Anti-bat tiger moth sounds: Form and function

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Abstract   The night sky is the venue of an ancient acoustic battle between echolocating bats and their insect prey. Many tiger moths (Lepidoptera: Arctiidae) answer the attack calls of bats with a barrage of high frequency clicks. Some moth species use these clicks for acoustic aposematism and mimicry, and others for sonar jamming, however, most of the work on these defensive functions has been done on individual moth species. We here analyze the diversity of structure in tiger moth sounds from 26 species collected at three locations in North and South America. A principal components analysis of the anti-bat tiger moth sounds reveals that they vary markedly along three axes: (1) frequency, (2) duty cycle (sound production per unit time) and frequency modulation, and (3) modulation cycle (clicks produced during flexion and relaxation of the sound producing tymbal) structure. Tiger moth species appear to cluster into two distinct groups: one with low duty cycle and few clicks per modulation cycle that supports an acoustic aposematism function, and a second with high duty cycle and many clicks per modulation cycle that is consistent with a sonar jamming function. This is the first evidence from a community-level analysis to support multiple functions for tiger moth sounds. We also provide evidence supporting an evolutionary history for the development of these strategies. Furthermore, cross-correlation and spectrogram correlation measurements failed to support a "phantom echo" mechanism underlying sonar jamming, and instead point towards echo interference [*Current Zoology* 56 (3): 358–369, 2010].

Key words   Acoustic aposematism, Sonar jamming, Arctiidae, Cross-correlation, Autocorrelation

Many tiger moths produce high frequency clicks in response to the hunting calls of insectivorous bats. These sounds provide a survival advantage to their possessors (Dunning et al., 1992) but the sensory mechanisms by which anti-bat sounds work have spurred considerable debate (see Ratcliffe and Fullard, 2005). Throughout the discussion one or a few key species often have served as "representative". In reality there is considerable variation in the anti-bat sounds produced by tiger moths and it is this variation that is the focus herein. The questions that we address are: (1) how in parameter space do tiger moth sounds vary; (2) do the sounds fall into discrete categories; (3) what does the variation tell us about the functions of anti-bat sounds; and (4) how do the sounds vary across tiger moth taxa?

Tiger moths (Family: Arctiidae) produce sounds by activating bilateral thoracic blisters of cuticle called tymbal organs. The diversity of acoustic "displays" of arctiids have been documented by Blest (1964), Fenton and Roeder (1974), Fullard and Fenton (1977), and Barber and Conner (2006), but they have never been probed for consistent patterns within and across taxo-nomic groups. One key characteristic, the degree of frequency modulation, a characteristic that may be important to their function, has never been explored in a comparative way.

Tymbal organs (Fig. 1A) are thoracic plates modified by cuticular thinning and striation to produce a complex sound radiator (Blest et al., 1963; Fullard and Heller, 1990). During activation by underlying muscles, a wave of deformation expands from its dorsal origin ventrally along striations (Fenton and Roeder, 1974) producing a train of discrete clicks. After a brief pause, elastic recoil of the structure triggers a return wave across the same striations to produce a second burst of clicks (Fig. 1B). The number of clicks produced per full cycle is determined by the number of striations on the structure, a morphological trait, and the extent to which they are traversed, a behavioral trait. Species can vary in both traits and in the rate at which they activate the structure. The bilateral tymbals can also be activated synchronously or asynchronously (Fullard and Fenton, 1977). During a cycle the peak frequency of each click varies typically (but not always) from the high frequency to a
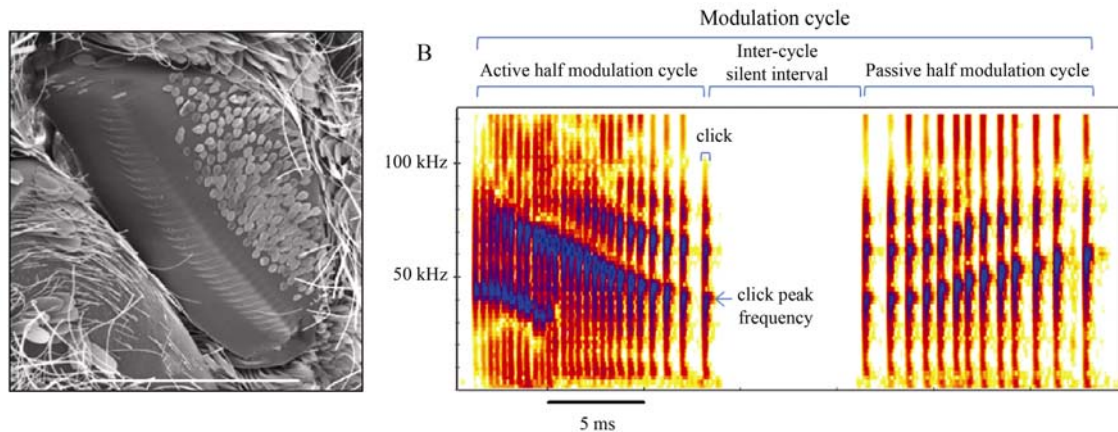

Fig. 1   Tiger moth sound producing tymbal organ (A) and spectrogram of tiger moth clicks with definitions (B)
Clicks are produced by the sequential buckling of the microtymbals (small ridges in A) inward and then outward to create the active and passive half-modulation cycles seen in B. The peak frequency of clicks changes over time. The highly developed tymbal and click recording are from the sonar-jammer, *Bertholdia trigona*. The tymbal in A is shown with dorsal side up and anterior to the left.

low frequency and back again (Blest et al., 1963). When the temporal characteristics of bat hearing are considered (Simmons et al., 1989) this pattern results in a frequency modulated (FM) structure reminiscent of the frequency sweep of bat calls. The frequency structure of a single click can also be complex. While considered broadband they often have one or more frequency peaks in a harmonic or pseudo-harmonic relationship.

The sensory mechanisms by which anti-bat sounds may function have traditionally been described as the triumvirate of startle, acoustic aposematism, and sonar jamming or some combination thereof. It has become increasingly apparent that this list first has proven too limiting and, second, that some categories can be subdivided into multiple distinct mechanisms. We here provide a brief summary of the proposed mechanisms.

