Acoustic Defence Strategies in Caterpillars

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Late instar *Drepana arcuata*. (Photo by Tom Eisner, presented to Jayne Yack)

Introduction

Caterpillars have many enemies, including invertebrate predators and parasitoids (e.g. wasps, flies, mantids, stink bugs, dragonflies, ants, and spiders) and vertebrate predators (e.g. bats, birds, lizards, rodents, toads) (Heinrich 1993; Montllor and Bernays 1993; Wagner 2005; Kalka and Kalko 2006; Greeney et al. 2012; Sugiura 2020). While vulnerable in their soft exoskeletons and with limited options for escape, they are not exactly helpless. In fact, caterpillars are well recognized for their many antipredator strategies, including crypsis, mimesis, deimatic displays, urticating and poisonous spines and bristles, irritating sprays, warning coloration,

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thrashing, dropping, and shelter building (Lederhouse 1990; Gentry and Dyer 2002; Greeney et al. 2012; Sugiura 2020). Research on antipredator tactics has focused on those operating in the visual and chemical realms, and comparatively less is understood about acoustic defences. Do caterpillars use sounds and vibrations to detect or repel enemies, or to avoid detection? Arguably caterpillars should be exploiting airborne sounds and solid-borne vibrations to avoid attack. Their enemies generate a diversity of acoustic signals and cues that can provide information to assess risk. Also, considering that many enemies of caterpillars have hearing capabilities, producing acoustic signals should be effective in communicating with these enemies. Additionally, caterpillars have limited visual capabilities, but live in rather complex vibroacoustic environments, being substrate-bound organisms (see Yack and Yadav 2021). These points considered, one is hard-pressed to explain the few examples of caterpillar acoustic defences in reviews covering the topics of acoustic defences in Lepidoptera (e.g. Minet and Surlykke 2003), acoustic defences in insects (e.g. Conner 2014), insect defences (e.g. Evans and Schmidt 1990; Ruxton et al. 2004; Sugiura 2020), or caterpillar defences (Lederhouse 1990; Stamp and Casey 1993; Gentry and Dyer 2002; Greeney et al. 2012). Still, there have been reports, many dating back to the 1800s, of caterpillars producing sounds or responding to them, purportedly, in the context of defence. In the past few decades, alongside a growing awareness of the importance of near-field sounds and solid-borne vibrations in insect communication, there has been an increasing number of experimental studies confirming that caterpillars live in rather complex acoustic environments. This chapter reviews the literature on caterpillar acoustic defences to gain an appreciation for the taxonomic diversity and functions of hearing and sound production in the context of defence, and to propose future lines of investigation.

First it is important to define the terms used in this chapter to discuss acoustic stimuli, how they are detected in insects, and how they might be relevant to an insect prey. Broadly speaking, acoustic events are vibrations transmitted through any elastic medium (Windmill and Jackson 2016). Vibrations travelling through air and water are commonly referred to as 'sounds', whereas those transmitted through solids such as plant material, silk, waxes, or soil are commonly referred to as 'vibrations', 'substrate-borne vibrations', or 'solid-borne vibrations'. Airborne vibrations are further categorized as 'far-field' and 'near-field' sounds, which describe the pressure and displacement components of sound respectively. Far-field sounds are pressure waves transmitted over long distances and detected by pressure detectors such as tympanal ears found in many adult insects and most vertebrates. Near-field sounds, resulting from the displacement component of a vibrating source, typically are transmitted over shorter distances (within a few meters) and are restricted to lower frequencies (less than 2 kHz). Near-field sound receptors have been described in adult and juvenile insects and include lightweight receivers such as hairs (i.e., trichoid sensilla) and antennae. Vibrations propagated through solids are used by insects in a variety of contexts. The sensory organs best known for vibration reception are subgenual organs in adults of some insect orders (see Yack 2016). In this Chapter, I use the terms *sound* to mean airborne vibrations in general, and *near- and far-field sounds* to distinguish between the displacement and pressure components respectively. I use the terms *vibrations* or *solid-borne vibrations* to describe waves transmitted through solids. For more in-depth discussions of the nomenclature associated with acoustic vibrations and sensory receptors in insects, see Hill (2008, 2014), Hill and Wessel (2016), Lakes-Harlan and Strauss (2014), Windmill and Jackson (2016), and Yack (2004, 2016).

Acoustic stimuli relevant to a discussion on caterpillar defences include those that arise from predators and parasitoids, as well as non-predators (conspecifics and heterospecifics), and these stimuli can be categorized as signals or cues. Here I use the term *cue* to refer to sounds and vibrations that have not evolved in the context of communication (i.e., they have not evolved to alter the behaviour of an intended recipient). Acoustic cues in this context include sounds and vibrations generated as a consequence of movement (e.g. flying, walking, digging). On the other hand, *signal* is used to describe a sound or vibration that evolved in the context of communication (i.e., conveying a message to an intended receiver). The intended receiver could be oneself (e.g. echolocation) or another recipient (e.g. alarm or mating call). For further discussion of the nomenclature relating to signals, cues, and communication, see Maynard-Smith and Harper (2003) and Yack et al. (2020).

Acoustic Antipredator Strategies in Insects

What acoustic strategies do insect prey use to avoid attack? To address this question, I have broadly categorized acoustic anti-predator strategies into acoustic crypsis, sound and vibration detection, and sound and vibration production. These categories are outlined below and in Fig. 1 with representative examples drawn from insects in general, and then further discussed in the context of caterpillar defences in sections "Acoustic crypsis in caterpillars", "Sound and vibration reception in caterpillars", and "Generating sounds and vibrations in caterpillars" of this chapter.

Crypsis can be defined as any trait, whether visual, chemical, tactile, electric, or acoustic, that minimizes the probability of being detected when potentially detectable by a predator (Conner 2014). Acoustic crypsis includes the following strategies: (i) reducing sounds that predators could use to locate prey. For example, some insects shut down advertisement or mating calls in the presence of a predator (e.g. Faure and Hoy 2000; Greenfield and Baker 2003; Hamel and Cocroft 2019) or cease movement to avoid being detected by vibration cues (e.g. Djemai et al. 2001; Takanashi et al. 2016); (ii) altering the physical characteristics of sound (e.g. amplitude, frequency) to be less conspicuous to an enemy (e.g. Nakano et al. 2008); (iii) rendering oneself inconspicuous to echolocating predators by reducing the amplitude of the echo through morphological features (e.g. Zeng et al. 2011); and (iv) blending into the background acoustically to avoid being detected or recognized as prey (e.g. Rydell 1998). Acoustic crypsis is believed to be an understudied defence strategy in insects (Conner 2014). The topic of acoustic crypsis in caterpillars is discussed in section "Acoustic crypsis in caterpillars".

