence*

Species	*N*1	%U	%T	Tscore	*N*2	maxDC	*N*3	First	Half	Max	2max
Amastus aconia (Herrich- Schaeffer)	18	50	17	0.2	2	2.30	6	1967	1430	300	417
Amplicincia near *mixta* (Moschler)	18	44	67	1.8	2	0.33	8	1438	913	538	588
Automolis sp.	2	50	100	2.5	2	15.45	12	1200	700	700	150
Bertholdia griscopalpis Rawlins	8	63	63	1	8	11.86	5	300	260	80	230
Bertholida femida Schaus	9	78	100	2.3	5	30.94	7	514	443	286	200
Calidota ruficollis Druce	8	0	25	0.5	*	*	*	*	*	*	*
Correbia lycoides Walker	2	50	100	3	2	31.68	1	700	500	200	50
Cosmosoma caecum Hampson	3	0	67	1	*	*	*	*	*	*	*
Cosmosoma cingulatum Butler	2	50	100	2.5	2	3.04	1	2100	1400	1200	1250
Cosmosoma orathidia Druce	5	0	60	1	*	*	*	*	*	*	*
Cosmosoma stibosticta Butler	5	20	100	2.6	6	0.45	1	2000	2000	1350	1350
Crambidia sp.	6	0	67	1.7	*	*	*	*	*	*	*
Crambomorpha sp.	22	55	9	0.2	2	2.25	11	473	445	345	314
Episcepsis mornata (Walker)	15	27	13	0.3	2	12.02	4	600	450	375	363
Episcepsis near *endodasia* 1 Hampson	2	100	100	3	2	12.73	2	400	350	200	250
Eucereon aroa Schaus	14	29	64	1.9	2	1.49	4	700	650	425	425
Eucereon coeruleocaput Rothschild	14	21	29	0.7	2	3.64	2	600	450	450	450
Eucereon decora Schaus	31	48	100	2.3	2	9.94	14	443	200	93	100
Eucereon near *abdominale* (Walker)	4	50	100	2.8	3	1.38	2	300	300	100	125
Eucereon near *aeolum* Hampson	2	50	100	2	2	3.85	1	600	600	200	250
Eucereon phaeoproctum Hampson	6	67	67	1.8	4	0.52	4	600	500	375	388
Eucereon setosum (Sepp.)	5	40	80	2.2	3	5.22	2	1000	900	600	700
Eucereon tarona Hampson	24	17	100	2.5	8	3.02	4	375	350	250	275
Eupseudosoma abberans Schaus	5	40	40	1.2	2	20.16	2	1400	950	750	800
Gymnelia sp. 1	18	17	56	1.6	13	3.76	6	483	133	67	17
Halysidota near *cirphis* Schaus	5	80	80	2.4	5	3.42	4	1475	1275	850	750
Hemihyalina near *alba* (Druce)	19	0	37	0.7	*	*	*	*	*	*	*
Hypocladia caita Dognin	11	9	56	1.2	5	9.40	1	1000	800	500	550
Hypomolis near *metarhoda* Schaus	4	75	100	2.8	4	48.24	2	1150	750	200	125
Idalus near *veneta* Dognin	17	88	24	0.6	4	35.75	13	1408	1254	885	881
Idalus sp. 4	4	0	100	2.5	*	*	*	*	*	*	*
Ischnocanipa sp. 2	11	82	100	2.8	2	50.66	9	1011	967	300	339
Lithosiinae: *Amplicincia* sp.	2	50	100	3	2	42.00	2	650	350	300	250
Lithosiinae: *Nodanza* sp.	9	44	89	2.7	3	3.05	5	1120	1020	860	840
Melese near *drucei* Rothschild	13	100	100	2.7	13	23.88	10	1830	1800	1010	1000
Napata walkeri (Druce)	2	0	100	2.5	*	*	*	*	*	*	*
Mean	10	42	73	2	4	14	5	960	763	475	463
s.d.	7	30	31	1	3	15	4	547	479	344	352
Cycnia tenera Huebner	65	83	94	2.6	24	8.50	19	895	605	253	255

*N*1, sample size for %U, %T and Tscore; %U, percentage of species responding to playback of echolocation attack; %T, percentage of species responding to tactile stimulation; Tscore, tactile threshold value; *N*2, sample size for max DC calculation; maxDC, maximum duty cycle; *N*3, sample size for temporal response to bat attack; First, average first response from end of attack; Half, average half-maximum response; Max, average maximum number of clicks from the end of the attack; 2max, average of two consecutive time bins with maximum number of clicks.

See Materials and methods for details.

the end of the terminal buzz. Two measures of maximum response, bin with most clicks and average of two consecutive bins with most clicks, occurred 475±344 ms and 463±352 ms, respectively, from the end of the attack; during the approach phase, before the onset of the terminal buzz.

Fig. 2 displays the temporal response of eight different arctiid species to simulated bat attack. Species like *Amplicincia* near *mixta* and *Melese* near *drucei* begin to call immediately after the playback begins, while other species (i.e. *Crambomorpha* sp. and *Episcepsis mornata*) do not call until over 1 s of playback has elapsed. However, all these species show a maximum response near the end of the approach phase