Startle   Bats appear to be startled by sounds produced by moths as a deimatic display (Edmunds, 1974; Hoy et al., 1989; Bates and Fenton, 1990; Hristov and Conner, 2005a, Barber and Conner, 2007). However the predators' behavioral response decays after a few stimuli and discussions have focused on whether bats experience tiger moth sounds frequently enough to allow habituation or whether they are sufficiently rare to allow for a startling advantage (Bates and Fenton, 1990; Miller, 1991; Hristov and Conner, 2005a; Ratcliffe and Fullard, 2005).

Aversion   Although rarely included as a mechanism it is possible that that moth sounds may be intrinsically repellent. Whether by virtue of their intensity or through their interaction with sensory processing, this mechanism deserves more attention (Ratcliffe and Fullard, 2005).

Aposematism or Warning   Many arctiids are unpalatable as a result of inherent toxins (Weller et al., 1999; Hristov and Conner, 2005a). Moth sounds could advertise these qualities to acoustic predators. Multiple studies show this as a primary defensive strategy for many tiger moth species (Dunning and Roeder, 1965; Dunning, 1968; Eckrick and Boppré, 1990; Acharya and Fenton, 1992; Dunning et al., 1992; Dunning and Krüger, 1995; Hristov and Conner, 2005b; Barber and Conner, 2007).

Mimicry   Where aposematism functions in nature it frequently supports Müllerian and Batesian mimicry. Dunning (1968) first suggested that tiger moths exploit acoustic mimicry, and Barber and Conner (2007) and Barber et al. (2009) provided conclusive evidence.

Jamming   Moth sounds confuse bats by hindering the normal processing of prey echoes. Psychophysical, behavioral, and neurophysiological experiments have long supported this idea (Fullard et al., 1979; Fullard et al., 1994; Miller, 1991; Tougaard et al., 1998; Tougaard et al., 2004); and recent behavior experiments with free flying bats and a high-duty-cycle moth have confirmed its utility (Corcoran et al., 2009). Precisely how moths accomplish sonar jamming remains an unanswered question.

Phantom Echo   The similarity of the moth clicks' power spectra, frequency time characteristics, and intensity to moth echoes prompted Fullard et al. (1979; 1994) to suggest that moth sounds create the illusion of multiple phantom targets as a form of acoustic camouflage (also see Blest et al., 1963).

Interference   Moth clicks could directly interfere with the bat's echo processing, thus rendering target

ranging less reliable (Miller, 1991; Masters and Raver, 1996; Tougaard et al., 1998).

Masking The presence of background sound can have a profound influence on the threshold of detection of acoustic signals including echoes (Barber et al., 2010). Tiger moth clicks, if sufficiently numerous and intense, could cause a bat to miss echoes in background noise.

Distraction The simultaneous processing of two data streams - in this case that of prey echoes and moth clicks - can make it difficult for a predator to attend to either (Barber et al., 2003).

Synthetic Hypotheses It should be noted that none of the above mentioned hypotheses need function in isolation as they are not mutually exclusive. It has recently been argued that the sounds produced by arctiids combine two of the above mechanisms (Ratcliffe and Fullard, 2005). They posit that moths sounds can both be aversive (by virtue of their ability to jam sonar) and warn of an underlying defense. This combination is proposed to be more potent that either by itself. Additional combinations are possible and even likely.

It is against this background of hypotheses that we now examine the rich diversity of tiger moth acoustic signatures. We herein analyze their sounds in temporal and frequency domains. While we consider tiger moth sound structure in the context of defense against bats, it should be noted that the sounds may also be used to defend against ultrasound sensitive terrestrial predators.

1 Methods and Materials

1.1 Field sites and moth collection

The adult moths used in this study were primarily collected at ultraviolet lights at two field sites: Tinalandia Lodge, 8 km east of Santo Domingo de los Colorados in western Ecuador in July of 2003 and at the Southwest Research Station near Portal, Arizona in July of 2009. Sound recordings of *Cycnia tenera* (Hübner) and *Euchaetes egle* Drury collected in Forsyth and Surry Counties in North Carolina were included as reference points since much of the work on the acoustic signaling of arctiids have focused on these species. A description of moth recordings from Ecuador and North Carolina were reported elsewhere (Barber and Conner, 2006), but are expanded upon here.

1.2 Sound recording procedures

Unless otherwise noted, all recording equipment and stimulation procedures replicate previously described methods (Barber and Conner, 2006). Briefly, moths were suspended in a sound-recording chamber (50 cm ×

20 cm × 20 cm) lined with sound-absorbent foam. Moths were held in a hemostat by their dorsally folded wings. Moth ultrasonic responses under such conditions are not different from the response in unrestrained flight (Fullard et al., 1994, W.E.C., J.R.B., *unpublished data*), however, because of the wing movements of the moth during flight bats in nature likely perceive more variation in moth sounds than reported here. Ultrasound was recorded using a Petterson D940 detector (Pettersson Elektronik AB, Uppsala, Sweden) connected via a National Instruments (Austin TX, USA) 6062E PCMCIA A/D sound card (250 kHz sampling rate) to a laptop computer running BatSound Pro v. 3.3 (Pettersson Elektronik AB, Uppsala, Sweden). For all recordings the detector's microphone was placed 5 cm lateral to the suspended moth, directly facing one of the moth's paired tymbals.

Moths were queried for ultrasonic responses using two methods presented in a random order: tactile stimulation (see Barber and Conner, 2006 for details), and ultrasonic playback of a bat echolocation attack sequence. For ultrasonic playback, a 2.1s laboratory recording of a trained big brown bat *Eptesicus fuscus* attacking a tethered moth in an anechoic flight room (5.8m × 4.0m × 3.0 m) was played back to each moth with a ScanSpeak ultrasonic speaker (Avisoft Bioacoustics, Berlin, Germany). The moth was suspended 5 cm away from the speaker, oriented with the moth's rear-facing ears (Scoble, 1995) directed towards the sound source. The bat calls were played back with a peak equivalent sound pressure level of 100 dB, as measured with a B&K ¼" microphone (grid off) at 5 cm. This SPL is similar to that recorded from bats attacking targets in a flight room (Boonman and Jones, 2002), but may be an underestimate of bat call intensities in the field. For further details of the recording, see Barber and Conner 2006. The vocalizations of *Eptesicus fuscus* are appropriate since it commonly occurs in North Carolina and Arizona where moths were collected, and its close relative possessing similar echolocation calls, *Eptesicus furinalis*, occurs at the collection site in Ecuador.