Acoustic Anti-predator Strategies in Insects

Acoustic Crypsis

A trait that minimizes the probability of being detected when potentially detectable by a predator or parasitoid.

Examples in Insects
- Reducing acoustic cues available to predators by ceasing movement, feeding, singing
- Adjusting sound characteristic (e.g. amplitude, frequency) to be out of predator hearing range
- Match or blend into background to be inconspicuous to echolocating predators

Sound and Vibration Detection

Receiving acoustic signals or cues of predators, or alarm calls or recruitment signals of non-predators.

Examples in Insects
- Detecting acoustic cues produced by an approaching predator (e.g. crawling vibrations, flight sounds, rustling leaves) (Cue by predator)
- Hearing echolocation calls or vibrational sounding signals (Signal by predator)
- Eavesdropping on communication calls, songs of predators (Signal by predator)
- Detecting alarm or recruitment signals by non-predators (Signal by non-predator)

Sound and Vibration Production

Producing sounds or vibrations that are directed at the predator to stop an attacker, or directed at non-predators to recruit help or coordinate defenses.

Examples in Insects
- Acoustic aposematism (Directed at predator)
- Deimatic displays (Directed at predator)
- Mimicry (Directed at predator)
- Jamming or interference (Directed at predator)
- Alarm signals (Directed at non-predator)
- Recruitment signals (Directed at non-predator)

Fig. 1 An overview of different acoustic defence strategies employed by insects, including acoustic crypsis, detecting sounds and vibrations, and generating sounds and vibrations. Examples (or lack thereof) of these strategies employed by caterpillars are discussed in the text

Detecting sounds and vibrations can be important for insect prey. Relevant sounds and vibrations generated by predators include incidental cues resulting from movement (e.g. wings flapping, leaves rustling, crawling). For example, some butterflies detect the flight sounds of insectivorous birds (Mikhail et al. 2018), and moths detect the rustling leaf sounds of foraging birds (Jacobs et al. 2008). Prey also attend to communication signals (e.g. advertisement songs, echolocation calls) of predators to assess risk. Many flying adult insects, including moths and butterflies, have evolved tympanal ears to detect the echolocation calls of bats (Hoy 1992; Miller and Surlykke 2001; Yack et al. 2007; Conner and Corcoran 2012; Yager 2012; Pollack 2016). There are no confirmed examples, to the best of my knowledge, of insects eavesdropping on the social calls of their predators, although this hypothesis has been proposed to explain hearing in some butterflies (Ribaric and Gogala 1996; Mikhail et al. 2018) and is a common strategy for assessing risk in vertebrate prey (see Yack et al. 2020). Relevant sounds and vibrations produced by non-predators include alarm and recruitment signals. There are several examples of adult social insects detecting and responding to the alarm calls of non-predators (Hunt and Richard 2013). The topic of caterpillar 'hearing' in the context of avoiding attack is discussed in section "Sound and vibration reception in caterpillars".

Insects also can generate sounds and vibrations when under attack or threat of attack. Such signals have been called distress, alarm, warning, and defence signals (Alexander 1967; Masters 1980; Conner 2014; Bura et al. 2016). Defence sounds directed at a predator may function as aposematic warning signals, deimatic displays, interference signals, or mimics of sounds advertising danger (Conner 2014; Low et al. 2021). Acoustic defence signals can also be directed at non-predators, such as conspecifics or heterospecifics, and these function primarily to warn kin, or recruit help from others (Cocroft and Hamel 2010; Hunt and Richard 2013). Despite the widespread occurrence of defence sounds and vibrations among insects, their survival benefits are not well understood (Conner 2014; Low et al. 2021). The topic of caterpillar sound and vibration production in the context of defence is discussed in section "Generating sounds and vibrations in caterpillars".

A review on the topic of acoustically mediated defences in caterpillars is due, for a couple of reasons. First, the subject has not previously been the focus of a review, although some aspects of the topic have been addressed in reviews on vibratory communication in insects (Yack 2016), vibratory communication in caterpillars (Yack and Yadav 2021), vibratory-mediated predator prey interactions in insects (Virant-Doberlet et al. 2019), and insect defence sounds (Low et al. 2021). Second, there have been an increasing number of experimental examples of acoustically mediated communication in caterpillars over the past two decades. It is now apparent that larval insects inhabit complex vibro-acoustic environments and attend to sounds and vibrations in a diversity of contexts, including territoriality and spacing (e.g. Yack et al. 2001; Fletcher et al. 2006; Scott et al. 2010; Yack et al. 2014), obtaining food (e.g. Ishay et al. 1974; McIver and Beech 1986), recruitment and coordinating group activities (e.g. Fletcher 2007, 2008; Yadav et al. 2017), mimicry to exploit resources (e.g. Travassos and Pierce 2000; Sala et al. 2014), and avoiding enemies (e.g. Castellanos and Barbosa 2006; Low 2008; Roberts 2017; Taylor and Yack 2019). In the majority of reports on larval acoustics, the sounds and vibrations are not easily detected by humans without the aid of recording equipment such as laser vibrometers and specialized microphones. However, with increasing awareness of the importance of vibro-acoustic communication in insects and the broader availability of specialized recording instruments, more examples are being reported for acoustic communication in juvenile insects.

Acoustic Crypsis in Caterpillars

> *Cryptic silence is to the ear what cryptic appearance is to the eye. The silence of which I speak is not a passive condition- a mere absence of sound. It is an active quality....* Cott (1940)

Predators and parasitoids of caterpillars use different sensory modalities, including their acoustic senses, to identify and locate prey. For example, stink bugs and parasitoid wasps eavesdrop on chewing and crawling movements of caterpillars (Pfannenstiel et al. 1995; Meyhofer et al. 1997), and bats use echolocation and passive listening to locate prey (Kalka and Kalko 2006; Wilson and Barclay 2006; Geipel et al. 2013; Page and Bernal 2020). Conceivably, caterpillars have evolved strategies to render themselves acoustically cryptic to their enemies. They have been shown to avoid both invertebrate and vertebrate predators by reducing movement and freezing (e.g. Heinrich 1993; Montllor and Bernays 1993) (Table 1). Although it is often assumed that this is a strategy to avoid visually hunting predators, reduction of movement could also render caterpillars acoustically cryptic. For example, the masked birch caterpillar (*Drepana arcuata*) ceased activities (chewing, movement) when approached by a predatory stink bug that uses vibrations to locate prey (Guedes et al. 2012). The apple leaf miner *Phyllonorycter malella* stops feeding and remains immobile in the presence of a parasitoid wasp *Sympiesis sericeicornis* that uses vibrations to locate its host (Meyhöfer et al. 1997). Other strategies that caterpillars could employ to render themselves acoustically cryptic would be to restrict feeding and movement activities to times of the day when predators are not hunting, to acoustically match their backgrounds to avoid detection by echolocating predators, or to mask vibrations caused by their activities by selecting noisy backgrounds. Hiding acoustically from predators and parasitoids that use sound and vibratory cues to identify and locate prey is a likely strategy used by caterpillars, and deserves further research attention.

