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Defensive Sound Production in the Tobacco Hornworm, *Manduca sexta* (Bombycoidea: Sphingidae)

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Abstract The tobacco hornworm (*Manduca sexta*) is a model organism extensively studied for many aspects of its biology, including its anti-predator strategies. We report on a novel component of this caterpillar's defence repertoire: sound production. Late instar caterpillars produce discrete clicking sounds in response to disturbance. Click trains range in duration from 0.3–20.0 s (mean 3.3±4.8 s) and contain 2–41 clicks (mean 7.1±9.5). Sounds are broadband with a dominant frequency of 29.8±4.9 kHz. We investigated the mechanism of sound production by selectively ablating three identified sets of ridges on the mandibles, and determined that ridges on the inner face strike the outer and incisor ridges on the opposing mandible to produce multi-component clicks. We tested the hypothesis that clicks function in defence using simulated attacks with blunt forceps. In single attack trials 77% of larvae produced sound and this increased to 100% in sequential attacks. Clicks preceded or accompanied regurgitation in 93% of multiple attack trials, indicating that sound production may function in acoustic aposematism. Sound production is also accompanied by other behaviours including directed thrashing, head curling, and biting, suggesting that sounds may also function as a general warning of unprofitability.

Keywords Sound production · caterpillar · acoustic communication · defence · *Manduca sexta*

Introduction

Caterpillars have been studied extensively for their anti-predator defences, and while the majority of these defences have focused on visual or chemical displays, little has been reported on acoustics. In one study, sound production was reported in caterpillars of the

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well known tobacco hornworm, *Manduca sexta* (Brown et al. 2007). In that study, which focused primarily on sound production in another caterpillar (*Antheraea polyphemus*), clicking sounds were reported to occur in response to forceps attacks. *Manduca sexta* is one of the most widely studied insects and serves as a model organism in neurobiology, hormonal and behavioural research (Tuttle 2007). Given the interest in this caterpillar as a model laboratory species, it is surprising that until recently no record of its ability to make sounds had been documented. Moreover, another study focusing specifically on the defensive behaviours of *M. sexta* (Walters et al. 2001) made no mention of sound production. Walters et al. (2001) simulated attacks on the larvae by delivering a pinch with forceps or a poke with a nylon filament to the prolegs, and recorded the larvae's reactions on videotape. Although the Walters et al. (2001) study reported directed thrashing, opening the mandibles (biting) and regurgitation as defensive behaviours, sound was not reported. Therefore, either the sounds recorded by Brown et al. (2007) were specific to that particular population, or sounds were simply not noted by Walters et al. (2001) due to the methodology used. Regardless, the phenomenon of sound production in *M. sexta* caterpillars requires confirmation and further examination.

The specific objectives of this study are to: (a) characterize the acoustic properties of these sounds; (b) experimentally test the mechanism of sound production; and (c) test the hypothesis that sounds function as part of the defensive repertoire in this species.

Methods

Animals

Manduca sexta Linneaus larvae (Fig. 1) were purchased from Canadian Feeders (Windsor, ON, Canada) and LiveFood (Mercier, QC, Canada). Larvae were initially reared on artificial diet provided by the company of origin, then transferred to potted

Fig. 1 A fifth instar *Manduca sexta* larva on a tomato plant. Scale bar, 1 cm

plants (based on availability; including datura (*Datura inoxia*), tobacco (*Nicotiana tabacum*), or tomato (*Solanum lycopersicum*)) in mesh cages, at least 24 h before experimentation to allow the caterpillars time to acclimate. Caterpillars were housed in an insect rearing facility at Carleton University. All trials were performed on larvae in their fifth instar.