1.3 Data analysis

Ten previously defined moth click parameters were measured as previously described (Barber and Conner, 2006; Fullard and Fenton, 1977), using BatSound Pro v.3.3 (Pettersson Elektroniks AB, Uppsala, Sweden), Raven Pro v1.4 (Cornell Lab of Ornithology, Ithaca, NY) or a custom LabView (National Instruments, Austin, TX) program. Five parameters were measured directly from the oscillogram trace of individual click modulation

cycles from the tactile stimulation recordings (*cdur*, click duration; *mhc*, modulation half-cycle duration; *mc*, modulation cycle duration; *isi* inter-cycle silent interval; *clicks*, number of clicks per mhc; Fig. 1). Three frequency measures (*d kHz*, dominant frequency; *-15 dB kHz*, frequency at -15 dB below d kHz; *+15 dB kHz*, frequency at -15 dB above d kHz) were taken from power spectra produced of a single modulation cycle created with 1024-point Fast Fourier Transforms (FFT) using a hanning window (Proakis and Manolakis, 2006). To measure maximum duty cycle (*MaxDC*), the bat playback recordings were divided into 100 ms sections, with the last division ending with the final echolocation call. The maximum number of clicks occurring within one of these divisions was recorded, multiplied by the average cdur of the species and divided by 100 ms to generate the MaxDC measurement. Maximum peak-to-peak intensity was measured from each tactile stimulation moth click recording and then converted to peak equivalent SPL (dB peSPL re. 2×10^{-5} µPa) using a reference tone of known intensity (Stapells et al, 1982). The intensity (rms) of the reference tone was measured using a Bruel and Kjaer 2610 measuring amplifier with a ¼" B&K microphone (grid off). Measurements were adjusted for the frequency response of the microphone (+/- 10 dB from 20-100 kHz) according to the dominant frequency of the clicks.

We also measured two novel parameters for quantifying the degree of frequency modulation across clicks of a half modulation cycle (*swp*, sweep rate; *stdev kHz*, standard deviation of click peak frequencies; Fig. 1B). Swp is defined as the difference in dominant frequencies between the first and last click of the active half modulation cycle divided by mhc. Some moths produce an initial series of clicks with peak frequencies that do not match the overall frequency modulated trend of the mhc (e.g., *B. trigona* Fig. 1). Under these conditions, swp was measured only from the clicks creating the predominant frequency modulation of the sound.

As part of our exploration of the diversity of tiger moth sounds, we used Principal Components Analysis (PCA) with varimax rotation to determine the axes of variation by which clicks of tiger moth species differ. Statistical analysis was conducted in SPSS 16.0 (Chicago, IL). To ensure the reliability of the analysis, we included only species with >3 individuals, and averaged values across individuals within a species. Our relatively small sample size (28 of >11,000 tiger moth species) precludes us from generalizing our results to the Arctiidae as a whole. Instead, we consider the results in the context of two tiger moth communities. We assessed normality of variables using skewness and kurtosis (Tabachnick and Fidell, 2007). Three variables were positively skewed (MaxDC, swp, and clicks). The skew of MaxDC and clicks resulted from a small number of species with relatively high values and were not transformed in order to retain their natural distributions. A square-root transform was applied to swp, producing a normal distribution. PCA is relatively robust to violations of normality when used for descriptive purposes, as we do here (Tabachnick and Fidell, 2007).

We looked for outliers using 2D scatter plots, and eliminated two cases. Principal components with Eigen values >1 were considered important sources of variation. Variables with component loadings > 0.5 were used in labeling the axis which each component represents. Correlation coefficients between variables loading on the same components were used to confirm the validity of the associations determined by the PCA (Tabachanick and Fidell, 2007). Finally, we analyzed 2D scatter plots of all significant principle components to identify trends in the diversity of tiger moth sounds.

1.4 Cross-correlation metrics

We conducted a series of cross-correlation analyses to test the plausibility of the phantom echo hypothesis and the interference hypothesis. Four echolocation calls representing search, approach, buzz 1 and buzz 2 were selected from the echolocation attack sequence used in the playback trials. Because the bat recording was made in a flight room, the calls represent only the short duration, fast repetition rate end of the bats' echolocation repertoire (Surlykke and Moss, 2000). However, because moths generally click late in an attack sequence (Fullard et al., 1994, Barber and Conner, 2006) - when bats shorten their sonar emissions - the range of calls used is reflective of the sounds bats make when moths typically click in nature. One modulation cycle from each moth recording was randomly selected, scaled to have equal peak-to-peak amplitude as the bat call, and cross-correlated against each bat call. Reported cross-correlation values were scaled relative to the peak autocorrelation value of each bat call. While early work suggested bats use a cross-correlation-like form of echolocation (Simmons, 1973), more recent work has demonstrated that bats do not perform as well as would be expected with such an echolocation system, particularly in the presence of interfering noise (Troest and Møhl, 1986). Others have suggested that bats use a process more similar to spectrogram cross-correlation (Altes, 1980; Saillant et al., 1993). If so, spectrogram

correlation (Clark et al., 1987; Masters and Raver, 1996) would be a better measure of the similarity of sounds as perceived by bats. Therefore, we also computed spectrogram correlations between moth clicks and bat calls. In this procedure the spectrograms of two sounds are overlaid and a correlation coefficient is computed using corresponding pixels from the two spectrograms. The shorter spectrogram is then shifted forward in time one pixel with respect to the longer spectrogram, and this process is serially repeated until the end of the longer spectrogram is reached. All spectrograms were created using a hanning window and a 176-point window. This window size corresponds to the 350 μs integration time required for bats to discriminate two sounds (Simmons et al., 1989).