Sound and Vibration Reception in Caterpillars

> *The fact that a considerable number of species is now known to respond [to sound]… suggests that the response to sound is characteristic of many, perhaps all, caterpillars.* (Minnich 1936).

Several species of caterpillars have been reported to respond behaviourally to air- or solid-borne vibrations. The sensory mechanisms used for sound and vibration reception in caterpillars, however, remain mostly unknown. Only in two species have acoustic receptors been experimentally confirmed to the best of my knowledge, and these are both trichoid sensilla used to detect near-field sounds (Markl and Tautz 1975; Taylor and Yack 2019). Receptors of solid-borne vibrations have not yet been identified in caterpillars despite the many confirmed examples of vibration reception based on behavioural experiments (Yack and Yadav 2021). Structures

Table 1 Sound an vibration detection in a defensive context based on behavioural responses

Taxon			Acoustic stimulus/stimuli				
Superfamily	Family	Species	Source	S/V[a]	Behavioural response	Proposed function	Reference(s)
Bombycoidea	Saturniidae	*Actias Luna*	Tuning forks (~200–1000 Hz)	S	Head retraction	N/A	Minnich (1936)
Bombycoidea	Saturniidae	*Automeris io*	Tuning forks (~200–1000 Hz)	S	Cessation of movement, body contraction	N/A	Minnich (1936)
Bombycoidea	Saturniidae	*Hylesia nigricans*	Playback sound of wing beat of wasp or insectivorous bird	S	Head flicking, ultrasound emission	Stimulate defensive aggregation	Breviglieri and Romero (2019)
Bombycoidea	Saturniidae	*Hylesia sp.*	Human voice, music, wasp flight	S	Jerking of anterior body	Avoiding parasites	Hogue (1972)
Bombycoidea	Saturniidae	*Samia cecropia (Hyalolophora cecropia)*	Tuning forks (~200–1000 Hz)	S	Head retraction	N/A	Minnich (1936)
Bombycoidea	Saturniidae	*Telea polyphemus (Antheraea polyphemus)*	Tuning forks (~200–1000 Hz)	S	Head retraction	N/A	Minnich (1936)
Drepanoidea	Drepanidae	*Drepana arcuata*	Crawling vibrations of predatory stink bug	V	Cessation of activity, signalling	Predator avoidance, deterrent	Guedes et al. (2012)
Geometroidea	Geometridae	*Semiothisa aemulataria*	Leaf vibration induced by wasps, stink bugs, 200 Hz sounds	V	Dropping by silk thread	Predator avoidance	Castellanos and Barbosa (2006)
Geometroidea	Geometridae	Species unidentified	Tuning forks (~200–1000 Hz)	S	Freezing, body contraction	N/A	Minnich (1936)
Gracillarioidea	Gracillariidae	*Phyllonorycter blancardella*	Vibrations simulating ovipositor insertions	V	Ceasing movement, evasive behaviour	Avoid parasitism	Djemai et al. (2001)

(continued)

Table 1 (continued)

Taxon			Acoustic stimulus/stimuli				
Superfamily	Family	Species	Source	S/V[a]	Behavioural response	Proposed function	Reference(s)
Gracillarioidea	Gracillariidae	*Phyllonorycter malella*	Insertion of ovipositor	V	Cease feeding or movement, increase movement	Avoid parasitism	Meyhöfer et al. (1997)
Lasiocampoidea	Lasiocampidae	*Bombyx quercus (Lasiocampa quercus)*	Shouting, whistling, hand clapping	S	Jerking heads and bodies	N/A	Johnson (1893)
Lasiocampoidea	Lasiocampidae	*Malacosoma pluviale (M. californicum)*	Simulated flight sound of parasitic fly	S	Head flicking	Avoid parasitism	Myers and Smith (1978)
Noctuoidea	*Erebidae*	*Callimorpha dominula*	Human voices	S	Lateral body thrashing	N/A	Tutt (1893)
Noctuoidea	*Erebidae*	*Empyreuma pugione*	100–350 Hz tones	S	Twitched violently	Avoiding predator or parasitoid	Conner and Wilson (2009)
Noctuoidea	Erebidae	*Euchaetias egle*	Tuning forks (~200–1000 Hz)	S	Cease movement, jerking anterior or posterior body laterally	N/A	Minnich (1936)
Noctuoidea	*Erebidae*	*Nemeophila plantaginis*	Human voices	S	Lateral thrashing	N/A	Tutt (1893)
Noctuoidea	Erebidae	Species unidentified	Tuning forks (~200–1000 Hz)	S	Cease movement, freezing, body contraction	N/A	Minnich (1936)
Noctuoidea	Noctuidae	*Barathra brassicae* (*Mamestra Brassicae*)	Flight sound of parasitoid (100–160 Hz), 40–1000 Hz sound	S	Cease movement, squirming, dropping	Avoid detection, escape	Markl and Tautz (1975), Tautz and Markl (1978)
Noctuoidea	Noctuidae	*Mamestra picta*	Tuning forks (~200–1000 Hz)	S	Anterior lateral thrashing	N/A	Minnich (1936)