Sound Recordings and Analysis

Sounds analysed for spectral, intensity and temporal characteristics were recorded in an acoustic chamber (Eckel Industries Ltd., Cambridge, MA, USA) or an enclosure lined with acoustic foam. Caterpillars were placed on sprigs of host plant and induced to signal using blunt forceps (see below). Temporal characteristics, including train duration, number of clicks per train, click duration and number of elements in a click were measured using AviSoft SASlab Pro (Avisoft Bioacoustics, Berlin, Germany) from sounds extracted as .wav files from video clips ($N=16$) of the attack trials (see below) using Quicktime 6.5.3. A train was defined as a string of clicks following an attack until sound production ceased, and one click was defined as the smallest unit of sound distinguishable by the human ear (Broughton 1963). Spectral characteristics were measured from five randomly chosen clicks from each of five animals using Raven 1.2 Bioacoustics Research Program (Cornell Laboratory of Ornithology, Ithaca, NY, USA). Sounds were recorded with a Brüel & Kjær (Naerum, Denmark) 1/4” microphone type 4939 placed 10 cm from the head capsule of the larva, amplified using a Brüel & Kjær Nexus conditioning amplifier type 2690, and recorded onto a Fostex FR-2 Field Memory Recorder (Gardena, CA, USA) at a sampling rate of 192 kHz. Spectra were produced using a 1024-point Fast Fourier Transform (FFT) (Hann window). Sound levels were calculated by recording sounds at a distance of 10 cm using a Brüel & Kjær 1/4” microphone and measuring voltages on a Tektronix THS720A oscilloscope. Voltages were converted to pascals (Pa) based on the sensitivity output of the Nexus amplifier and converted to dB SPL values.

Sound Production Mechanism

Mandibles were dissected from caterpillars that had been previously confirmed to produce sounds. Dissected dried mandibles were sputter coated with gold-palladium and examined using a VEGA II XMU variable pressure scanning electron microscope (Tescan USA Inc., Cranberry Twp., PA). Sets of ridges were defined according to their relative location on the mandible (outer and inner faces, and the incisor edge) following nomenclature used by Bernays (1991).

To determine how mandible movements were associated with sound production, mouthparts were videotaped using a Sony HDR-HC7 HD Handycam (Tokyo, Japan) equipped with a Sony ECM-MS957 microphone and a macro lens. Videos were analyzed using iMovie 3.0.3 to determine how mandible movements were associated with sound production.

To determine how mandibles interacted to produce sounds, different sets of ridges were ablated on both mandibles. Larvae that were confirmed to be sound producers were anesthetised using carbon dioxide, and selected mandible ridges were ground down (i.e. removed) using a Vogue Professional 6700 nail drill (Woodland Hills, CA, USA) equipped with diamond dental burs. There were three experimental groups: (i) only inner ridges removed (i.e. those on the inner face, $N=16$); (ii) only outer ridges removed (i.e. those on the outer face, $N=8$); (iii) only incisor ridges removed (i.e. those on the incisor edge, $N=12$). There was also a control group ($N=18$) where caterpillars were treated similarly to the experimental animals, but instead, a smooth drill bit that did not change the structure of the mandibles was used. Pre- and post-operation attack trials were performed on each larva from all 4 groups to test for sound production. Sound traces from pre- and post-operative conditions were analysed for the presence or absence of sound production, as well as for changes in temporal characteristics (i.e. number of elements per click) using Raven 1.2.

Attack Experiments

Attack trials were performed to assess behaviours associated with different forms of attack, and the relationships between sound production and other behaviours. All trials were carried out on caterpillars that had been isolated on a sprig of host plant for a minimum of 30 min prior to experimentation. Defensive behaviours were recorded using a Sony Mini-DV DCR-HC85 Handycam (Tokyo, Japan) and a Sony ECM-MS907 microphone placed 4 cm away from the heads of the larvae. Different approaches were used to replicate methods from previous experiments (Brown et al. 2007; Walters et al. 2001) as well as to simulate an attack by an avian predator to test our hypothesis on the function of sound production. In the first experiment, intended to simulate an attacking bird (c.f. Bowers 2003; Grant 2006), pinches were delivered to the head capsule using blunt forceps. A pinch was delivered one, three or five times to individual caterpillars with 5 s between consecutive pinches. These trials were analyzed to determine the mean number of clicks in the first 60s of a trial, the occurrence of clicking and regurgitation, and the temporal relationship between the two. In a second experiment, following Walters et al. (2001), five pinches were delivered to the prolegs using sharp forceps; three to one side of the animal and two to the other with approximately 3 s between each pinch ($N=10$). In a third experiment, five pokes to the prolegs were administered using a stiff piece of fishing line with 3 s between attacks ($N=5$). Results from experiments 2 and 3 were analysed for the number of animals that produced sound, and how caterpillars responded behaviourally to these attacks. Individual caterpillars were not re-used between trials.