We conducted a second set of correlation analyses to determine the disruptive potential of moth clicks. First, the audio recordings of a bat call and a moth click modulation cycle were linearly combined. To standardize for differences in intensity that could affect correlation values, the moth clicks were set to have peak-to-peak SPLs 10 dB greater than the bat calls, replicating the natural situation for at least one bat-moth interaction (Corcoran et al., 2009). The autocorrelation function was then calculated for the bat call in the presence of moth clicks and scaled relative to the autocorrelation value of the bat call absent of interfering sound. This process was repeated by shifting the bat call forward in time 1 ms until the end of the moth click modulation cycle was reached. All calculated values for a given moth click modulation cycle were then averaged. This process was completed using standard cross-correlation and spectrogram correlation.

2   Results

Our acoustic samples - 15 from Ecuador, nine from Arizona and two from North Carolina - captured considerable variation in tiger moth anti-bat sounds (Table 1; Fig. 2 for examples). The dominant frequency varied from 27.7 kHz to 82.2 kHz and the number of clicks per modulation cycle varied from 1.0 to 21.5. The maximum duty cycle varied from 0.3% to 50.7% and the absolute value of the FM sweep varied from 0.0 to 6.9 kHz/ms. Three key species with known behavioral functions, namely *Cycnia tenera*, which has been shown to produce sounds that warn predators of their underlying bad taste (Hristov and Conner, 2005a,b), *Euchaetes egle*, a Batesian mimic of the first (Barber and Conner, 2007) and *Bertholda trigona*, a known sonar jammer (Corcoran et al., 2009), are highlighted throughout to ground

truth the data set.

A principal components analysis of the characteristics of tymbal sounds partitions variation along three main axes or Principal Components (PC1 – PC3; Table 2). These, in order of the strength of their loading are a frequency axis (including peak frequency, +/- 15dB measurements, and click duration), a duty cycle and frequency modulation (FM) axis (including a negative correlation with isi), and a modulation cycle structure axis (including the duration of the modulation half cycle and click number). These three components account for 74.9 percent of the total variation of the 11 parameters characterizing tymbal sounds.

To visualize the partitioning of tymbal sound space we graphed binary combinations of the principal components (Fig. 3). Plots of PC1 and PC2 and PC1 and PC3 resulted in homogenous data clouds that appeared to reveal little about underlying function (Fig. 3A, B). The PC2-PC3 plot, however, revealed a clustering into two groups (Fig. 3C). The first cluster includes all species in the bottom two and top-left quadrants of the PC2-PC3 plot. The second cluster includes the six species contained within the top-right quadrant of the PC2-PC3 plot. The distinction between these two clusters, and the labeling of the two groups can better be observed in a simple 2D plot of two variables that heavily weight PC2 and PC3 -- maximum duty cycle and click number (Fig. 3D). Here, cluster one is primarily composed of species with low to medium number of clicks (1–8) and low MaxDC (< 12%). Two species with high click numbers (17–21), but low MaxDC values are included in this group. The aposematic *C. tenera* and mimetic *E. egle* also fall in this group. The second cluster is marked by medium to high click numbers (5–22) and notably higher MaxDC values (24% –51%). The sonar-jammer, *B. trigona* falls in group two. It is also noteworthy that *C. tenera* and its proven mimic *E. egle* are closer together in all four comparisons than either is to the proven jammer *B. trigona*. Finally, species in the subfamily lithosiinae (gray numbers in Fig.2B) are restricted to cluster one, whereas arctiines (black numbers in Fig. 2B) are found in both clusters.

To further probe the relevance of tymbal sound structure to function we carried out cross-correlation and spectrogram cross-correlation analyses of four species of arctiids (*B. trigona*, *Carales arizonensis*, *Cisthene martini*, *Ctenucha venosa*) that span the full range of tymbal sound complexity, or variation in duty cycle, frequency modulation, and click number. Cross-correlations were calculated relative to the search, approach, buzz 1