Noctuoidea	Noctuidae	*Spodoptera exigua*	Honeybee flight	S	Stops feeding	Avoid detection	Tautz and Rostas (2008)
Noctuoidea	Notodontidae	*Cerura borealis*	175–180 Hz and 330–360 Hz tones	S	Rearing head, moving tentacles, extending flagella	Avoiding parasitoids	White et al. (1983)
Noctuoidea	Notodontidae	*Cerura scitiscripta* (*Tecmessa scitiscripta*)	Human voice	S	Thrashing anterior and posterior ends	Defence reaction	Klots (1969)
Noctuoidea	Notodontidae	*Datana ministra*, *D. perspicua*	512 and 728 Hz tones	S	Anterior and posterior flicking, lateral thrashing	N/A	Abbott (1927)
Papilionoidea	Nymphalidae	*Basilarchia arthemis* (*Limenitis arthemis*)	Tuning forks (~200–1000 Hz)	S	Cease movement, freezing, body contraction	N/A	Minnich (1936)
Papilionoidea	Nymphalidae	*Danaus plexippus*	Buzzing sounds of flying bumble bees and wasps, aircraft, human voices	S	Ducking, agitation of tubercles, twitching, volatile release	Antipredator display	Rothschild and Bergström (1997)
Papilionoidea	Nymphalidae	*Danaus plexippus*	50–900 Hz tones	S	Contraction, freezing, vertical anterior flicking	Predator or parasitoid avoidance	Taylor and Yack (2019)
Papilionoidea	Nymphalidae	*Danaus plexippus*	Tuning forks (~200–1000 Hz)	S	Anterior jerking	N/A	Minnich (1936)
Papilionoidea	Nymphalidae	*Vanessa antiopa* (*Nymphalis antiopa*)	Tuning forks (~200–1000 Hz), piano, human voice, organ, violin	S	Body contraction, head retraction, cessation of locomotion	N/A	Minnich (1925)

(continued)

Table 1 (continued)

Taxon			Acoustic stimulus/stimuli				
Superfamily	Family	Species	Source	S/V[a]	Behavioural response	Proposed function	Reference(s)
Papilionoidea	Nymphalidae	*Vanessa atalanta*	Tuning forks (~200–1000 Hz)	S	Cessation of movement, freezing, body contraction	N/A	Minnich (1936)
Papilionoidea	Nymphalidae	*Vanessa cardui*	Tuning forks (~200–1000 Hz)	S	Cessation of movement, freezing, body contraction	N/A	Minnich (1936)
Papilionoidea	Nymphalidae	*Vanessa urticae (Aglais urticae)*	Human voice	S	Lateral thrashing	N/A	Tutt (1893)
Papilionoidea	Papilionidae	*Papilio polyxenes*	Tuning forks (~200–1000 Hz)	S	Cessation of movement, freezing, body contraction	N/A	Minnich (1936)
Papilionoidea	Papilionidae	*Papilio turnus*	Tuning forks (~200–1000 Hz)	S	Cessation of movement, freezing, body contraction	N/A	Minnich (1936)
Papilionoidea	Pieridae	*Colias philodice*	Tuning forks (~200–1000 Hz)	S	Cessation of movement, freezing, body contraction	N/A	Minnich (1936)

[a] S/V = Sound/Vibration. The acoustic stimulus is reported as being either sound (airborne) or vibration (solid-borne) based on either what is proposed by the authors of the published paper, or what is inferred by the source of the stimulus. This does not mean that the caterpillar is necessarily responding to that form of stimulus however. For example, if a caterpillar responds to the sounds of a tuning fork, it could conceivably be receiving these vibrations via air (near-field receptors) or solids (vibration receptors), particularly if the receptor is undescribed

proposed to detect solid-borne vibrations in caterpillars include antennae (Dethier 1941), various scolopidia located in the thorax or abdomen (Hasenfuss 1992), and trichoid sensilla on the prolegs (Rosi-Denadai 2018). A possible mechanism for detecting far-field airborne sounds is through resonating internal structures (see Shaw 1994 for discussion of these in adult cockroaches), although currently there is no evidence for caterpillars detecting far-field sounds. In the context of avoiding predators, there are several reports of caterpillars responding to acoustic cues generated by flying, crawling, and ovipositing insect enemies. Also, there is limited evidence that caterpillars detect signals of non-predators to coordinate defences. These are discussed below.

Detecting Sounds and Vibrations Generated by Predators

Detection of Near-Field Sounds

Reports on caterpillars responding to sound date back more than 200 years (reviewed in Minnich 1936). Sound sources evoking responses have included tuning forks, highway noise, jet aircraft, human voices, flying insects, human voices, various musical instruments, hand clapping, and tones played from speakers (e.g. Tutt 1893; Johnson 1893; Minnich 1925, 1936; Abbott 1927; Hogue 1972; Markl and Tautz 1975; Myers and Smith 1978; Rothschild and Bergström 1997; Davis et al. 2018) (Table 1). Behavioural responses to these sounds include flicking different body parts, freezing, body contraction, squirming, increased heart rate, cessation of movement, and dropping from silk threads. Despite the numerous reports over the past two centuries, there has been little formal research on the adaptive significance and sensory mechanisms associated with caterpillar 'hearing'. The best studied species to date include larvae of the cabbage moth *Mamestra brassicae* (Noctuidae) and the monarch butterfly *Danaus plexippus* (Nymphalidae).

Cabbage moth (*Mamestra brassicae*) larvae respond to sounds in a number of ways, including ceasing locomotion, contracting, squirming, and dropping from the substrate (Markl and Tautz 1975). Caterpillars respond to pure tones between 40 and 1000 Hz, with best sensitivity at 100–600 Hz (Markl and Tautz 1975). Eight thoracic trichoid sensilla function as near-field sound receptors (Markl and Tautz 1975; Tautz 1977, 1978). Tautz and Markl (1978) demonstrated that defensive behaviours were evoked by flight sounds of the parasitoid wasp *Dolichovespula media* (Vespidae). When the wasp flies close to the larva, the sensilla are deflected, evoking defensive responses in the caterpillar. Responses varied with loudness of the sounds, with low amplitude sounds causing larvae to freeze, and higher amplitude sounds causing them to squirm and drop from the plant (Tautz and Markl 1978). Experimental tests involving sensory ablation showed that significantly more larvae were attacked if their sensilla had been removed compared to controls with intact sensilla (Tautz and Markl 1978). The resonance frequency of sensilla is ~150 Hz, matching the wingbeat frequency of *D. media* (Tautz and Markl 1978).

This comprehensive series of experiments confirmed that trichoid sensilla function in hearing, and that an adaptive function of hearing is to detect parasitoid wasps.