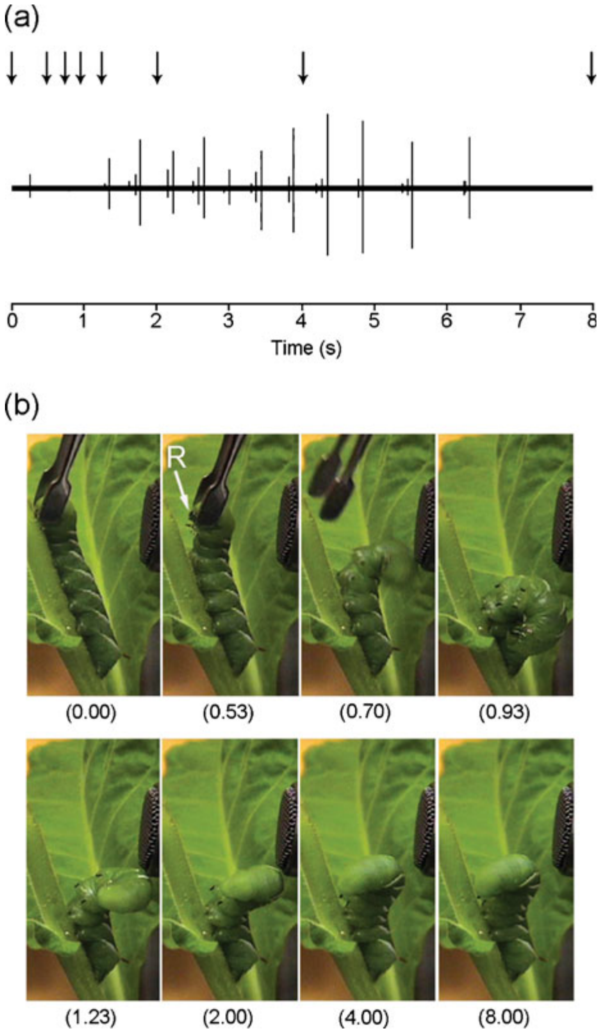
Results

Manduca sexta caterpillars exhibited a variety of behaviours in response to attack including clicking, regurgitation, directed thrashing, biting, and an inward curling of the head (Fig. 2). The relationships between these behaviours and details of sound production are discussed below.

Sound Characteristics

Larvae that produced sounds after being pinched once with blunt forceps were used to determine the temporal characteristics of the clicks (Table 1). Trains ranged from

Fig. 2 Behavioural response to an attack with forceps near the head region. **a** Oscillogram of the click train produced by the larva during the first eight seconds following attack. Arrows correspond to video frames in **b**. **b** Video frames showing typical defensive responses (thrashing and regurgitation) following attack. Times of occurrence for each frame are indicated in brackets. Regurgitant (R) can be seen in the second frame



0.3 to 20.0 s in duration and contained 2–41 clicks (Fig. 3, Table 1). Individual clicks were 23.1±32.6 ms in duration and consisted of one to five individual components (i.e. elements) (Fig. 3b, Table 1). Although the clicks are audible to the human ear,

Table 1 Temporal characteristics of sounds produced by larval *Manduca sexta*.