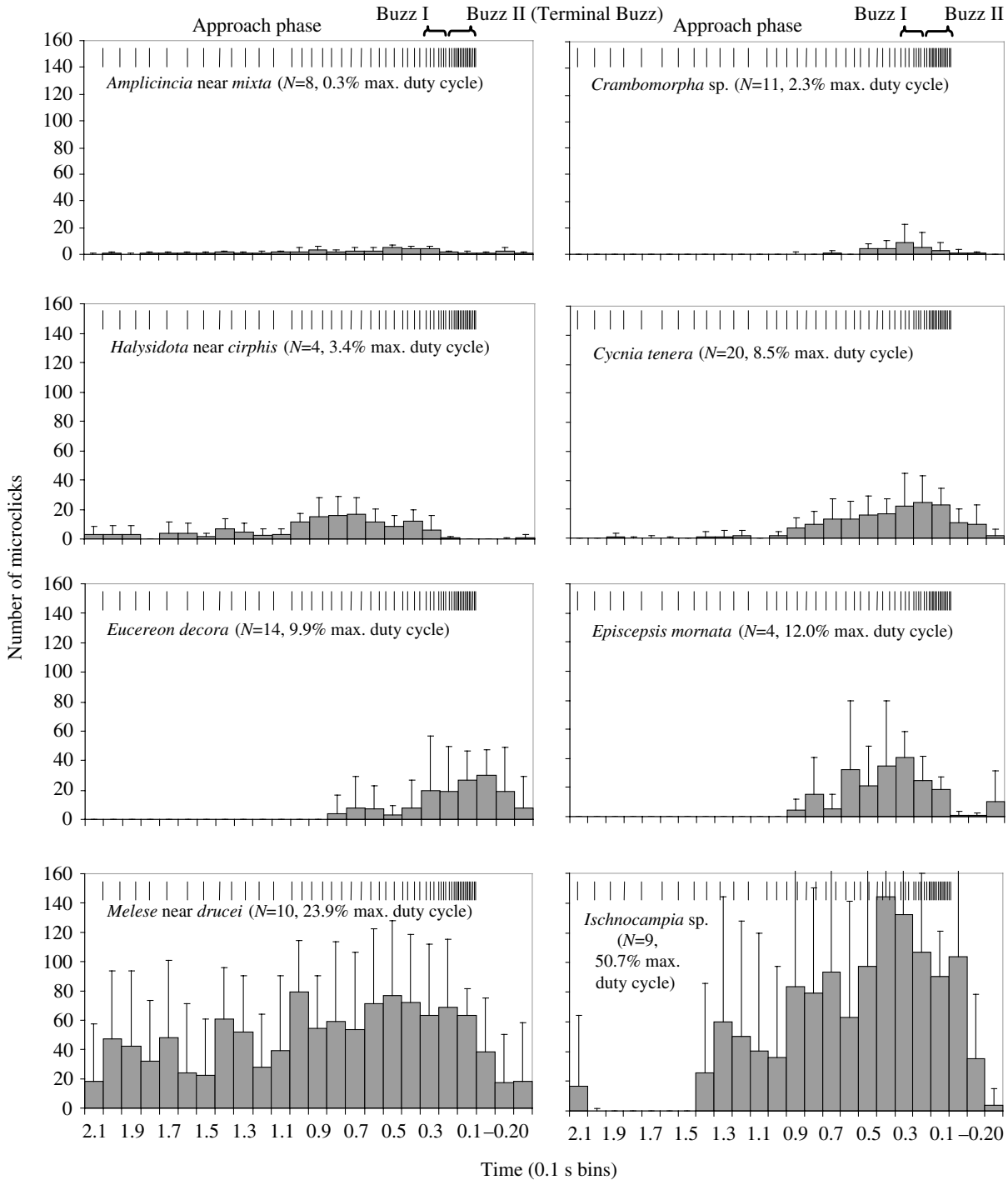

Fig. 2. Response profiles of seven Ecuadorian tiger moths and *Cycnia tenera* responding to a played back echolocation attack. The echolocation attack sequence is cartooned above each response profile. The stages of the attack are labeled above the top two panels. Values are means ± 1 s.d. See Materials and methods for details.

of the echolocation attack sequence. To ascertain if click density across species, quantified as maximum duty cycle, is associated with temporal response to the echolocation attack, as suggested by proponents of a jamming function [phantom echo hypothesis (Fullard et al., 1994); or interference hypothesis (Tougaard et al., 1998)] for arctiid sounds, we examined the dataset with a series of stepwise multiple regressions. All analyses were performed on log-transformed data to meet the assumptions of multiple regression modeling (Sokal and Rohlf, 1995).

A stepwise multiple regression failed to produce a model explaining max. duty cycle from timing of response to the reproduced bat attack, whether time bin of first moth click, time bin with half-maximum number of clicks, time bin with maximum number of clicks, or average of two consecutive time bins with the most clicks was used to assess response. Inspection of the zero-order correlations between each measure of timing and max. duty cycle revealed that none were statistically significant (all $P>0.32$), accounting for why none entered the regression equation. To confirm that this negative result was not an artifact of the way max. duty cycle was calculated we also examined the relationship between the maximum number of clicks in a 100 ms bin and our measures of timing, and again found no relationship using stepwise multiple regression. Zero-order correlations were all non-significant (all $P>0.28$).

A series of stepwise regression analyses predicting temporal response to the bat echolocation attack sequence (using our four timing measures) from arctiid calls (parameters included cdur, mhc, isi, clicks, dB pe SPL, dfreq, –15 dB kHz, +15 dB kHz; see Appendix Table A1 for abbreviations) revealed no significant predictors of timing. Inspection of the zero-order correlations between each call parameter and timing revealed that none were statistically significant (all $P>0.25$). However, a stepwise regression model predicting max. duty cycle from arctiid call parameters [same parameters included as above with average microclick duration (cdur) excluded due to its inclusion in the calculation of max. duty cycle] retained intensity (dB pe SPL) of the call, number of microclicks in the active modulation half cycle (clicks) and intra-cycle silent interval (isi) (Table 2, $R^2_{adj}=0.42$; $F_{(3,25)}=7.74$; $P=0.001$). The combination of two temporal parameters (clicks and isi) reflects the role of increased click production rate on duty cycle. The retention of intensity likely replicates the effect of more and longer clicks in the receiver's temporal integration window, resulting in a greater perceived intensity by the bat (see Discussion).

Additional stepwise multiple regression analyses, including our four timing measures, revealed no relationship with the percentage of a tiger moth species responding to tactile stimulation, ultrasonic stimulation, or tactile score. Zero-order correlations between timing and percentage of tactile responders (all $P>0.34$), percentage of ultrasound responders (all $P>0.08$) and tactile score (all $P>0.23$) were not significant accounting for why no models were produced. Interestingly, max. duty cycle is related only to percentage of playback responders ($R^2_{adj}=0.17$; $F_{(1,27)}=6.87$; $P=0.01$), not to the percentage of tactile responders or tactile score ($R^2_{adj}=–0.03$; $F_{(1,27)}=0.25$; $P=0.62$; $R^2_{adj}=–0.02$; $F_{(1,27)}=0.38$; $P=0.55$). This observation supports a role for increased duty cycle of arctiid calls in aerial interactions with echolocating bats.

There was a strong relationship between tactile score and percentage of a species that responded to tactile stimulation ($R^2_{adj}=0.93$; $F_{(1,34)}=440.02$; $P=0.0001$, Table 1). This relationship confirms the logical assumption that the more likely the species was to respond to tactile stimulation, the lower that species' threshold of response. Threshold of tactile response showed no relationship with percentage of biosonar playback responders ($R^2_{adj}=0.00$; $F_{(1,34)}=1.04$; $P=0.31$). Additionally, no connection was found between percentage of tactile responders and percentage of playback responders ($R^2_{adj}=–0.02$; $F_{(1,34)}=0.17$; $P=0.68$).

Discussion

General acoustic behavior

Two-thirds of the tropical assemblage of tiger moths sampled produced ultrasonic clicks when challenged with predator-mimicking stimuli; either tactile stimulation or playback of a bat echolocation attack. Given the roughly 11 000 species of tiger moths worldwide, thousands of arctiids are signaling predators acoustically and many of those are answering echolocating bats. The average dominant frequency of the tiger moths in our sample that responded to playback of a bat attack sequence (31 species) was 58.2±17.6 kHz (mean ± s.d.). This closely matches the dominant frequency in the biosonar cries of ten insectivorous bats known to occur in the area of Ecuador that we sampled (P. Jarrin, personal communication, from survey at Tinalandia, Eucador) (Albuja-V., 1999): –59.6±23.7 kHz [*Tadarida brasiliensis* (Simmons et al., 1978); *Micronycteris megalotis* and *Mimon Crenulatum*

Table 2. *Stepwise multiple regression analysis of arctiid call parameters by max. duty cycle*

Predictor	ΔR^2	Cumulative adjR^2	Beta weight	P (ΔR^2)
Step 1: clicks	0.228	0.199	0.192	0.009
Step 2: intensity	0.118	0.296	0.458	0.039
Step 3: isi	0.135	0.419	–0.412	0.017

Clicks, number of microclicks in the active modulation half-cycle; intensity, peak equivalent sound pressure level in decibels (dB pe SPL); isi, intra-cycle silent interval.

(Belwood, 1988); *Molossus molossus* (Kössl et al., 1999); *Rhynchonycteris naso* (Fenton et al., 1999); *Myotis nigricans* (Siemers et al., 2001); *Peropteryx macrotis*, *Mormops megalophylla*, *Eptesicus furinalis* and *Myotis keasyi* (Rydell et al., 2002)]. However, this close match in frequency should be interpreted with caution as we have no way of knowing if the bat and moth assemblages were sampled randomly or the predator/prey dynamics between these assemblages.