Table 1 Tiger moth click parameters

Species	Sp. #	Site	N1	stdev kHz	swp	N2	MaxDC	N3	cdur	mhc	mc	isi	clicks	dB pe SPL	d kHz	-15 dB kHz	+15 dB kHz
Subfamily Arctiinae																	
Bertholdia femida	1	EC	4	7.9±0.7	0.9±0.2	5	30.9	5	0.26±0.04	7.3±0.3	22.1±0.9	7.4±0.7	7.2±0.8	88.4±0.8	53.9±7.5	47.6±6.7	64.1±3.3
Bertholdia trigona	2	AZ	6	11.4±1.8	3.9±0.6	6	43.8	6	0.28±0.07	12.2±3.2	29.5±5.9	5.3±1.0	21.5±5.4	80.7±2.1	48.7±8.7	21.9±10.9	83.1±5.6
Carales arizonensis	3	AZ	5	6.6±7.1	0.2±1.0	5	38.4	5	0.41±0.05	11.4±2.2	28.6±9.7	6.2±3.0	13.0±2.2	76.8±3.1	53.8±19.4	34.8±24.2	67.3±23.5
Cosmosoma stibasticta	4	EC	4	N/A	N/A	6	0.5	6	0.45±0.14	0.45±0.14	11.4±7.2	10.4±7.0	1.0±0.0	90.4±0.6	43.6±1.9	38.4±3.0	49.6±2.5
Ctenucha venosa	5	AZ	5	0.5±0.6	0.2±0.3	4	3.3	5	0.55±0.17	1.9±1.9	9.8±6.4	6.0±2.6	1.6±0.8	77.2±2.6	29.3±3.1	16.6±4.0	34.6±2.4
Cycnia tenera	6	NC	8	1.0±0.7	1.2±0.7	24	8.5	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
Eucereon aroa	7	EC	5	7.1±3.6	3.9±3.0	4	1.5	9	0.15±0.02	7.5±1.9	19.3±2.9	5.6±1.6	8.6±2.4	74.9±0.6	72.5±4.6	65.5±5.1	78.4±5.8
Eucereon decora	8	EC	5	5.4±3.7	0.0±0.4	2	9.9	10	0.19±0.03	14.0±2.8	36.3±6.8	7.1±1.5	20.3±5.1	85.7±2.4	54.5±3.8	43.5±6.7	63.6±3.9
Eucereon near *abdominale*	9	EC	4	0.7±0.6	0.2±0.1	3	1.4	4	0.51±0.02	10.6±2.1	56.5±14.0	13.6±4.2	6.8±3.5	89.6±0.2	30.5±1.9	25.1±2.5	34.0±2.0
Eucereon phaeproctum	10	EC	4	10.3±8.8	5.8±6.1	4	0.5	4	0.11±0.02	3.1±1.0	12.0±0.8	8.2±2.4	4.5±0.6	70.0±9.1	69.4±0.4	61.5±3.5	77.4±4.2
Eucereon tarona	11	EC	5	4.2±0.2	1.6±0.9	8	3.0	8	0.39±0.06	15.5±7.7	38.9±12.7	14.4±3.3	6.7±2.1	84.5±0.9	60.5±6.2	53.5±4.6	70.8±6.1
Euchaetes egle	12	NC	5	2.3±1.9	0.3±0.4	4	3.1	5	0.17±0.02	12.6±3.9	40.5±4.7	14.4±2.7	6.4±1.8	78.3±2.8	66.3±4.4	47.0±7.1	80.1±7.1
Euchaetes antica	13	AZ	6	7.0±5.0	1.2±1.0	1	4.0	6	0.17±0.03	6.0±1.9	19.6±4.7	6.5±3.1	8.5±4.1	78.6±3.0	62.5±4.6	24.2±7.6	78.1±7.4
Gymnelia sp. 1	14	EC	5	0.3±0.6	0.2±0.4	13	3.8	13	0.41±0.13	1.8±3.4	11.8±8.1	9.2±7.0	1.8±1.9	67.6±4.1	40.8±2.3	34.6±4.7	46.2±5.3
Halysidota near *cirphis*	15	EC	4	5.6±2.2	2.4±1.8	5	3.4	5	0.18±0.02	10.3±2.2	33.9±6.1	9.3±3.7	17.4±6.5	85.5±2.9	51.2±3.6	39.9±9.2	59.1±4.8
Hemihyalea edwardsii	16	AZ	6	0.6±0.4	0.3±0.2	N/A	N/A	6	0.33±0.12	6.1±6.9	29.5±17.7	19.2±5.7	2.4±1.2	84.5±4.6	82.2±17.3	67.2±9.8	101.9±18.3
Hemihyalea near *alba*	17	EC	5	0.5±0.6	0.0±0.2	N/A	N/A	6	0.28±0.07	9.4±2.8	30.3±7.0	13.1±2.9	7.2±1.8	90.1±0.1	27.7±2.6	23.5±1.6	32.6±2.2
Idalus near *veneta*	18	EC	5	10.7±2.8	6.9±7.4	4	35.8	4	0.38±0.01	6.8±1.6	21.1±2.7	8.9±1.5	5.6±0.9	89.0±3.2	44.7±5.0	39.3±2.6	50.3±6.6
Ischnocampa sp. 2	19	EC	4	11.1±2.2	0.1±0.2	2	50.7	10	0.27±0.04	5.8±1.2	16.0±4.6	4.1±1.0	8.9±1.1	86.0±2.3	54.5±5.9	46.0±8.0	63.1±7.8
Melese near *drucei*	20	EC	5	7.6±3.3	2.4±1.0	13	23.9	13	0.19±0.04	9.6±1.1	24.9±2.5	5.0±1.1	11.6±1.7	76.7±0.7	77.8±3.0	64.3±6.5	90.1±3.7
Pygarctia roseicapitis	21	AZ	5	2.8±1.4	-0.80.9	4	6.1	5	0.20±0.03	10.0±2.2	38.4±8.2	18.7±5.1	3.5±0.4	76.9±4.8	54.0±8.4	24.1±6.2	75.2±21.6
Virbia fragilis	22	AZ	8	6.5±5.5	2.1±2.7	5	4.5	8	0.12±0.03	6.1±3.5	22.1±10.5	9.4±7.4	6.0±2.4	69.1±6.0	60.6±11.3	33.3±11.7	109.5±9.7
Subfamily Lithosiinae																	
Amplicincia near *mixta*	23	EC	5	3.4±1.7	1.6±1.6	2	0.3	8	0.11±0.02	3.7±1.1	12.9±2.0	5.1±0.8	6.4±3.0	76.6±0.1	72.2±3.8	63.9±6.3	79.4±6.6
Cisthene martini	24	AZ	7	5.2±5.8	0.6±1.5	4	5.7	7	0.25±0.07	4.1±1.6	16.7±1.8	8.9±2.2	4.9±1.4	74.6±7.7	60.9±7.9	34.5±11.2	73.3±9.3
Cisthene tenuifaschia	25	AZ	6	4.5±4.2	0.8±1.5	6	11.6	6	0.33±0.05	3.9±1.5	14.3±0.8	6.3±2.3	4.8±2.2	72.0±6.4	58.4±5.5	35.2±13.8	68.8±7.0
Crambidia sp.	26	EC	4	3.8±2.7	1.5±2.0	N/A	N/A	4	0.15±0.03	6.1±0.8	15.5±1.6	5.6±1.9	10.0±1.8	78.3±0.7	70.2±4.2	61.3±6.1	76.3±1.5