	Train duration (s)	Number of clicks per train	Click duration (ms)	Number of elements per click
Mean±s.d.	3.3±4.8	7.1±9.5	23.1±32.6	2.1±1.1
Range	0.3–20.0	2–41	0.04–149.2	1–5
Number of clicks	-	-	113	113
Number of animals	16	16	16	16

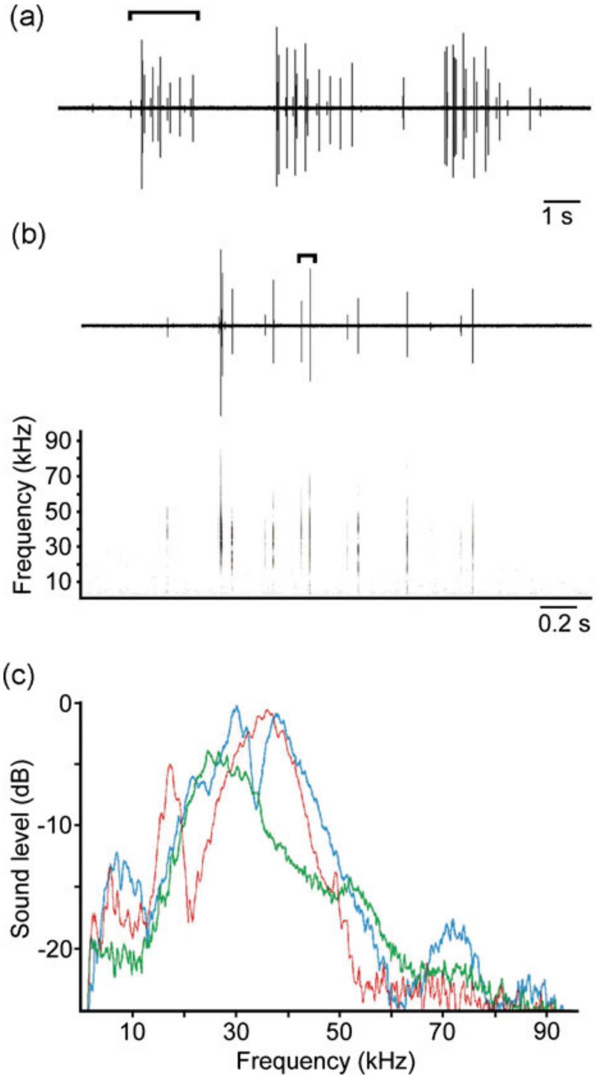


Fig. 3 Sounds made by a fifth instar larva following attack. **a** Three click trains elicited by three sequential attacks to the head capsule. The bar outlines one click train expanded in **b**. **b** Expanded click train from (**a**) to show the individual components of the clicks (one click represented by *smaller bar*). The accompanying spectrogram illustrates the frequency range. **c** Power spectra of clicks from three individuals

spectral analysis revealed that most energy occurs between 20–45 kHz (peak frequency 29.8±4.9, N (number of animals) = 5, n (number of clicks) = 25; Fig. 3b, c). Maximum intensity levels ranged between 82 and 93 dB SPL, measured at 10 cm from the source (N=5; n=60).

Sound Production Mechanism

Video analysis supports the hypothesis that clicks are produced using the mandibles. One mandible slides against the inner surface of the opposing mandible to produce an individual click. This motion can be repeated several times to produce a click train. Scanning electron micrographs revealed the mandibles to be highly serrated with three prominent ridges: outer, incisor and