Monarch butterfly (*Danaus plexippus*) caterpillars were first formally tested for their hearing capabilities by Minnich (1936), who reported that larvae responded to tuning forks by freezing, contracting, and jerking their anterior ends. Rothschild and Bergström (1997) subsequently reported that monarch caterpillars responded to sounds of passing aircraft, 'buzzing' sounds, and human voices, by making 'sudden ducking or twitching movements'. More recently, Davis et al. (2018) demonstrated that the sounds of traffic noise caused monarch larvae to increase their heart rates. Taylor and Yack (2019) conducted a series of experiments to characterize the behavioural responses to sounds and their tuning characteristics, and to identify the primary hearing organs. Late instar (4th and 5th) larvae responded to pure tone sounds by freezing, contracting, and vertically flicking their thorax (Fig. 2a). These responses were evoked by sound frequencies ranging between 50 and 900 Hz, with best sensitivity at 100–200 Hz. Sound amplitude affected the type of response, with low amplitudes causing freezing and contraction, and higher amplitudes evoking vigorous dorsoventral flicks (Taylor 2009; Taylor and Yack 2019). This result suggests that caterpillars respond differently as the enemy approaches, first by freezing to purportedly render themselves acoustically or visually cryptic and then by flicking their bodies and tubercles to knock off the predator or prevent egg laying by a parasitoid. Caterpillars were shown to habituate to sounds upon repeated exposures. This result has implications for conservation of monarch butterflies, as a larva's ability to detect and respond to enemies could be compromised in the presence of anthropogenic noise. The primary sensory receptors were confirmed, using ablation experiments, to comprise a pair of prothoracic trichoid sensilla. It is not known whether these receptors are homologous to those in *M. brassicae*, but given that these species are distantly related and exhibit different responses to sound, it is probable that sound reception resulted from convergent evolution. It is proposed that monarchs evolved hearing in response to flight sounds of aerial predators such as wasps and tachinid flies. However, experiments with live predators or parasitoids have not yet been conducted.

Behavioural responses to sounds have been reported for caterpillar species belonging to several lepidopteran taxa (Table 1). In addition to the above-mentioned examples, there are reports of tent caterpillars responding to sounds by flicking their heads and dropping from their tents (Myers and Smith 1978; Taylor 2009), notodontid larvae thrashing tentacles (White et al. 1983), and gregarious saturniid caterpillars raising their heads and generating alarm calls (Breviglieri and Romero 2019). Given the diversity of behavioural responses observed in distantly related species, and the likelihood that near-field receptors are presumably relatively 'easy' to evolve, it would not be surprising if sound reception evolved multiple times in caterpillars. Trichoid sensilla that detect air currents and near-field sounds tend to be long (>500 μm) and filiform in shape (see Keil 1997), and these probably evolve as specializations of the many trichoid sensilla (i.e. innervated hairs) that cover the bodies of larval Lepidoptera. Future studies on 'hearing' should involve testing of more species for their behavioural responses to sound, either played through

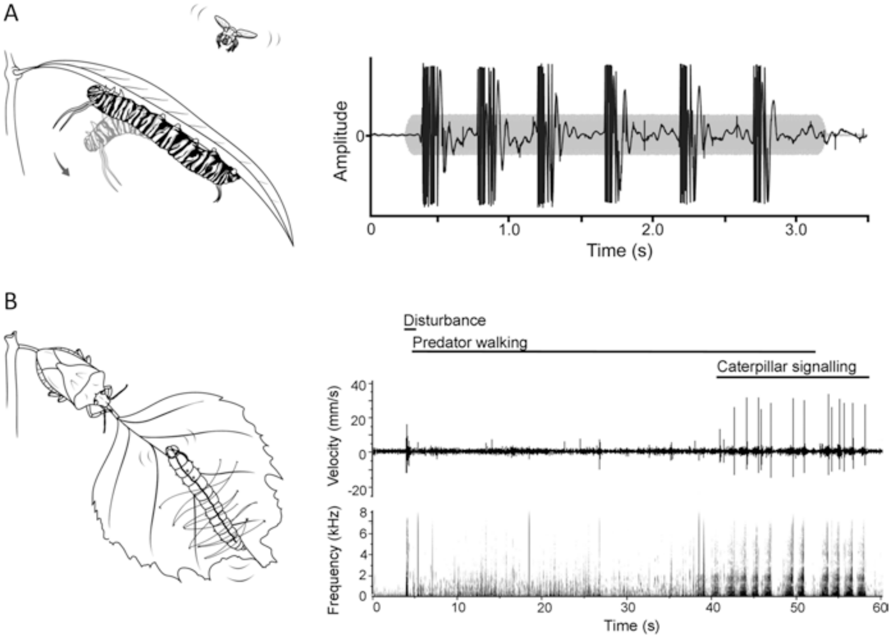

Fig. 2 Defensive sound and vibration detection in caterpillars. (**A**) Monarch (*Danaus plexippus*) caterpillars detect low frequency sounds (~100–500 Hz) by freezing, contracting, and flicking their anterior bodies. Sound frequencies match those generated by a flying insect predator or parasitoid. The waveform illustrates a late instar caterpillar responding to a sound by dorsally flicking. The dark part of the trace shows a laser vibrometer recording from a milkweed leaf, showing six consecutive flicks of the caterpillar. The grey part of the trace indicates the timing of a 300 ms, 200 Hz sound played to the caterpillar through a speaker (adapted from Taylor and Yack 2019). (**B**) The masked birch caterpillar (*Drepana arcuata*) responds to plant-borne vibration cues resulting from the walking movements of a predatory stink bug (*Podisus* sp.). Caterpillars typically first freeze upon detecting the predator, and then signal when the predator is close. The trace shown is a laser vibrometer recording from a birch leaf upon which the caterpillar is residing in its silk shelter. Crawling vibrations of the stink bug are shown to occur prior to the caterpillar signalling. The disturbance marks the application of the predator to the leaf twig (adapted from Guedes et al. 2012)

speakers in the lab, or in the presence of live predators. Experiments should also focus on identifying the receptors, and ascertaining the capabilities of these receptors for encoding sound frequency, amplitude, and direction, characteristics that could convey information about the location and type of enemy.

Detection of Solid-Borne Vibrations

Caterpillars are substrate-bound organisms residing primarily on or within plants (e.g. leaves, twigs) or silk (e.g. silk mats on leaves, or tents). Consequently, solid-borne vibrations generated by predators or parasitoids should be important for risk assessment. Predator-generated vibrations could include cues resulting from the predator approaching the prey, signals used for hunting (i.e. echolocation), or signals used for communicating with others such as conspecifics. These types of cues and signals could conceivably be transmitted to the prey directly through the solid substrate, or indirectly, by air-borne sounds vibrating the substrate (see Caldwell 2014; Yack 2016). While there are many sources of vibrations of potential interest to caterpillar prey, there are currently few experimentally confirmed examples of caterpillars using these vibrations to assess risk. Late instar masked birch caterpillars (*Drepana arcuata*) (Drepanidae) respond to low-frequency crawling vibrations generated by an approaching predatory stink bug (*Podisus* sp.) (Guedes et al. 2012) (Fig. 2b). The caterpillars respond differently depending on the distance of the approaching enemy, by first ceasing activity, and then signalling when the predator is close or has launched an attack. *Semiothisa aemulataria* (Geometridae) larvae respond to plant-borne vibrations resulting from approaching predators (stink bugs, wasps) (Castellanos and Barbosa 2006). Late instar larvae could distinguish between vibrations caused by different sources, including predators, non-predators, and abiotic sources. They also showed evidence of being able to discriminate between vibrations of wasps and stinkbugs by escaping on different lengths of silk thread. Apple leaf miners *Phyllonorycter malella* (Gracillariidae) stop feeding upon detecting vibrations produced by a parasitic wasp *Sympiesis sericeicornis* (Eulophidae) inserting its ovipositor into a mine; the caterpillar resumes feeding only after the parasitoid leaves (Meyhöfer et al. 1997).