All temporal values are listed in ms. Abbreviations: Sp. #, species number; Site, collection site; AZ, Arizona; EC, Ecuador; NC, North Carolina; N1, sample size for frequency modulation measurements; stdev kHz, standard deviation of click frequency in kHz; sweep, click sweep rate in kHz/ms; N2, sample size for duty cycle measurements; MaxDC, maximum duty cycle over 100 ms interval; N3, sample size for modulation cycle parameter measurements; cdur, click duration; mhc, active half modulation cycle duration; mc, modulation cycle duration; isi, inter-cycle silent interval; clicks, number of clicks in active half modulation cycle; dB pe SPL, peak equivalent sound pressure level in decibels re. 20 µPa; d Khz, dominant frequency in kHz; -15 dB kHz, frequency -15 dB below d kHz; +15 dB kHz, frequency -15 dB above d kHz. Values are mean ± standard deviation.
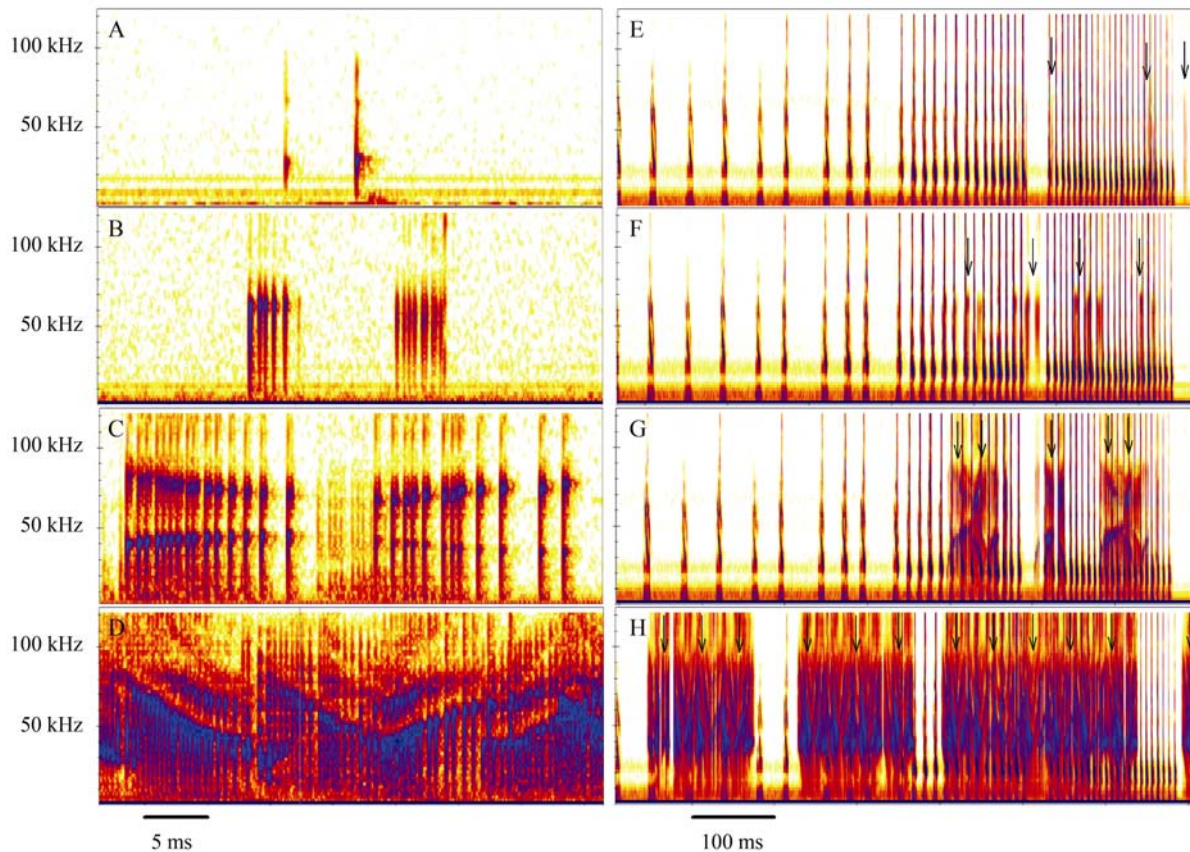
Fig. 2   Variation in the complexity of anti-bat tiger moth sounds as illustrated by spectrograms of moth click modulation cycles (A–D) and moth response to bat attack playbacks (E–H)

Modulation cycle click numbers and duty cycles increase from top to bottom. The following tiger moth species are depicted: *Ctenucha venosa* (A, E), *Cisthene martini* (B, F), *Carales arizonensis* (C, G), and *Bertholdia trigona* (D, H). Single modulation cycles are shown in A–C, whereas in D parts of two overlapping, asynchronous modulation cycles are shown. The bat calls depicted in E-H increase in production rate over time as the recorded bat neared its insect prey. Moth clicks in E-H are indicated by arrows.

Table 2   Component matrix and Eigen values for principal component analysis of tiger moth click parameters

Parameter	Component		
	1	2	3
kHz	**0.941**	0.117	0.006
cdur	**−0.930**	−0.029	−0.185
+15 dB kHz	**0.863**	0.137	0.132
-15 dB kHz	**0.671**	0.132	−0.086
stdev kHz	0.298	**0.829**	0.269
isi	−0.153	**−0.798**	0.138
MaxDC	−0.235	**0.785**	0.379
mhc	0.121	−0.053	**0.946**
clicks	0.147	0.303	**0.843**
dB pe SPL	−0.484	0.035	**0.515**
swp	0.466	0.485	−0.046
Eigen values	4.07	2.5	1.52

For abbreviations, see Table 1. Bold values indicate the primary parameters comprising each component, and having absolute value of component loadings >0.5.

and buzz 2 cries of the big brown bat *E. fuscus* (Table 3). Cross-correlations were very low (0.01 to 0.21) and showed little pattern across search, approach, buzz 1 and buzz 2 bat cries. Spectrogram cross-correlations values were marginally better with the highest values (0.21 to 0.37) found for the approach, buzz 1 and buzz 2 bat cries.