Even those moths that clicked solely in response to tactile stimulation could still be influencing bat receivers. Arctiids are often dropped after capture with no discernable damage (Acharya and Fenton, 1992; Hristov and Conner, 2005a; Ratcliffe and Fullard, 2005) likely due to defensive odors [i.e. pyrazine (Scoble, 1995), reflex bleeding (Scoble, 1995) and bad tasting scales (Rossini et al., 2004; Hristov and Conner, 2005b)]. Clicks stimulated by contact with the wing and tail membranes would only speed prey discrimination by the bat. Almost all species that responded to playback of bat attack continued to click for a few hundred milliseconds after the end of the feeding buzz, when they would be enveloped in the bat's membranes (Figs 2 and 3). Still the peak of arctiids' acoustic response to bat attack occurred near the end of the approach phase of the echolocation attack sequence.

Fit with predictions of the jamming hypothesis

The predictions of the phantom-echo and interference versions of the jamming hypothesis (see Introduction), are not supported by the similar response profiles of our assemblage of tiger moths. On average, our sample of arctiids first answered the echolocation attack almost 1 s before the end of the terminal buzz, reached a half-maximal response over 700 ms from the end of the buzz and peaked in response 0.5 s before the end of the attack. In short, much of tiger moth response to bat attack occurs outside of the jamming hypotheses' predictions (Fullard et al., 1994; Tougaard et al., 1998; Tougaard et al., 2004). Furthermore, no relationship exists between the duty cycle of a tiger moth's call and its temporal response to bat attack. Fig. 3 shows spectrograms of three species of arctiids that span the duty cycle spectrum, from 0.3% to 31% max. duty cycle, responding similarly to bat attack.

One reviewer pointed out that under the interference hypothesis tiger moths with low duty cycles can be expected to be under stronger selective pressure to time their response to the terminal phase of the attack (the opposite of the usual argument), where the probability of hitting the narrow jamming window is greatest, than high duty cycle moths who have a larger margin of error for effective jamming. While this postulate has not been supported by proponents of the interference hypothesis, it is a logical prediction and yet, we find no support for it here. There is no difference in temporal response profiles based on duty cycle of an arctiid's call and thus its probability of placing clicks within the jamming window.

It is tempting to surmise from the failure of our average values to fit the assumptions of the jamming hypothesis that

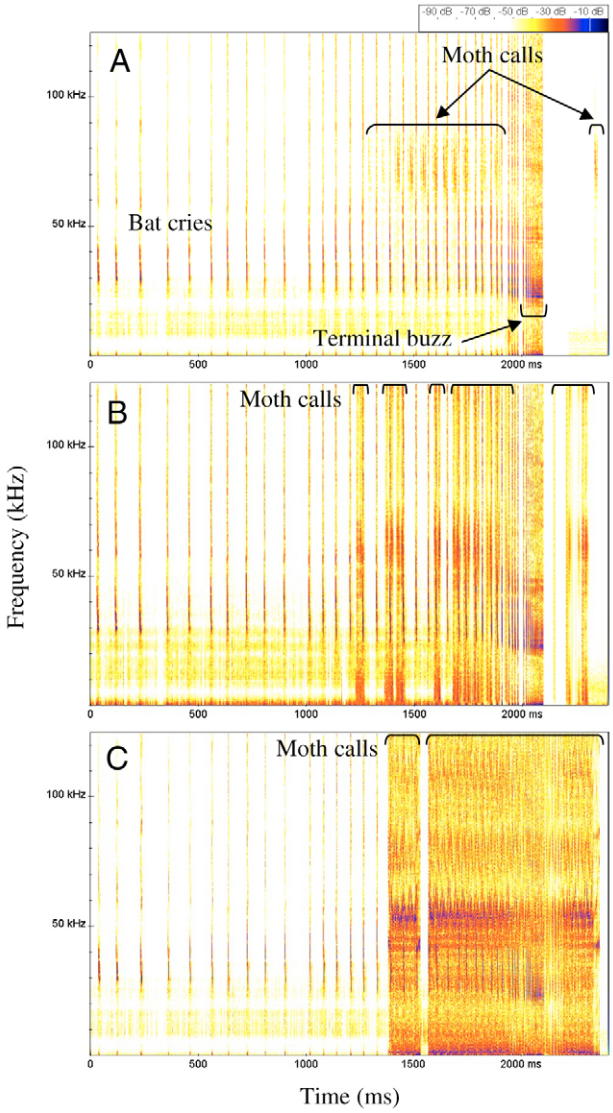

Fig. 3. Spectrograms of three tiger moths responding to a played back bat echolocation attack sequence. The *y*-axis is frequency in kHz. Note the bat cries increasing in rate towards the terminal buzz- shortly after which the bat would envelop the moth in its wing and tail membranes. The sequences are presented in order of maximum duty cycle: (A) *Amplicinia* near *mixta*; 0.3% (B) *Eucereon decora*; 9.9% (C) *Bertholdia femida*; 31%.

the entire postulate should be dismissed. We caution that the data we present here allows only a test of the stated assumptions behind the jamming hypothesis across an assemblage of arctiids and not its efficacy in bat/moth aerial battles. In fact, on a species by species basis some of our data could be construed to support the jamming hypothesis, as two of our moths (*Bertholdia griscopalpis* and *Eucereon decora*) do meet the hypotheses' predictions in their production of reasonably high duty cycle calls (~10%), produced maximally during the terminal buzz [defined by (Kick and Simmons, 1984)]; analogous to buzz II (Schnitzler et al., 1987). However, the two other tiger moths that responded maximally during the

terminal buzz produce clicks at 1.4% (*Eucereon* near *abdominale*) and 3.8% (*Gymnelia* sp. 1) duty cycles and seem unlikely to be producing clicks for a disruptive function. Five members of the assemblage and *Cycnia tenera* responded maximally during the early part of the buzz (buzz I) and ranged in duty cycle from 3% (*Eucereon tarona*) to 48.2% (*Hypomolis* near *metarhoda*). The remaining 20 species of arctiids peaked in response to the bat attack during the approach phase and again represent a diverse range of duty cycles. Perhaps the most informative finding to arise from this database is the lack of relationship between duty cycle (or any other arctiid call parameter) and timing. Why do moths that have little probability of disrupting the biosonar of an approaching bat call at or near the same time as arctiids that appear to be hallmarks of the jamming hypothesis?

Why call late?

Given that tiger moths, regardless of duty cycle, respond similarly to playback of bat attack, what are some alternative hypotheses for calling late? The most convincing alternative is that bats are unlikely to hear the sounds offered by arctiids any earlier than near the end of the attack. Given a hearing threshold for bats of 20 dB pe SPL [including noise (Surlykke et al., 1999)], an arctiid signal produced at 55 kHz and 84 dB (the averages of our data set) would be attenuated to the bat's hearing threshold (given atmospheric attenuation and spherical spreading loss) at approximately 5 m from the moth. Estimating an average flight speed of 5 m s^{-1} (Norberg and Rayner, 1987; de la Cueva Salcedo et al., 1995), an attacking bat would hear the warning about 1000 ms before capture. The actual distance at which a bat hears the moth is likely to be even smaller given the additional perturbations of temperature, wind and humidity gradients on natural signals (Lawrence and Simmons, 1982).

Arctiids that call early in the bat echolocation attack sequence may also unnecessarily give away their position until the moth is certain it is under attack. Even if some moth calls have a jamming function, evidence indicates that the disruption of encoding echolocation information only occurs in a narrow temporal window, leaving a substantial portion of time in-between returning echoes for passive sound localization (Barber et al., 2003). In aerial-feeding bats passive localization may be poor (Koay et al., 1998) but nonetheless may direct the echolocation beam towards the target.