There are likely to be many instances of caterpillars using vibrations generated by predators and parasitoids. To document these cases, predator-prey interactions should be staged on natural substrates while recording with vibration sensors to assess what vibrations are available to caterpillars. Playing back these vibrations to prey can be helpful in assessing a prey's response to these vibrations, although vibratory playbacks can be methodologically complex (Cocroft et al. 2014). Identifying the receptors used for vibratory sensing is also needed to better understand vibratory-mediated risk assessment in caterpillars.

Detecting Sounds and Vibrations Made by Non-predators

Caterpillars communicate with non-predators, including conspecifics and heterospecifics, to coordinate defences against their common predators (Costa 2006). For example, some species form assemblages with conspecifics to enhance warning displays, or to build protective shelters. Other species form relationships with ants for protection. The roles of sound and vibration detection in caterpillars remain to be tested in most cases, but there are a few inferential examples. Breviglieri and Romero (2019) report that social *Hylesia nigricans* (Saturniidae) caterpillars respond to ultrasonic alarm signals generated by conspecifics that are being attacked by wasp and bird predators, and these sounds are proposed to function in coordinating group defences. Other examples of caterpillars detecting non-predator sounds and vibrations in the context of defence are discussed in section "Sending signals to non-predators", which focuses on signal generation in caterpillars.

Summary of Defensive Sound and Vibration Detection

Although caterpillars lack tympanal ears that are commonly used in adult Lepidoptera for avoiding predators, they have nonetheless evolved mechanisms to detect near-field sounds and solid-borne vibrations to avoid attack. Eavesdropping on the acoustic cues produced by enemies has been reported numerous times, and is thought to be widespread among caterpillars. It is very likely that caterpillars also use sounds and vibrations to coordinate defences in social groups, and possibly, to eavesdrop on the communication signals of predators such as insectivorous birds. Future lines of investigation should involve staging interactions with natural predators while recording air- and solid-borne vibrations to gain a better appreciation for the cues and signals available to larvae during these interactions. Once hearing and vibration reception has been confirmed based on behavioural experiments, the sensory mechanisms involved should be identified. Also, it is worth considering the effects of anthropogenic noises, both airborne and vibratory, on the abilities of caterpillars to respond to predators.

Generating Sounds and Vibrations in Caterpillars

> *The larva of the North American Saturnian moth Telea polyphemus can, in the third and fourth stages, by rubbing the powerfully constructed mandibles against each other produce a tolerably loud, tapping sound, which is audible at the distance of several meters. That here is question of a means of intimidation is not to be doubted, for if the larva is left in peace it keeps perfectly quiet, but when the larva-cage is touched, or the larvae are taken out, they make this peculiar tapping sound, resembling the ticking of a watch.* (Federley 1905).

Defence sounds in Lepidoptera are taxonomically widespread and highly variable with respect to the types of sounds and mechanisms of sound production. In adults, these sounds, which primarily function to warn, frighten, or confuse echolocating bats, are well documented (reviewed in Minet and Surlykke 2003; Conner and Corcoran 2012; Greenfield 2014; Kawahara and Barber 2015). Comparatively less is understood about defensive sounds in juveniles, even though disturbance sounds have been documented for both pupae and larvae of many species (e.g. Hinton 1948; Devries 1991a; Bura et al. 2016; Dolle et al. 2018). Caterpillars conceivably would benefit from communicating acoustically with their vertebrate predators (i.e. birds, rodents, bats, frogs, and lizards) which have well-developed hearing. Other caterpillars, such as those living in social groups, or those attended by ants, could benefit from sending recruitment or alarm signals to gain protection or coordinate a defence. Caterpillar sound production in the context of defence is discussed below under two categories: caterpillars that send signals to predators (section "Sending signals to predators") and those that send signals to non-predators (section "Sending signals to non-predators").

Sending Signals to Predators

Many species of silk and hawkmoth (Bombycoidea) caterpillars produce sounds upon being disturbed (Table 2). Earlier reports variously described these sounds in different species as 'singing' (Reed 1868), 'tcep or tceep' (Sanborn 1868), 'squeaking' (Packard 1904), 'crepitating noise' (Packard 1904), 'ticking of a watch' (Federley 1905), and 'crackling-rasping noises' (Heinrich 1979), although the functions of these sounds remained untested. More recently, these sounds have been shown to be widespread throughout the superfamily, variable in their signal characteristics in mechanisms, and to function in defence (see Brown et al. 2007; Bura et al. 2009; Bura et al. 2011; Bura et al. 2012; Bura et al. 2016; Dookie et al. 2017; Rosi-Denadai et al. 2018; Sugiura et al. 2020). In a study of 61 species of late instar larvae, Bura et al. (2016) showed that 31% of species and 45% of genera produced sounds following simulated attacks. Four distinct sound types and respective mechanisms were reported: clicking (mandibular stridulation), chirping (mandibular stridulation), whistling (forced air out of spiracles), and vocalizing (forced air out of buccal cavity). It is proposed that these sounds are directed primarily at vertebrate predators, and function as warning signals (acoustic aposematism), as startle displays, or to mimic alarm calls of a predator. Acoustic aposematism is predicted to occur in species that use a chemical defence, with sounds preceding or accompanying chemical release. Bura et al. (2016) demonstrated that in species with 'high' chemical scores (i.e. chemical production through regurgitation or release from scoli occurring promptly following attack), sound production preceded or accompanied chemical release. These sounds tend to be short-duration clicks or chirps and are proposed to warn the predator of an impending defence. In a study using live predators, Brown et al. (2007) showed that clicking *Antheraea polyphemus* caterpillars (Fig. 3a) survived attacks by chickens following sound production, and mice were repelled by the chemical regurgitant. Other sounds are proposed to startle predators. These sounds tend to be loud and long in duration, such as whistles and vocalizations, and are not typically associated with a chemical defence. Bura et al. (2016) demonstrated that species with low chemical scores (i.e. rarely produced a chemical following multiple attacks) tended to produce sounds with these characteristics. Trials with live predators showed that whistles of the walnut sphinx, *Amorpha juglandis* (Fig. 3b), caused yellow warblers (*Dendroica petechia*) and red winged black birds (*Agelaius phoeniceus*) to escape by diving or flying away (Bura et al. 2011; Dookie et al. 2017). Another hypothesis explaining the function of caterpillar defence sounds is mimicry. The whistles of *A. juglandis* caterpillars resemble the 'seet' warning calls of insectivorous birds, and it was proposed that these sounds mimic the alarm calls of avian predators (Dookie et al. 2017).