A second analysis quantified the degree to which the tiger moth sounds degraded the autocorrelation of bat cries. When using cross-correlation the moth clicks had no effect on the autocorrelation values; all were near 1.0. When using spectrogram correlation the moth clicks degraded the autocorrelation values to a great degree (Table 3). In this case the degree of degradation was strongly correlated with the degree of tiger moth call complexity. The clicks of *B. trigon*a were the most effective followed by *C. arizonensis*, *C. martini*, and *C. venosa*.
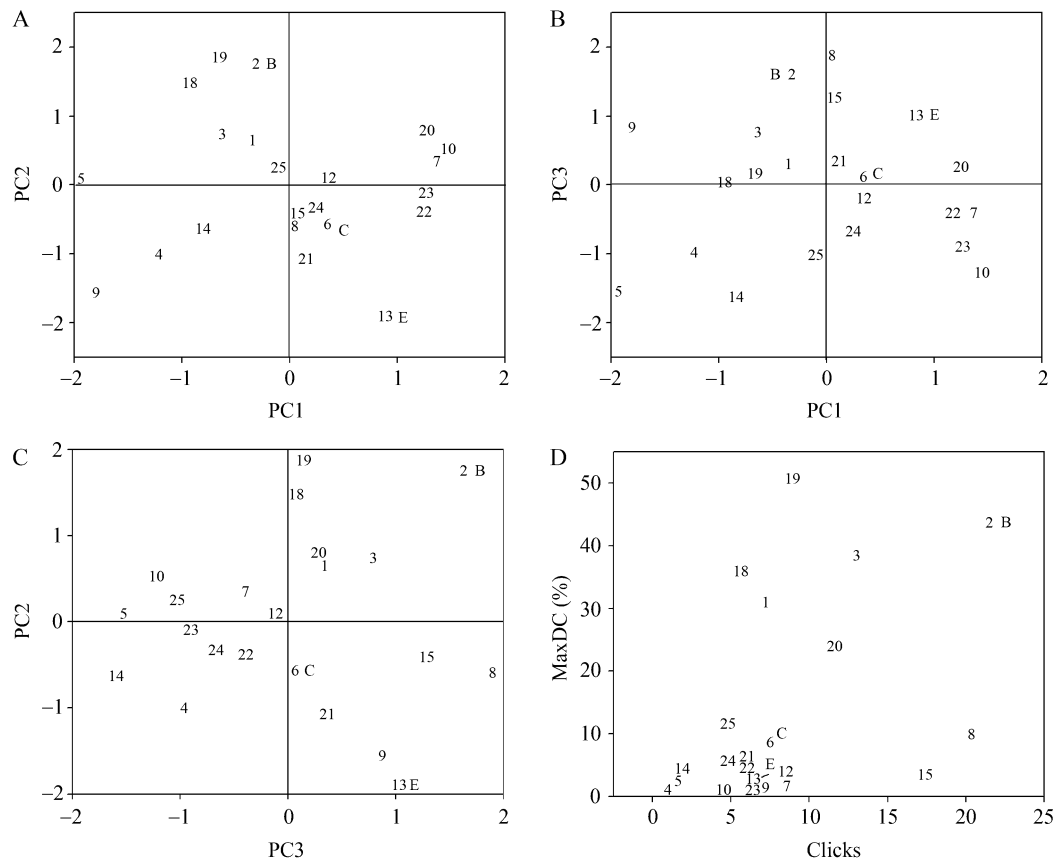
Fig. 3 **Principal Components (PC) plots of tiger moth sound parameters. Numbers indicate species as listed in Table 1**
For PC loadings, see Table 2. The sonar jammer, *Bertholdia trigona*, aposematic *Cycnia tenera,* and mimic *Euchaetes egle* are indicated by the letters "B", "C", and "E", respectively. Black numbers (1–22) are used for species in the subfamily Arctiinae and gray numbers (23–25) for subfamily Lithosiinae. Species that did not click in response to bat calls are not included.

Table 3 **Sound similarity and disruptive capacity of tiger moth clicks compared to bat echolocation calls**

	Species	Search	Approach	Buzz 1	Buzz 2	mean
Clicks-bat call CC	BETR	0.13	0.19	0.14	0.12	0.15
	CAAR	0.07	0.19	0.13	0.12	0.13
	CIMA	0.06	0.08	0.03	0.05	0.05
	CTVE	0.01	0.12	0.18	0.21	0.13
	mean	0.09	0.16	0.10	0.10	0.11
Clicks-bat call SC	BETR	0.22	0.21	0.29	0.32	0.26
	CAAR	0.14	0.28	0.34	0.30	0.27
	CIMA	0.18	0.21	0.18	0.21	0.20
	CTVE	0.15	0.25	0.37	0.37	0.28
	mean	0.16	0.23	0.30	0.31	0.25
ACC in clicks	BETR	0.99	1.02	1.01	1.01	1.01
	CAAR	1.00	0.97	1.02	1.00	1.00
	CIMA	0.99	1.01	1.02	0.99	1.00
	CTVE	1.00	0.97	0.98	1.01	0.99
	mean	1.00	0.99	1.00	1.00	1.00
ASC in clicks	BETR	0.34	0.36	0.38	0.51	0.40
	CAAR	0.54	0.49	0.53	0.61	0.54
	CIMA	0.54	0.59	0.58	0.72	0.61
	CTVE	0.91	0.79	0.75	0.84	0.82
	mean	0.63	0.59	0.58	0.70	0.62

Abbreviations: CC, cross-correlation; SC, spectrogram correlation; ACC, auto-cross-correlation; ASC, auto-spectrogram correlation; Four moths representing the full spectrum of number of clicks per half modulation cycle were chosen (from low to high: CTVE, *Ctenucha venosa*; CIMA, *Cisthene martini*; CAAR, *Carales arizonensis*; BETR, *Bertholdia trigona*). Search, approach, buzz 1 and buzz 2 indicate the phase of big brown bat echolocation call used in each calculation.

3   Discussion

Clearly, tiger moth sounds are not homogenous. They vary along frequency, duty cycle/frequency modulation, and modulation cycle structure axes. This variation undoubtedly reflects multiple functions and provides a comparative strategy for further study of the interactions of these charismatic insects and predators. The most instructive axes of variation appear to be those of duty cycle/FM and modulation cycle structure. We propose that these axes divide the arctiids into animals with two coherent strategies: one capable of advertizing bad taste as typified by *C. tenera* and mimicked by *E. egle* (Barber and Conner, 2007) and a second capable of sonar jamming as typified by *B. trigona* (Corcoran et al., 2009). According to this hypothesis we predict that most species that cluster with *C. tenera* and *E. egle* are unpalatable, supporting a minority of palatable species thorough Batesian mimicry. In contrast, we predict that most moth species that broadly cluster with *B. trigona* will prove to be palatable to bats because their clicks are a sufficient defense. Blest et al. (1963) reports that several high-duty cycle moths appear palatable, however further surveys are needed. A further test of this hypothesis would be to determine the threshold of duty cycle (a component of which is click number) that allows moth clicks to effectively jam the sonar of bats that use FM bat calls. We predict the duty cycle threshold to occur near the boundary separating the two moth groups – about 15% – 20% (Fig. 3D). One could determine this threshold by broadcasting playbacks of different moth clicks to bats attacking tethered moths (Dunning and Roeder, 1965, Miller et al., 2004). It would be essential, however, to broadcast the clicks from a location very close to the tethered moth – for example from a miniature ultrasonic speaker also suspended from the tether – to ensure bats are unable to use directional cues to filter the interfering stimuli.