Producing clicks is obviously a conditional strategy that is not constantly deployed (Edmunds, 1974). Using a combination of bat cry rate and intensity to determine threshold of response (Northcott and Fullard, 1996) may prevent alerting unheard, nearby bats that are naïve to the relationship between the moth's sound production and defensive chemistry. Calling too early may also allow experienced bats more time to discover Batesian mimics (Dunning, 1968). In addition, the postulate that moths sending an aposematic message need call early to give the bat time to process the meaning of the signal belies the associative learning principle that the smaller time interval between the conditioned and unconditioned stimulus the more effective the learning of that association (Domjan, 2003). Moreover, the true time interval between arctiid sound production and a bad taste in the bat's mouth includes several tens of milliseconds of handling time, as the bat transfers the moth from its wing membranes to its tail and then, to its mouth – time that the tiger moth can use to offer its acoustic warning; again allowing even those moths that do not respond to bats during the echolocation attack an opportunity to transmit their message of unpalatability. We do not mean to entirely dismiss the assertion of previous workers (Fullard et al., 1994) that there is some temporal limit on bats ability to process signal meaning but a response late in the echolocation attack is apparently enough time for such processing (Hristov and Conner, 2005a; Ratcliffe and Fullard, 2005) (J.R.B. and W.E.C., unpublished observations).

The dogbane tiger moth – Cycnia tenera

To compare our field-based methodology with the laboratory methods of Fullard et al. (Fullard et al., 1994), we tested *Cycnia tenera* and our results closely agree with their work: 253 ms (this study) *vs* 195 ms time of maximum response as measured from the end of the attack sequence. The slight difference in peak clicking and stage of response to bat attack [buzz I, this study; buzz II (Fullard et al., 1994)] could be attributable to the differences in echolocation attack sequences used as stimuli or overall differences in methodology. Our wild-caught *C. tenera* responded with lower overall click density than Fullard et al.'s sample (Fullard et al., 1994) and may indicate the role age and/or laboratory overwintering of pupae plays in click production. Interestingly, 83% (54 of 65) of the *C. tenera* we examined responded to playback yet only 47% in Fullard et al.'s investigation responded at the same intensity of playback (Fullard et al., 1994). This could again be due to the age/experience level of our moths, differences between populations, and/or an artifact of laboratory emergence.

Despite recurring claims that the three hypotheses for tiger moth sounds are not mutually exclusive (Miller, 1991; Fullard et al., 1994; Tougaard et al., 1998; Tougaard et al., 2004; Hristov and Conner, 2005a; Ratcliffe and Fullard, 2005), concrete evidence in aerial bat–tiger moth interactions only exists for startle (which appears to function ephemerally) and acoustic aposematism (Hristov and Conner, 2005a; Ratcliffe and Fullard, 2005). As of yet, the only behavioral evidence for jamming comes from reduced laboratory paradigms where bats do not use natural echolocation attack behavior (e.g. Miller, 1991; Masters and Raver, 1996). Both studies that pitted tiger moths against flying bats used *Cycnia tenera*. Therefore, we must conclude that the timing and call of *C. tenera* provides a sufficient associative learning stimulus to indicate nasty taste (acoustic aposematism) in two bat species, *Eptesicus fuscus* (Hristov and Conner, 2005a) and *Myotis septentrionalis* (Ratcliffe and Fullard, 2005). As *C. tenera*'s temporal response to synthetic bat attack is near the median value of our tropical assemblage of tiger moths, it seems many arctiid calls may function aposematically.

Appendix

Table A1. *Call parameters for 38 species of Ecuadorian tiger moths*

Species	*N*	cdur	mhc	mc	isi	clicks	dB pe SPL	d kHz	–15 dB kHz	+15 dB kHz
Amastus aconia (Herrich-Schaeffer)	2	0.20±0.1	15.5±5.4	54.7±13.0	22.5±0.5	3.5±0.7	87.7±0.3	116.7±2.2	102.5±7.5	133.7±2.8
Amplicincia near *mixta* (Moschler)	8	0.11±0.02	3.7±1.1	12.9±2.0	5.1±0.8	6.4±3.0	82.8±4.3	72.2±3.8	63.9±6.3	79.4±6.6
Automolis sp.	2	0.41±0.04	9.4±9.4	23.1±1.4	4.4±0.8	9.3±0.9	86.2±1.1	50.0±11.2	43.5±14.6	58.8±10.7
Bertholdia griscopalpis Rawlins	2	0.36±0.06	7.8±0.1	25.5±5.2	9.4±3.6	10.5±2.1	97.4±0.1	55.8±0.6	46.6±2.6	69.7±8.3
Bertholida femida Schaus	5	0.26±0.04	7.3±0.3	22.1±0.9	7.4±0.7	7.2±0.8	90.8±4.2	53.9±7.5	47.6±6.7	64.1±3.3
Calidota ruficollis Druce	2	0.26±0.06	1.5±0.4	11.3±3.18	8.4±2.0	2.0±0.0	79.0±3.0	44.7±3.5	41.1±3.0	52.0±0.4
Correbia lycoides Walker	2	0.15±0.01	8.2±0.8	32.8±0.8	7.2±0.7	10.0±1.4	84.7±1.6	58.4±0.8	49.5±0.0	66.2±4.0
Cosmosoma caecum Hampson	2	0.05±0.0	2.6±1.0	9.3±1.1	4.5±0.1	4.0±0.0	76.5±3.3	41.8±1.4	29.8±5.2	56.2±5.4
Cosmosoma cingulatum Butler	2	0.04±0.0	7.6±1.7	24.9±3.5	4.7±0.7	18.0±1.4	73.9±2.5	37.2±0.1	33.1±2.7	40.0±1.7
Cosmosoma orathidia Druce	2	0.21±0.01	32.7±15.6	135.4±1.3	76.7±23.5	4.5±0.7	71.3±1.8	41.5±16.7	33.6±11.2	54.2±8.8
Cosmosoma stibosticta Butler	6	0.45±0.14	0.45±0.14	11.4±7.2	10.4±7.0	1.0±0.0	76.0±4.4	43.6±1.9	38.4±3.0	49.6±2.5
Crambidia sp.	4	0.15±0.03	6.1±0.8	15.5±1.6	5.6±1.9	10.0±1.8	89.7±4.0	70.2±4.2	61.3±6.1	76.3±1.5
Crambomorpha sp.	2	0.19±0.05	19.0±3.6	95.7±14.4	61.4±30.0	4.2±0.7	81.9±6.4	44.8±2.3	27.1±6.6	63.9±21.3
Cycnia tenera Huebner	20	0.23±0.04	6.5±1.4	22.7±4.4	8.1±2.8	7.5±2.1	86.5±4.7	63.5±6.6	53.5±6.4	71.9±7.1
Episcepsis mornata (Walker)	2	0.21±0.05	6.7±1.0	18.6±4.1	3.8±2.1	12.0±2.8	76.9±1.4	43.1±4.1	33.7±3.5	49.9±2.6
Episcepsis near *endodasia* 1 Hampson	2	0.19±0.01	6.7±0.6	18.9±0.0	4.8±0.6	14.5±0.7	86.3±0.3	59.6±1.6	50.1±1.7	65.2±3.3
Eucereon aroa Schaus	9	0.15±0.02	7.5±1.9	19.3±2.9	5.6±1.6	8.6±2.4	80.8±6.0	72.5±4.6	65.5±5.1	78.4±5.8
Eucereon coeruleocaput Rothschild	3	0.11±0.02	4.3±0.3	36.8±5.4	28.3±6.0	6.5±1.3	78.6±2.2	67.6±2.5	61.4±1.3	73.5±3.9
Eucereon decora Schaus	10	0.19±0.03	14.0±2.8	36.3±6.8	7.1±1.5	20.3±5.1	90.0±4.4	54.5±3.8	43.5±6.7	63.6±3.9
Eucereon near *abdominale* (Walker)	4	0.51±0.02	10.6±2.1	56.5±14.0	13.6±4.2	6.8±3.5	88.6±5.9	30.5±1.9	25.1±2.5	34.0±2.0
Eucereon near *aeolum* Hampson	2	0.05±0.0	22.9±1.7	61.9±4.7	18.3±0.7	8.0±0.0	61.9±3.0	28.4±0.9	18.4±0.1	72.8±2.5
Eucereon phaeoproctum Hampson	4	0.11±0.02	3.1±1.0	12.0±0.8	8.2±2.4	4.5±0.6	73.8±0.3	69.4±0.4	61.5±3.5	77.4±4.2
Eucereon setosum (Sepp.)	3	0.18±0.11	5.4±1.2	29.2±1.6	17.2±5.8	5.7±1.5	82.1±6.6	69.9±1.2	57.1±9.9	82.0±6.4
Eucereon tarona Hampson	8	0.39±0.06	15.5±7.7	38.9±12.7	14.4±3.3	6.7±2.1	88.6±2.1	60.5±6.2	53.5±4.6	70.8±6.1
Eupseudosoma abberans Schaus	2	0.16±0.28	10.1±1.1	27.1±4.5	4.5±0.5	16.2±1.2	90.6±1.3	66.7±3.6	55.4±2.1	77.2±9.0
Gymnelia sp. 1	13	0.41±0.13	1.8±3.4	11.8±8.1	9.2±7.0	1.8±1.9	77.8±5.6	40.8±2.3	34.6±4.7	46.2±5.3
Halysidota near *cirphis* Schaus	5	0.18±0.02	10.3±2.2	33.9±6.1	9.3±3.7	17.4±6.5	80.9±5.2	51.2±3.6	39.9±9.2	59.1±4.8
Hemihyalina near *alba* (Druce)	6	0.28±0.07	9.4±2.8	30.3±7.0	13.1±2.9	7.2±1.8	88.9±4.0	27.7±2.6	23.5±1.6	32.6±2.2
Hypocladia caita Dognin	5	0.20±0.09	2.9±1.3	14.8±6.6	8.8±5.0	3.3±0.4	80.1±7.4	53.7±4.6	41.7±12.7	65.3±5.5
Hypomolis near *metarhoda* Schaus	4	0.36±0.07	6.0±1.8	18.6±2.0	8.2±0.5	7.0±1.3	88.2±2.5	48.3±3.8	35.7±5.3	61.0±3.3
Idalus near *veneta* Dognin	4	0.38±0.01	6.8±1.6	21.1±2.7	8.9±1.5	5.6±0.9	97.7±1.4	44.7±5.0	39.3±2.6	50.3±6.6