Table 2 Caterpillars producing sounds and vibrations in a defensive context

Taxon (of sender)			Acoustic signal		Target animal (proposed)	Function (proposed)	Reference(s)
Superfamily	Family	Species	Descriptors of sound, mechanism	NF/FF/V[a] (proposed)	Predator, non-predator, parasitoid		
Adeloidea	Heliozelidae	*Antispila nysaefoliella*	Abdominal movements	V	Parasitoids	Defence against parasitoids	Low (2008)
Bombycoidea	Saturniidae	*Actias Luna*	Stridulation, mandibles, clicking	FF	Predators	Aposematism	Bura et al. (2016)
Bombycoidea	Saturniidae	*Antheraea pernyi*	Stridulation, mandibles, clicking	FF	Predators	Aposematism	Bura et al. (2016)
Bombycoidea	Saturniidae	*Antheraea polyphemus*	Stridulation, mandibles, clicking	FF	Predators	Aposematism	Brown et al. (2007), Bura et al. (2016)
Bombycoidea	Saturniidae	*Callosamia promethea*	Stridulation, mandibles, clicking	FF	Predators	Aposematism	Bura et al. (2016)
Bombycoidea	Saturniidae	*Calosaturnia mendocino*	Stridulation, mandibles, chirping	FF	Predators	Aposematism	Bura et al. (2016)
Bombycoidea	Saturniidae	*Citheronia lobesis*	Stridulation, mandibles, chirping	FF/V	Predators	Aposematism	Bura et al. (2016)
Bombycoidea	Saturniidae	*Hylesia nigricans*	Ultrasound emission	FF	Non-predators (conspecifics)	Recruitment	Breviglieri and Romero (2019)
Bombycoidea	Saturniidae	*Rhodinia fugax*	Forced air, spiracles, whistling	FF	Predators	Startle display	Sugiura et al. (2020)
Bombycoidea	Saturniidae	*Saturnia pyri*	Stridulation, mandibles, chirping	FF	Predators	Aposematism	Bura et al. (2016, 2009)
Bombycoidea	Saturniidae	*Schausiella santarosensis*	Stridulation, mandibles, chirping	FF	Predators	Aposematism	Bura et al. (2016)

(continued)

Table 2 (continued)

Taxon (of sender)			Acoustic signal		Target animal (proposed)	Function (proposed)	Reference(s)
Superfamily	Family	Species	Descriptors of sound, mechanism	NF/FF/V[a] (proposed)	Predator, non-predator, parasitoid		
Bombycoidea	Sphingidae	*Acherontia atropos*	Stridulation, mandibles, clicking	FF	Predators	Aposematism	Bura et al. (2016)
Bombycoidea	Sphingidae	*Amorpha juglandis*	Forced air, spiracles, whistling	FF	Predators	Startle display	Bura et al. (2011, 2016)
Bombycoidea	Sphingidae	*Amphion floridensis*	Forced air, buccal cavity, vocalizing	FF	Predators	Startle display	Bura et al. (2016), Rosi-Denadai et al. (2018)
Bombycoidea	Sphingidae	*Eumorpha satellitia*	Stridulation, mandibles, clicking	FF	Predators	Aposematism	Bura et al. (2016)
Bombycoidea	Sphingidae	*Langia zenzeroides*	Forced air, spiracles, whistling	FF	Predators	Defence against invertebrate attackers	Sugiura and Takanashi (2018)
Bombycoidea	Sphingidae	*Manduca pellenia*	Stridulation, mandibles, clicking	FF	Predators	Aposematism	Bura et al. (2016)
Bombycoidea	Sphingidae	*Manduca sexta*	Stridulation, mandibles, clicking	FF	Predators	Aposematism	Bura et al. (2012, 2016)
Bombycoidea	Sphingidae	*Nyceryx magna*	Forced air, buccal cavity, vocalizing	FF	Predators	Startle display	Bura et al. (2016)
Bombycoidea	Sphingidae	*Pachygonidia drucei*	Forced air, buccal cavity, vocalizing	FF	Predators	Startle display	Bura et al. (2016)
Bombycoidea	Sphingidae	*Phyllosphingia dissimilis*	Forced air, spiracles, whistling	FF	Predators	Startle display	Bura et al. (2016)

Bombycoidea	Sphingidae	*Sphecodina abbottii*	Forced air, buccal cavity, vocalizing	FF	Predators	Startle display	Packard (1904), Heinrich (1979), Bura et al. (2016)
Drepanoidea	Drepanidae	*Drepana arcuata*	Percussion, stridulation mandibles, anal oars	V	Predators (stink bug)	Deterrent to predators	Guedes et al. (2012)
Gelechioidea	Oecophoridae (Lypusidae)	*Diurnea fagella*	Thoracic leg hook scraping on leaf surface	V	Arthropods and parasitoids	Refuge defence	Hunter (1987)
Noctuoidea	Notodontidae	*Cerura* sp. *Dicranura* sp.	Stridulation, mandibles	V	NA	Intimidation	Federley (1905)
Papilionoidea	Lycaenidae	*Cupido argiades* *Jalmenus evagoras* *Lycaena phaleas* *Maculinea alcon* *Scolitintides orion* *Thereus pedusa* etc.	N/A	V	Non-predator (ants)	Increase survival	DeVries (1990), (1991a), Travassos and Pierce (2000), Riva et al. (2017)
Papilionoidea	Lycaenidae	*Arhopala madytus*	Stridulation, abdominal segment 5 and 6	V	Non-predator (ant)	Protection from ants	Hill (1993)
Papilionoidea	Lycaenidae	*Hypolycaena othona*	Rhythmic muscle contractions, croaking	V	N/A	Maybe alarm calls to ants	Fiedler (1992a)

(continued)

Table 2 (continued)