Do moths gain an advantage because their clicks and /or modulation cycles (FM sweeps) are perceived as bat calls or their echoes? If they do we would expect clicks (and here trains of clicks) that more closely resemble echoes to better disrupt echolocation. We found a wide range of cross-correlations (0.01 – 0.21) and spectrogram correlations (0.14 – 0.37) between moth clicks and bat calls. To determine whether the observed correlation ranges are sufficient to degrade sonar performance through a phantom echo strategy, we consider two previously published cases: (1) clicks occurring asynchronously with target echoes (e.g. Surlykke and Miller,

1985), and (2) clicks that overlap or closely precede echoes in time (e.g. Miller, 1991). Surlykke and Miller (1985) demonstrated that clicks played at random with respect to the timing of echoes were ineffective at diminishing sonar performance. This is the natural situation with low-duty-cycle moth clicks. The clicks Surlykke and Miller played had a cross-correlation with bat calls of 0.16 – a value near the maximum of the cross-correlations we found. It therefore appears highly unlikely that clicks presented asynchronous to echoes are misperceived by bats as echoes. Miller (1991) demonstrated up to 4000% degradation in ranging ability caused by clicks played in a 1–2 ms time window prior to echoes. Fullard et al. (1994) argued that this degradation might be caused by the bat confusing clicks for echoes in this narrow time window. Masters and Raver (1996) tested this hypothesis by playing an array of sounds ranging from random noise to a perfect bat call replica in the narrow interference window found by Miller (1991). As expected, the perfect bat call replicas caused the greatest degradation of sonar performance. However, unexpectedly, all sounds other than perfect bat call replicas caused the same reduced degree of sonar interference. That is, random noise caused as much sonar interference as sounds that only slightly differed in structure from the bat's call. Therefore, a moth would have to nearly perfectly mimic each bat's call to gain advantage through a phantom echo strategy. Our measured correlation values demonstrate that this does not occur. Moths therefore do not appear to gain advantage by making the time-frequency structure of clicks resemble that of bat calls.

While the frequency modulation of moth click bursts appears insufficient to mimic bat calls, we gathered evidence suggesting that frequency modulation is associated with high duty cycle clicks, such as that used by *B. trigona* to jam bat sonar. Moths may therefore be using a strategy akin to "sweep jamming" used in human electronic warfare (Weik, 1989; John Irza, MathWorks, personal communication). This allows a jammer to disrupt a wide range of frequencies, while maximizing the instantaneous power present at each frequency. In the case of moths, this could make the defense effective against an array of bat predators using different sonar frequencies.

Our autocorrelation results indicate that tiger moths answering bats with high duty cycles and modulation cycles with many clicks (e.g. *B. trigona*) may be effective simply because they provide spectrally rich noise that interferes with or masks the echoes returning to the

bat from the moth. Both high duty cycle and high click numbers are likely selected to maximize the probability of clicks arriving in the precise time window (just prior to the arrival of an echo) necessary for range interference (Miller, 1991; Tougaard et al., 1998). Since masking requires sound intensities several orders of magnitude more intense than interference (Møhl and Surlykke, 1989), interference remains the most likely mechanism at this time.

In our view the effectiveness of moths sounds with different characteristics (duty cycle, frequency modulation, and the number of clicks per modulation cycle) and the true mechanisms of sonar jamming will best be determined through the careful design of empirical experiments. One approach would be to use a tiny omnidirectional speaker with a mealworm reward in lieu of a tethered moth. Using such a system one could vary the characteristics of the moth sounds and the palatability of the mealworm reward to address the full range of possible strategies utilized by moths to avoid bat predation.

The frequency of moth sounds is likely important in defending against bats. A cursory inspection of the data suggests that peak frequency is not a function of the size of the moth. Instead it would be interesting to investigate the relationship between tiger moth tymbal frequency and the cry frequency of the bat species that feed on each moth. Bats that forage in the open typically use lower frequencies than bats that forage close to vegetation (Aldridge and Rautenbach, 1987). Little is known about where different moth species fly, however, we might predict that moths that fly in the open would use lower frequency clicks than moths that fly close to vegetation in order to match the sonar and auditory frequencies of their predators, regardless of the anti-bat mechanism. Such a match would be analogous to the relationship between moth auditory sensitivity and bat echolocation assemblages (Fullard, 1982).

Detailed phylogenetic hypotheses (trees) for the Arctiidae are in a state of flux but one aspect of all studies whether based on traditional morphology or molecular characteristics is the monophyletic stability of two subfamilies, the Lithosiinae and the Arctiinae (Weller et al., 2009). The Lithosiinae are considered a basal group and are comprised of species that feed in their larvae stages on lichens, free-living algae, and bryophytes which render at least some species unpalatable to vertebrate predators (Acharya and Fenton, 1992; Hesbachler et al., 1995; Bowers, 2009). The Arctiinae are extremely diverse in feeding strategy and include species that are quite unpalatable by virtue of plant toxin sequestration

and species that can be considered highly palatable (Hristov and Conner, 2005b; Bowers, 2009). Provided this context, our data suggest that in the early evolution of the Arctiidae, species in the Lithosiinae and the sister Arctiinae developed tymbals that made few clicks per modulation cycle with low duty-cycles (Fig. 3D). These sounds would be useful for advertising the defensive chemistry typical of both groups, and other palatable species would gain advantage through Batesian mimicry (Barber and Conner, 2007). A jamming strategy requiring high duty-cycles and many clicks per modulation cycle appears to have evolved later within the Arctiinae. This relieved some species from the constraints of aposematism (acquiring toxins) and mimicry (timing and abundance dependent on aposematic models). Once the phylogenetic tree of the Arctiidae stabilizes it will be possible to map and more rigorously test hypotheses concerning the evolution of tymbal sounds and their functions.

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