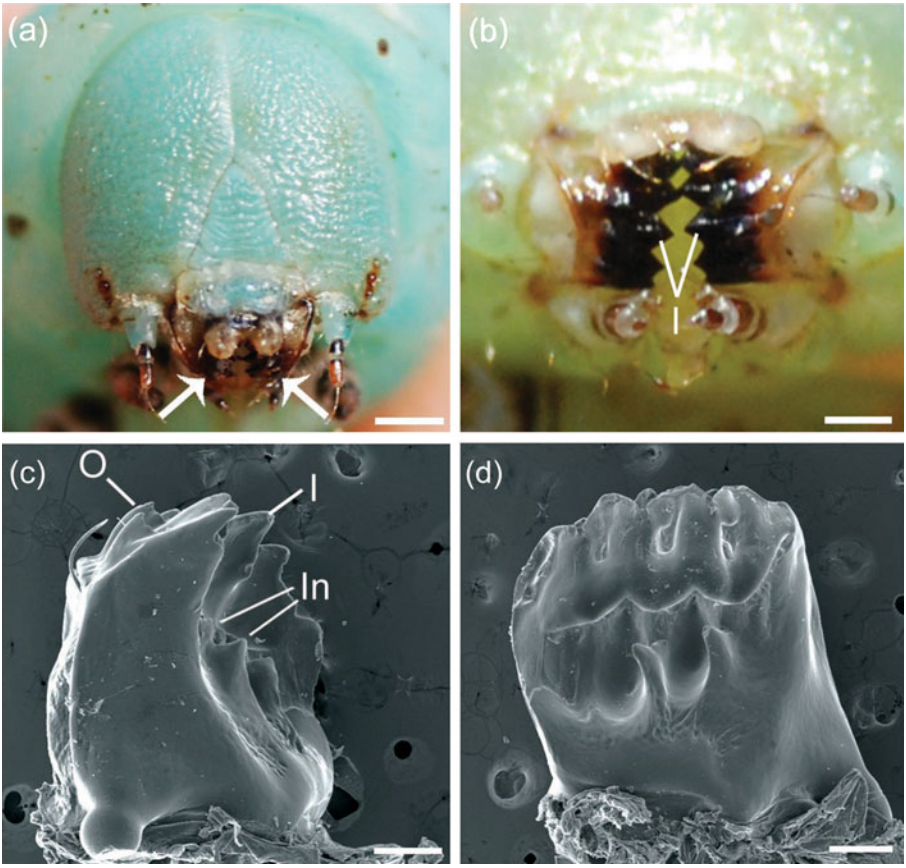
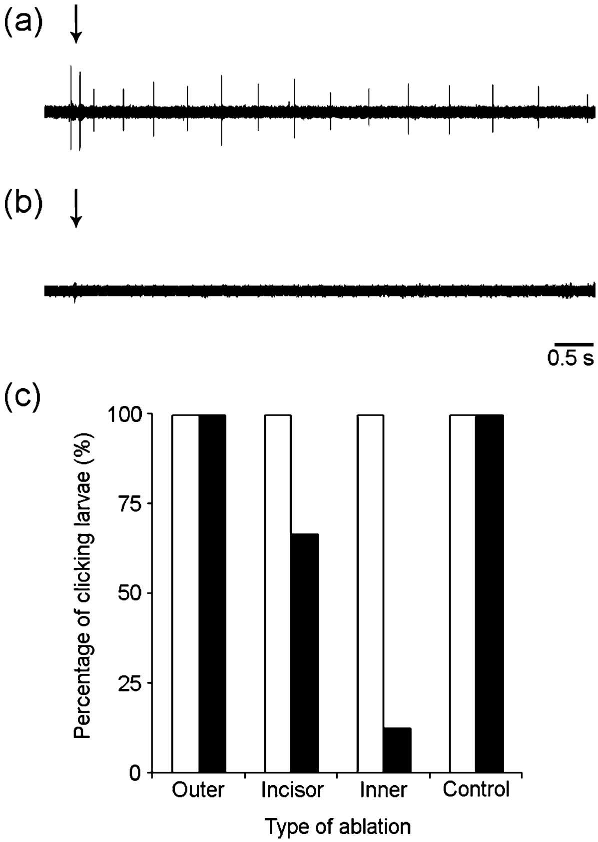


Fig. 4 Sound producing structures of *Manduca sexta*. **a** Close up of the head capsule. *Arrows* indicate the location of the mandibles. Scale bar 1 mm. **b** Close up of the mandibles; incisor ridges (I) are clearly visible. *Scale bar*, 0.5 mm. **c** Ventral view of the right mandible showing the location of the different ridges: outer (O), incisor (I) and inner (In). *Scale bar*, 0.25 mm. **d** Inner face of the left mandible, *Scale bar*, 0.25 mm

inner (Fig. 4). We propose that clicks are produced when the outer and incisor ridges of one mandible catch on the inner ridge of the opposing mandible. This proposed mechanism is supported by the ablation experiments (Fig. 5). When the inner ridges were ablated, sound production was eliminated in 14/16 (87.5%) caterpillars. All 18 control animals continued to click following the ‘sham’ ablations. Ablation of the outer and incisor ridges resulted in silencing of the individual in 0/8 (0%) and 4/12 (33.3%) cases respectively (Fig. 5c). Even though ablation of the outer and incisor ridges did not result in removing sound production in the majority of trials, in those animals that continued to produce sounds following the ablation, the temporal characteristics of the clicks were changed with respect to the number of elements occurring per click. In pre-ablated individuals the majority of clicks contained two or more elements (outer 34/50, incisor 41/60), but following ablations, this was reduced to 10/50 in outer ridge ablations and 9/60 in incisor ablations. We conclude that clicks are produced by stridulation of