Table A1. *Continued*

Species	*N*	cdur	mhc	mc	isi	clicks	dB pe SPL	d kHz	–15 dB kHz	+15 dB kHz
Idalus sp. 4	2	0.17±0.03	2.3±0.7	19.5±4.3	16.6±5.5	2.5±0.7	78.5±3.6	46.9±9.2	42.1±5.6	54.0±12.4
Ischnocanipa sp. 2	10	0.27±0.04	5.8±1.2	16.0±4.6	4.1±1.0	8.9±1.1	90.9±1.7	54.5±5.9	46.0±8.0	63.1±7.8
Lithosiinae: *Amplicincia* sp.	2	1.0±0.01	4.2±0.3	12.5±0.5	6.0±0.08	5.3±0.4	71.7±5.7	78.9±2.1	67.5±2.8	87.8±1.2
Lithosiinae: *Nodanza* sp.	3	0.12±0.02	2.6±0.1	16.2±2.4	10.4±3.8	8.7±3.5	80.0±8.7	77.1±14.0	75.0±13.2	79.1±14.2
Melese near *drucei* Rothschild	13	0.19±0.04	9.6±1.1	24.9±2.5	5.0±1.1	11.6±1.7	92.5±1.7	77.8±3.0	64.3±6.5	90.1±3.7
Napata walkeri (Druce)	2	0.23±0.05	7.9±2.1	19.5±3.7	3.8±0.5	19.0±1.4	91.2±1.2	50.8±7.1	43.4±5.6	54.3±3.4

See Fig. 1 for tiger moth call description. All temporal values are listed in ms. Abbreviations: cdur, microclick pulse duration; mhc, modulation half cycle duration; mc, modulation cycle; isi, intercycle silent interval; clicks, microclicks per active modulation half cycle; dB pe SPL, peak equivalent sound pressure level in decibels; d kHz, dominant frequency in kHz; –15 dB kHz, frequency 15 dB below the d kHz; +15 dB kHz, frequency 15 dB above the d kHz. It is important to note that dfreq is listed for the primary harmonic and the ±15 dB frequency bandwidth usually, but not always, captured prominent second harmonics. Additionally, most calls contained some energy at lower frequencies (but always outside our ±15 dB bandwidth) that permitted us to hear the animals responding when held close to the ear. Noise from echoes within our recording chamber and insects calling outside our recording room prevented a detailed analysis of lower frequencies.

Listed below are (a) arctiid species tested that did not produce sound (*N*) and (b) arctiid species that produced sound but whose files were not analyzable due to corrupted recordings or small sample size (*N*, number responding to ultrasound stimulation, number responding to tactile stimulation).

(a) *Automolis* near *albimaculifera* Hampson (1), *Automolis* near *iheringhi* Schaus (4), *Calidota ruficollis* (Druce) (2), *Castrica phalaenoides* (Drury) (3), *Coreura simsoni* Druce (1), *Correbia raca* (Druce) (1), *Correbidia calopteridia* (Butler) (1), *Correbidia fana* (Druce) (1), *Correbidia striata* (Druce) (1), *Mesothen* near *ockendeni* Druce (3), *Cosmosoma caecum* Hampson (1), *Cosmosoma* near *auge* (L.) (1), *Cosmosoma* near *gaza* Schaus (1), *Delphyre* near *dizona* (Druce) (1), *Delphyre nigra* (Schaus) (1), *Dinia* near *chrysogastrides* Draudt (1), *Ecpantheria cotyera* Druce (7), *Ecpantheria* near *cotyera* Druce (5), *Epanycles imperialis* (Walker) (1), *Eucereon aroa* Schaus (1), *Eucereon discolor* Walker (4), *Eucereon lineata* Dognin (1), *Eucereon* near *aroa* Schaus (3), *Eucereon patrona* Schaus (2), *Eucereon varium* (Walker) (1), *Eupseudosoma abberans* Schaus (1), *Cosmosoma metallicum* (Rothschild) (2), *Cosmosoma* near *lucens* (Dognin) (2), *Gymnelia* sp. (2), *Halysidota rhomboidea* (Sepp.) (1), *Halysidota distincta* Rothschild (1), *Halysidota dognini* Rothschild (1), *Halysidota* near *distincta* Rothschild (1), *Halysidota* near *pseudomanda* Rothschild (2), *Halysidota tolimensis* Rothschild (5), *Halysidota underwoodi* Rothschild (4), *Ischnocampa* sp. (2), *Napata* sp. (1), *Opharus bimaculata* (Dewitz) (1), *Pachydota nervosa* (Felder) (1), *Pericopis grassator* Hering (5), *Pericopis* near *lycaste* Klug. (1), *Robinsonia* sp. (4), *Saurita* near *obscura* Klages (3), *Thyragis* sp. (2), *Turuptiana neurophylla* (Walker) (2).