Fig. 5 **a** Pre-operation oscillogram showing a click train following an attack (*arrow*). **b** Post-operation oscillogram of an inner ridge ablation showing the removal of sound production following an attack (*arrow*). **c** Percentage of larvae that clicked prior to (*white bars*) and following (*black bars*) different ridge ablations



opposing mandibular ridges, where the inner ridges are caught on the edges of the opposing incisor and outer ridges, producing multi-element clicks.

Attack Trials

Sound production was induced by different attack methods, including those using blunt forceps to pinch the head capsule, leg pinching, and leg poking. In experiments using blunt forceps, both acoustic signalling and defensive regurgitation increased with the degree of disturbance (Fig. 6a–c). In one-pinch trials 77% of larvae produced sound ($N=22$). This increased to 85% in three-pinch trials ($N=20$) and 100% in five-pinch trials ($N=20$). Larvae pinched five times clicked significantly more (29.6±22.1 clicks) than those pinched one (6.2±10.3 clicks) or three times (9.6±7.9 clicks) in a 60 s period (Fig. 6b, Mann–Whitney U, $P<0.001$ and $P=0.001$, respectively). There was also an association between signalling and regurgitation (Fig. 6c). During regurgitation, a distinct droplet was produced, typically after 1–3 pinches. Caterpillars were able to aim the droplet towards the site of attack, and also re-imbibe the regurgitant after a period of time. Based on these characteristics, *M. sexta* can be considered a primary regurgitator (Grant 2006). Although signalling can occur in the absence of regurgitation (C+R−, 63.6% and 25% of one and five pinch

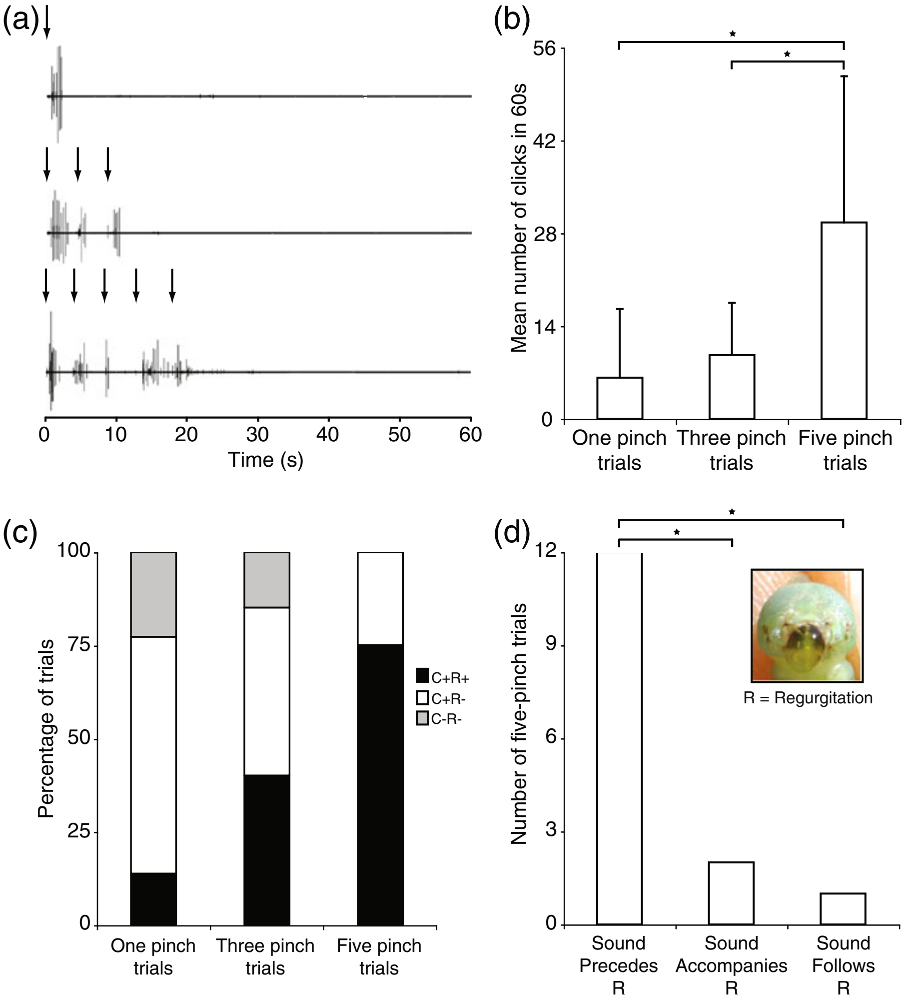


Fig. 6 **a** Oscillograms of click trains following one-, three- and five-pinch trials. Arrows indicate when larvae were attacked. **b** Mean number of clicks produced during the first 60 s following the initial pinch in one-, three-, and five-pinch trials. **c** Behavioural responses to attack by forceps in one-, three- and five-pinch trials. C+R+, both clicking and regurgitation; C-R-, neither clicking nor regurgitation. **d** The occurrence of clicking with respect to regurgitation (inset) in C+R+ five-pinch trials. Clicking preceded the appearance of regurgitation in most cases

trials, respectively), regurgitation never occurred in the absence of clicking (C−R+) (Fig. 6c). Responses with both clicking and regurgitation (C+R+) increased with increasing attack, accounting for 13.6% in one pinch attacks and 75% in five pinch attacks. In five-pinch trials where both clicking and regurgitation occurred, the first click preceded regurgitation significantly ($\chi^2=14.8$, $P=0.001$; Fig. 6d).

Sound production was also reliably produced when we used attack methods similar to those employed by Walters et al. (2001). Clicks were recorded in 8/10 individuals from the leg pinch trials and 3/5 individuals from the leg poke trials. Larvae in these trials also regularly bit the forceps, a behaviour also reported in Walters et al. (2001).

Discussion

This study demonstrates that tobacco hornworms produce sounds when they are attacked, confirming an earlier report by Brown et al. (2007). Interestingly, there have been other papers on predator–prey interactions for *M. sexta* (e.g. Thurston and Prachuabmoh 1971; Stamp 2001; Thaler and Griffin 2008) and at least one study dedicated to the defensive responses (Walters et al. 2001), yet there has been no mention of sound production. A possible explanation for this is that the caterpillars were stimulated in ways that did not elicit sound production, though we varied the methods of attack in our experiments to match those of Walters et al. (2001), and sound was produced in each scenario. Another possibility is that sound production is a regional phenomenon found only in certain populations. We recorded from two sources in our experiments, one from eastern Quebec and the other from southern Ontario, and Brown et al. (2007) recorded from a third population in south-central Nova Scotia. These locations are all from areas of eastern Canada, but are widely distributed within the region. Yet, since all individuals were from established laboratory colonies, they all may in fact have originated from a single source in North Carolina (Kingsolver 2007). Experiments using wild-caught specimens and congeners should be carried out to determine if sounds occur outside of these colonies. At least one congener from Costa Rica, *Manduca pellenia*, also produces clicking sounds in response to attack (VLB, unpublished). Another plausible explanation may relate to the characteristics of the sounds; though they would be audible at close distances in a typical temperate forest environment (noise floor is 30 dB SPL, Goerlitz et al. 2008) and can be detected in a quiet room by the unaided human ear up to 2 m, the sounds became indistinguishable from the background at about 1 m in noisier environments. Also much of the energy is in the ultrasonic range, so they may simply have gone unnoticed by other experimenters.