(b) *Agylla argentifera* (Walker) (5,3,1), *Amaxia erythrophleps* Hampson (2,1,1), *Autochloris mathani* Rothschild (5,0,3), *Automolis diluta* (Felder) (3,0,1), *Automolis* near *metallica* Joicey (4,1,1), *Automolis tanialoides* Rothschild (1,0,1), *Automolis vittipes* (Walker) (1,0,1), *Bertholdia* near *yashoquintela* Rawlins (2,1,1), *Cercopimorpha* near *dolens* Schaus (1,0,1), *Cosmosoma eumelis* (Druce) (1,0,1), *Cosmosoma galatea* Schaus (2,0,2), *Mesothen* near *ockendeni* Druce (2,0,1), *Cosmosoma metallescens* (Menée) (6,0,1), *Cosmosoma orathidia* Druce (3,0,2), *Cosmosoma sectinota* Hampson (2,0,1), *Ctenuchini* sp. (1,0,1), *Dixophlebia quadristrigata* (Walker) (2,0,1), *Elysiles cingulata* (Walker) (1,0,1), *Episcepsis inornata* (Walker) (4,2,1), *Episcepsis* near *endodasia* Hampson (1,0,1), *Episcepsis* sp. (1,0,1) *Eucereon atrigutta* Druce (1,1,1), *Eucereon lineate* (Dognin) (2,0,1), *Eucereon setosum* (Sepp.) (3,0,3), *Eucereon* sp. (2,0,2), *Eucereon striata* (Druce) (1,1,0), *Halysidota* near *bicolor* Walker (11,0,9), *Halysidota* near *alsus* (Cramer) (1,1,0) *Halysidota* near *pseudomanda* Rothschild (2,1,1), *Halysidota alsus* (Cramer) (3,0,1), *Hemihyalina* near *alba* (Druce) (7,0,1), *Holophaea* sp. (1,0,1), *Hyaleuceria vulnerata* Butler (4,0,2), *Idalus dognini* Rothschild (1,1,1), *Idalus* near *rosea* (Schaus) (1,0,1), *Idalus sp.* (6,0,3), *Idalus* sp. 2 (2,0,2), *Idalus* sp. 3 (1,0,1), *Macrocneme* near *chrysitis* (Guérin) (7,2,5), *Mapeta* sp. (4,0,3), *Napata albiplaga* (Walker) (1,0,1), *Pelochyta cinera* (Walker) (5,0,1), *Phaeomolis lepida* Schaus (3,1,0), *Pheia elegans* (Druce) (1,0,1), *Robinsonia multimaculata* Rothschild (1,1,1), *Xenosoma nigrcosta* (Walker) (1,0,1).

Diversity of tiger moth calls

These data presented here do not address the function of high duty cycles in tiger moths, but given the description of calls with higher duty cycles than previously quantified (i.e. *Bertholdia femida*; Fig. 2C) (but see Blest et al., 1963) and the diverse range cataloged (Table 1), it is relevant to briefly discuss alternative hypotheses for duty cycle evolution in the Arctiidae. Recent work has produced no direct evidence for jamming (Miller et al., 2004; Hristov and Conner, 2005a; Ratcliffe and Fullard, 2005). It is possible that the systems used were not sensitive enough to uncover any subtle jamming effects of the clicks and that more robust signals (i.e. higher duty cycles) are needed to reveal such a function. However, high click density calls could also produce benefits in an aposematic context. Increased learning rates of higher duty cycle signals and increased avoidance by predators of signals more elaborate than the original learning stimulus may be driving signal evolution (Gamberale-Stille and Tullberg, 1999; Lindström et al., 1999). Also, depending upon how bats categorize ultrasonic insect warning sounds, higher duty cycles may be more effective acoustic mimics. In habitats where arctiids are rare, startle may play a driving role if higher duty cycles produce greater startle magnitudes (Hoy, 1989; Blumenthal, 1996).

The suggestions above describe potential evolutionary driving mechanisms but they fail to explain the persistence of low duty cycle calls. Weak selective pressure is doubtful to explain maintenance of such diversity. We postulate that much of this stabilization is driven by the role of tiger moth sounds in sex; both in species identification and sexual selection. Many tiger moths have been shown to use sound in sex (Krasnoff, 1987; Krasnoff and Yager, 1988; Cerny, 1990; Sanderford and Conner, 1990; Sanderford and Conner, 1995; Simmons and Conner, 1996; Sanderford et al., 1998), including the most commonly used arctiid in bat-tiger moth studies, *Cycnia tenera* (Conner, 1987) (S. E. Garrett and W.E.C. unpublished data). Tiger moth sounds' role in sexual communication may also explain the broad range of dominant frequencies in our sample (28–116 kHz; Appendix) that are not likely to be solely explained by the mosaic of predators (bats and otherwise) that arctiids face in the wild. We envision the mechanisms underlying this conjecture to involve sender–receiver matching for optimal receptor stimulation not frequency discriminations, as moths have been shown to lack such ability (Roeder, 1967).

Arctiid call parameters and the bat receiver

The hypotheses presented above concerning the temporal dimensions of tiger moth calls are inextricably linked with the effect of increased number of clicks per unit time on perceived intensity by the bat. The arctiid call parameters that predicted a significant amount of variance in max. duty cycle of our tropical assemblage were: number of microclicks per half-modulation cycle, intra-cycle silent interval, and intensity (Table 2; see Fig. 1 for moth call description). The inclusion of number of microclicks per half-modulation cycle is not surprising and confirms that increasing this parameter increases click rate. Also, the incorporation of a negative relationship between intra-cycle silent interval and duty cycle in the model likely reflects the connection between modulation cycle production rate and a fast intra-cycle recovery, and thus more microclicks per unit time. Perhaps the most interesting parameter included in the model is intensity.

Assuming a fixed intensity of a single microclick and that bats function as perfect power integrators, an additional microclick within the bat receiver's integration window would increase the perceived intensity of the moth signal by approximately 3 dB (Zwislocki, 1960; Au et al., 1988). However, given the large variation in microclick intensity and duration both across species and even within a single modulation cycle of one moth, the relationship between number of microclicks and intensity is not that clearcut. As in the regression model, an animal receiver would perceive more microclicks per unit time as more intense. The details of such a relationship would also depend upon the behavioral integration time of the receiver. Using a double click paradigm this value has been estimated at 0.2 ms in *Megaderma lyra* (Weißenbacher et al., 2002) and 2.4 ms in *Eptesicus fuscus* (Surlykke and Bojesen, 1996). In humans, integration time may depend upon stimulus type (for a review, see Brown and Maloney, 1986). Although, in *M. lyra* integration time has been shown to be independent of echolocation use (Weißenbacher et al., 2002), it remains unclear how different stimulus types influence these processes in bats. The above studies have also shown some variation across individuals. Taken together these results indicate that integration time likely varies both across species and situations. Our use of 100 ms to standardize intensity measurements allows a comparison of relative values but cannot predict the perceived intensity by the bat receiver.