We propose that individual clicks are produced by the inner ridges of one mandible catching on the incisor and outer ridges of the opposing mandible. The manner in which the different ridges catch onto each other may determine the number of elements in each click. Mandible clicking has been reported in two other species of Bombycoidea caterpillars (*Antheraea polyphemus* and *Actias luna*, Brown et al. 2007), and is one of the limited options available for sound production in soft bodied insects. Mandible clicking is not common in other insects, but has been reported in some grasshoppers during encounters with conspecifics and as a reaction to disturbance (Alexander 1960; Blondheim and Frankenberg 1983).

Our data support the hypothesis that clicks produced by *M. sexta* caterpillars function in defence. Clicks are produced when the animal was attacked and the amount of clicking increases significantly with the number of attacks. Sounds were not observed in conjunction with other behaviours like crawling or feeding, or during interactions with conspecifics. The clicks are short, spectrally broadband with most energy between 5 and 50 kHz, and audible at close distances, thus resembling other insect disturbance signals (Masters 1979, 1980). The energy range overlaps with the optimal hearing frequencies of most birds (Schwartzkopff 1955; Dooling 1991), which are important predators of sphingid caterpillars (Pittaway 1993; Tuttle 2007). In addition, the dominant frequency of *M. sexta* clicks is ultrasonic, which falls into the hearing ranges of mammalian predators such as bats and mice.

Gleaning bats may be an important predator of caterpillars (Kalka and Kalko 2006; Wilson and Barclay 2006) and mice have been shown to respond to sounds produced by insects with similar sound frequencies (e.g. bee hissing, Kirchner and Röschard 1999).

Our results also provide preliminary evidence for the hypothesis that these signals function in acoustic aposematism. A key prediction for this hypothesis is that the sounds be associated with an honest defence. We show that there is an association between clicking and regurgitation and, in the majority of C+R+ trials clicking preceded regurgitation significantly more than it followed regurgitation. When an animal is presented with the signal prior to receiving a stimulus it will be more likely to remember the association between the two. There is also indirect evidence that the regurgitant of *M. sexta* caterpillars has deterrent properties. Tobacco hornworn caterpillars feed on plants from the family Solanaceae that are known to contain tropane alkaloids which can act as lethal neurotoxins (Nishida 2002). While *M. sexta* caterpillars have been shown to store these alkaloids in their tissues (Rothschild *et al*. 1979) there is no direct evidence that these are contained in the oral secretions; however, this is quite likely since secondary compounds are present in the regurgitated gut contents of other insects (cf. Sword 2001). Since, as primary regurgitators, *M. sexta* caterpillars have the ability to aim their regurgitant, this defence may function by irritating the sensitive mucous membranes (i.e. eyes, nose, mouth) of their vertebrate predators (Roth and Eisner 1962).

Other behaviours were also observed in response to attack, including biting and thrashing, and these behaviours typically occurred after the onset of sound production. Walters et al. (2001) suggested that the thrashing behaviour exhibited by the caterpillars decreases the incidence of successful attacks by avian predators based on observed field encounters. This would increase the time spent in one place, a potentially dangerous activity for birds that are prey animals themselves (Kaby and Lind 2003). In addition, if the biting caterpillar came into contact with the delicate eye of a bird it could possibly be capable of inflicting serious damage. Therefore, sounds may also signal general unprofitability, to warn an attacking predator that its time would be better spent elsewhere.

This study demonstrates that mandibular clicking commonly occurs when tobacco hornworm caterpillars are attacked and supports the hypothesis that sounds function in defence, and perhaps more specifically, acoustic aposematism. Anti-predator defences have been studied extensively in caterpillars (Lederhouse 1990; Bowers 1993; Stamp and Wilkens 1993), but most research has focused on those perceived by the predator in the visual domain (e.g. camouflage, aposematism, mimicry). Less is known about the role of non-visual anti-predator strategies (see Ruxton 2009). Recent studies on silk and hawk moth (Bombycoidea) caterpillars indicate that defensive sounds may be widespread (Brown et al. 2007; Bura et al. 2009; Bura et al. 2011) and may function in mimicry, startle or warning. Further comparative studies of sound production in the Bombycoidea, and experiments using live predators should be performed to test hypotheses to explain evolutionary origins and specific functions of defensive sounds in caterpillars.

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