Thus, the addition of microclicks may be one method that arctiids have used to increase the apparent intensity of their calls to bat predators. Louder calls would produce a greater startle response (Blumenthal, 1996), increase the statistical chances of signal detection (Tougaard, 1998) and be more salient aposematic learning signals (Domjan, 2003). Also, louder signals would be more likely to match the intensity of returning echoes from the moth's body during the final advance of the bat attack. Such a match between bisonar echo and moth clicks would support the phantom-echo hypothesis (Fullard et al., 1979; Fullard et al., 1994). This hypothetical match would also support the interference hypothesis as Tougaard et al. showed (Tougaard et al., 1998) that clicks of equal or greater intensity than near simultaneously delivered FM signals (mimicking biosonar echoes) produced suppression of neural units in the lateral lemniscus of the big brown bat. Most cells were unaffected if the clicks were not as intense as the FM sweeps. Assuming these neural results can be broadly applied to behavior, jamming would only be effective over that time range where the moth clicks were equal to or louder than returning echoes, supporting jamming proponents contention that a jamming moth should call late.

Conclusions

We do not argue that this data set speaks directly to the function of arctiid sound production. However, we do assert that timing of response is *not* a diagnostic parameter of a jamming function for arctiid clicks and there are other, equally convincing reasons that arctiids should call late to a bat echolocation attack sequence. It is possible that onset differences in arctiids' response to bat attack may be found to be important in future work, particularly when search phase calls are used in echolocation attack stimuli. It also remains unclear whether the proximal stimulus triggering tiger moth response to bat attack is temporal pattern recognition or stimulus intensity and what the interplay is between these parameters (but see Northcott and Fullard, 1996). The pattern of response times shown here demonstrates that a similar time/intensity algorithm governs tymbal response to bats in arctiids with diverse duty cycles. The most telling future research on tiger moth assemblages will incorporate tiger moth palatability and acoustics in a phylogenetic framework; this work awaits the refinement of evolutionary hypotheses in the Arctiidae (Weller et al., 1999).

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References

Acharya, L. and Fenton, M. B. (1992). Echolocation behavior of vespertilionid bats (*Lasiurus cinereus* and *Lasiurus borealis*) attacking airborne targets including arctiid moths. *Can. J. Zool.* **70**, 1292-1298.

Albuja V., L. (1999). *Murciélagos del Ecuador (2nd edn).* Quito, Ecuador: Cicetrónica Cía.

Au, W. W. L., Moore, P. W. B. and Pawloski, D. A. (1988). Detection of complex echoes in noise by an echolocating dolphin. *J. Acoust. Soc. Am.* **83**, 662-668.

Barber, J. R., Razak, K. A. and Fuzessery, Z. M. (2003). Can two streams of auditory information be processed simultaneously? Evidence from the gleaning bat *Antrozous pallidus. J. Comp. Physiol. A* **189**, 843-855.

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.

Belwood, J. J. (1988). Foraging behavior, prey selection and echolocation in phyllostomine bats (Phyllostomidae). In *Animal Sonar* (ed. P. E. Nachtigall and P. W. B. Moore), pp. 601-605. New York, London: Plenum Press.

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 Biol. Sci.* **158**, 196-207.

Blumenthal, T. D. (1996). Inhibition of the human startle response is affected by both prepulse intensity and eliciting stimulus intensity. *Biol. Psychol.* **44**, 85-104.

Brown, C. H. and Maloney, C. G. (1986). Temporal integration in two species of Old World monkeys: blue monkeys (*Cercopithecus miti*s) and grey-cheeked monkeys (*Cercocebus albigena*). *J. Acoust. Soc. Am.* **79**, 1058-1064.

Cerny, K. (1990). Untersuchungen zur ökophysiologie der gattung *Setina* schrank (Lepidoptera: Arctiidae). PhD thesis, Universität Innsbruck, Innsbruck, Austria.

Conner, W. E. (1987). Ultrasound: its role in the courtship of the arctiid moth, *Cycnia tenera. Experientia* **43**, 1029-1031.

de la Cueva Salcedo, H., Fenton, M. B., Hickey, M. B. C. and Blake, R. W. (1995). Energetic consequences of flight speeds of foraging red and hoary bats (*Lasiurus borealis* and *Lasiurus cinereus*; Chiroptera: Vespertilionidae). *J. Exp. Biol.* **198**, 2245-2251.

Domjan, M. (2003). *The Principles of Learning and Behavior*. Belmont, CA: Thomson Wadworth.

Dunning, D. C. (1968). The warning sounds of moths. *Z. Tierpsychol.* **25**, 129-138.

Dunning, D. C. and Krüger, M. (1995). Aposematic sounds in African moths. *Biotropica* **27**, 129-138.

Dunning, D. C. and Roeder, K. D. (1965). Moth sounds and the insect-catching behavior of bats. *Science* **147**, 173-174.

Dunning, D. C., Acharya, L., Merriman, C. B. and Ferro, L. D. (1992). Interactions between bats and arctiid moths. *Can. J. Zool.* **70**, 2218-2223.

Eckrich, M. and Boppré, M. (1990). Chemical vs. acoustic cues in the defense of arctiid moths (Lepdioptera) against small mammals. *Verh. Dtsch. Zool. Ges.* **83**, 632.

Edmunds, M. (1974). *Defence in Animals: A Survey of Anti-predator Defences*. Burnt Mill, UK: Longman.

Fenton, M. B., Rydell, J., Vonhof, M. J., Eklöf, J. and Lancaster, W. C. (1999). Constant-frequency and frequency-modulated components in the echolocation calls of three species of small bats (Emballonuridae, Thyropteridae, and Vespertillionidae). *Can. J. Zool.* **77**, 1891-1900.

Fullard, J. H. (1982). Echolocation assemblages and their effects on moth auditory systems. *Can. J. Zool.* **60**, 2572-2576.

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 behavioral analyses of the sounds produced by some species of Nearctic Arctiidae (Lepidoptera). *Can. J. Zool.* **55**, 1213-1224.

Fullard, J. H. and Heller, B. (1990). Functional organization of the arctiid moth tymbal (Insecta, Lepidoptera). *J. Morphol.* **204**, 57-65.

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., Simmons, J. A. and Saillant, P. A. (1994). Jamming bat echolocation: the dogbane tiger moth *Cycnia tenera* times its clicks to the terminal attack calls of the big brown bat *Eptesicus fuscus. J. Exp. Biol.* **194**, 285-298.

Gamberale-Stille, G. and Tullberg, B. S. (1999). Experienced chicks show biased avoidance of stronger signals: an experiment with natural color variation in live aposematic prey. *Evol. Ecol.* **13**, 579-589.

Harvey, P. H. and Pagel, M. D. (1991). *The Comparative Method in Evolutionary Biology*. Oxford: Oxford University Press.

Holderied, M. W., Corine, C., Fenton, M. B., Parsons, S., Robson, S. and Jones, G. (2005). Echolocation call design and intensity in the aerial hawking bat *Eptesicus bottae* (Vespertilionidae) studied using stereo videogrammetry. *J. Exp. Biol.* **208**, 1321-1327.

Hoy, R. R. (1989). Startle, categorical response, and attention in acoustic behavior of insects. *Annu. Rev. Neurosci.* **12**, 355-375.

Hristov, I. H. and Conner, W. E. (2005a). Sound strategy: acoustic aposematism in the bat-tiger moth arms race. *Naturwissenschaften* **92**, 164-169.

Hristov, I. H. and Conner, W. E. (2005b). Effectiveness of tiger moth (Lepidoptera, Arctiidae) chemical defenses against an insectivorous bat (*Eptesicus fuscus*). *Chemoecology* **15**, 105-113.

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.

Koay, G., Kearns, D., Heffner, H. E. and Heffner, R. S. (1998). Passive sound-localization ability of the big brown bat (*Eptesicus fuscus*). *Hear. Res.* **119**, 37-48.

Kössl, M., Mora, E. C., Coro, F. and Vater, M. (1999). Two-toned echolocation calls from *Molossus molossus* in Cuba. *J. Mammal.* **80**, 929-932.

Krasnoff, S. B. (1987). The chemical ecology of courtship communication in

some nearctic arctiids (Lepidoptera: Arctiidae). PhD thesis, Cornell University, Ithaca, New York, USA.

Krasnoff, S. B. and Yager, D. D. (1988). Acoustic response to a pheromonal cue in the arctiid moth *Pyrrharctia isabella. Physiol. Entomol*. **13**, 433-440.

Kroodsma, D. E., Byers, B. E., Goodale, E., Johnson, S. and Liu, W.-C. (2001). Pseudoreplication in playback experiments, revisited a decade later. *Anim. Behav*. **61**, 1029-1033.

Lawrence, B. D. and Simmons, J. A. (1982). Measurements of atmospheric attenuation at ultrasonic frequencies and the significance for echolocating bats. *J. Acoust. Soc. Am.* **71**, 585-590.

Lindström, L., Alatalo, R. V., Mappes, J., Riipi, M. and Vertainen, L. (1999). Can aposematic signals evolve by gradual change? *Nature* **397**, 249-251.

Masters, W. M. and Raver, K. A. (1996). The degradation of distance discrimination in big brown bats (*Eptesicus fuscus*) caused by different interference signals. *J. Comp. Physiol. A* **179**, 703-713.

Miller, L. A. (1991). Arctiid moth clicks can degrade the accuracy of range difference discrimination in echolocating big brown bats, *Eptesicus fuscus*. *J. Comp. Physiol. A* **168**, 571-579.

Miller, L. A., Futtrup, V. and Dunning, D. C. (2004). How extrinsic sounds interfere with bat biosonar. In *Echolocation in Bats and Dolphins* (ed. J. A. Thomas, C. F. Moss and M. Vater), pp. 380-385. Chicago: University of Chicago Press.

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. and Rayner, J. M. (1987). Ecological morphology and flight in bats (Mammalia: Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **316**, 335-427.

Norman, A. P. and Jones, G. (2000). Size, peripheral auditory tuning and target strength in noctuid moths. *Physiol. Entomol*. **25**, 346-353.

Northcott, M. and Fullard, J. H. (1996). The closed-loop nature of the tymbal response in *Cycnia tenera*. *Brain Behav. Evol*. **48**, 130-136.

Ratcliffe, J. M. and Fullard, J. H. (2005). The adaptive function of tiger moth clicks against echolocating bats: an experimental and synthetic approach. *J. Exp. Biol.* **208**, 4689-4698.

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

Rossini, C. A., Bezzerides, A., Gonzalez, M., Eisner, M. and Eisner, T. (2004). Chemical defense: incorporation of diet-derived pyrrolizidine alkaloid into the integumental scales of a moth (*Utetheisa ornatrix*). *Chemoecology* **13**, 199-205.

Rydell, J., Arita, H. T., Santos, M. and Granados, J. (2002). Acoustic identification of insectivorous bats (order Chiroptera) of Yucatan, Mexico. *J. Zool*. **257**, 27-36.

Sanderford, M. V. and Conner, W. E. (1990). Courtship sounds of the polka-dot wasp moth, *Syntomeida epilais. Naturwissenschaften* **77**, 345-347.

Sanderford, M. V. and Conner, W. E. (1995). Acoustic communication in *Syntomeida epilais* Wlk. (Lepidoptera: Arctiidae, Ctenuchinae). *J. Insect Behav*. **8**, 19-31.

Sanderford, M. V., Coro, F. and Conner, W. E. (1998). Courtship behavior in *Empyreuma affinis* Roths. (Lepidoptera, Arctiidae, Ctenuchinae): acoustic signals and tympanic organ response. *Naturwissenschaften* **85**, 82-87.

Schnitzler, H.-U., Kalko, E., Miller, L. and Surlykke, A. (1987). The echolocation and hunting behavior of the bat, *Pipistrellus kuhli*. *J. Comp Physiol. A* **161**, 267-274.

Schnitzler, H.-U. and Kalko, E. K. (2001). Echolocation by insect-eating bats. *Bioscience* **51**, 557-569.

Scoble, M. J. (1995). *The Lepidoptera: Form, Function and Diversity*. Oxford: Oxford University Press.

Siemers, B. M., Kalko, E. K. V. and Schnitzler, H. U. (2001). Echolocation behavior and signal plasticity in foraging Neotropical *Myotis nigricans* (Schinz, 1821) (Vespertilionidae): a convergent case with pipistrelles? *Behav. Ecol. Sociobiol*. **50**, 317-328.

Simmons, J. A., Lavender, W. A., Lavender, B. A., Childs, J. E., Hulebak, K., Rigden, M. R., Sherman, J., Woolman, B. and O'Farrell, M. J. (1978). Echolocation by free-tailed bats (*Tadarida*). *J. Comp. Physiol. A* **125**, 291-299.

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.

Simmons, R. B. and Conner, W. E. (1996). Ultrasonic signals in the defense and courtship of *Euchaetes egle* Drury and *E. bolteri* Stretch (Lepidoptera: Arctiidae). *J. Insect Behav*. **9**, 909-919.

Sokal, R. R. and Rohlf, F. J. (1995). *Biometry*. New York: W. H. Freeman.

Stapells, D. R., Picton, T. W. and Smith, A. D. (1982). Normal hearing threshold for clicks. *J. Acoust. Soc. Am*. **72**, 74-79.

Surlykke, A. and Bojesen, O. (1996). Integration time for short broad band clicks in echolocating FM-bats (*Eptesicus fuscus*). *J. Comp. Physiol. A* **178**, 235-241.

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.

Surlykke, A. and Moss, C. F. (2000). Echolocation behavior of big brown bats, *Eptesicus fuscus*, in the field and the laboratory. *J. Acoust. Soc. Am*. **108**, 2419-2429.

Surlykke, A., Filskov, M., Fullard, J. H. and Forrest, E. (1999). Auditory relationships to size in noctuid moths: bigger is better. *Naturwissenschaften* **86**, 238-241.

Tougaard, J. (1998). Detection of short pure-tone stimuli in the noctuid ear: what are temporal integration and integration time all about? *J. Comp. Physiol. A* **183**, 563-572.

Tougaard, J., Cassedy, J. H. and Covey, E. (1998). Arctiid moths and bat echolocation: broad-band clicks interfere with neural responses to auditory stimuli in the nuclei of the lateral lemniscus of the big brown bat. *J. Comp. Physiol. A* **182**, 203-215.

Tougaard, J., Miller, L. A. and Simmons, J. A. (2004). The role of arctiid moth clicks in defense against echolocating bats: interference with temporal processing. In *Echolocation in Bats and Dolphins* (ed. J. A. Thomas, C. F. Moss and M. Vater), pp. 365-371. Chicago: University of Chicago Press.

Watson, A. and Goodyear, D. T. (1986). *Catalogue of the Neotropical Tiger-moths (Occasional Papers on Systematic Entomology, No. 1)*, 71 pp. London: British Museum.

Weißenbacher, P., Wiegrebe, L. and Kössl, M. (2002). The effect of preceding sonar emission on temporal integration in the bat, *Megaderma lyra*. *J. Comp. Physiol. A* **188**, 147-155.

Weller, S. J., Jacobson, N. L. and Conner, W. E. (1999). The evolution of chemical defenses and mating systems in tiger moths (Lepidoptera: Arctiidae). *Biol. J. Linn. Soc. Lond.* **68**, 557-578.

Zwislocki, J. (1960). Theory of temporal auditory summation. *J. Acoust. Soc. Am*. **32**, 1046-1060.