Taxon (of sender)			Acoustic signal		Target animal (proposed)	Function (proposed)	Reference(s)
Superfamily	Family	Species	Descriptors of sound, mechanism	NF/FF/V[a] (proposed)	Predator, non-predator, parasitoid		
Papilionoidea	Lycaenidae	*Lycaena dispar, L. helle, L. phlaeas*	N/A	N/A	Natural enemies	Signal and repel natural enemies	Riva et al. (2017)
Papilionoidea	Lycaenidae	*Surendra florimel*	N/A	V/FF	Non-predator (ant), other predator	Protection from ants, distress calls	Fiedler (1992b)
Papilionoidea	Riodinidae	*Eurybia* sp.	N/A	V	Non-predator (ants)	Increase survival	DeVries (1990, 1991a)
Papilionoidea	Riodinidae	*Juditha molpe* *Nymphidium* sp. *Synargis mycone* *Thisbe irenea* *Theope* sp. Etc.	Stridulation, vibratory papillae, and epicranial granulations	V	Non-predator (ants)	Increase survival	DeVries (1990, 1991a, 1991b)

[a] NF/FF/V = Near-field sound, far-field sound, vibration (solid-borne). These describe the proposed (or suggested) mode of transmission to the receiver

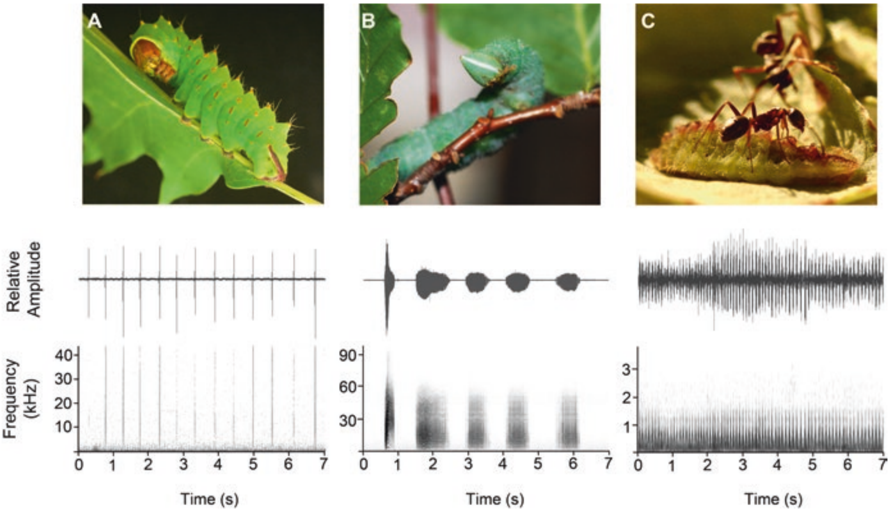

Fig. 3 Caterpillars that generate sounds and vibrations to avoid attack. (**A**) Aposematic warning sounds. When attacked, the silkmoth caterpillar *Antheraea polyphemus* (Saturniidae) produces clicking sounds by stridulating its mandibles. These sounds are followed by regurgitation and function as warning sounds (see Brown et al. 2007). The waveform and spectrogram show a train of clicks following a simulated attack to the caterpillar with blunt forceps. (**B**) Startle sounds. The walnut sphinx *Amorpha juglandis* produces whistles by forcing air out of its eighth abdominal spiracles. These sounds have been shown to startle avian predators (see Bura et al. 2011; Dookie et al. 2017). The oscillogram and spectrogram show a train of five whistles following a simulated attack with blunt forceps. (**C**) Vibratory recruitment signals. Parasitic larvae of the butterfly *Scolitantides orion* generate acoustic signals to recruit ants for protection. The oscillogram and spectrogram show a train of acoustic signals generated by the larva. The mechanism of signal production is unknown. Sounds and photographs for A and B are from the Yack lab, and for C are provided courtesy of Francesca Barbero and Marco Gherlenda

Some caterpillars are proposed to generate solid-borne vibrations directed at an attacker, although the functional significance of these vibratory signals is not clear. Tupelo leaf miners, *Antispila nysaefoliella*, generate vibrations when disturbed by a parasitoid (Low 2008). The vibrations were described as ‘ticks’ and ‘rattles’ produced by specialized structures on the abdomen. Signalling is proposed to interfere with foraging in parasitic wasps, although this hypothesis remains untested. The masked birch caterpillar, *Drepana arcuata*, generates drumming and scraping vibrations when pursued by a stink bug predator (*Podisus* sp.), and these signals appeared to stop the attack (Guedes et al. 2012). It is possible that the vibrations signal to the predator that the prey is unprofitable to pursue. *Diurnea fagella* larvae produce vibratory signals by scraping a hook on their thoracic leg against the leaf surface (Hunter 1987). It was postulated that signalling is directed at intruding spiders, but the anti-predator functions of these signals were not tested.

Sending Signals to Non-predators

Caterpillars also send acoustic signals to non-predators in the context of defence. These signals are primarily vibratory, and function, or are proposed to function, as alarm or recruitment signals to coordinate a defence or recruit others for protection. Currently, the majority of examples involve myrmecophilic (ant-loving) butterfly larvae. Larvae of Lycaenidae and Riodinidae butterflies can generate vibratory signals to recruit and maintain relationships with ants in mutualistic, commensalistic, and parasitic relationships (reviewed in Devries 1991a; Riva et al. 2017; Schönrogge et al. 2017; Casacci et al. 2019) (Table 2). Lycaenidae larvae can produce a variety of vibrations described as pulses, drums, grunts, and hisses to communicate with ants (Travassos and Pierce 2000; Schönrogge et al. 2017). While the mechanisms of signal production are not well understood, one such mechanism involves an abdominal stridulatory apparatus (Hill 1993). Other Lycaenidae species have been described to produce vibrations by a 'shivering' behaviour, which is probably a form of tremulation (e.g. Devries 1991a). Riodinidae larvae also produce vibrations to call to ant hosts. Many species generate signals using a stridulatory mechanism comprising two structures: vibratory papillae and epicranial granulations (Devries 1990, 1991a). Vibratory papillae are grooved rod-like appendages located on the prothorax that strike against textured (granulated) surfaces on the head to produce vibrations as the head oscillates. One of the benefits that caterpillars gain from their relationships with ants is protection from predators and parasitoids. In species that use vibratory signals to gain acceptance into the ant colony, the anti-predator benefits derived from calling are indirect, as being tended by ants provides protection from predators and parasitoids (Pierce et al. 1987; Devries 1991b). However, in cases where myrmecophilous species live within the ant territory but outside of the ant nest, larvae generate vibratory and chemical signals to recruit ants for protection (Schönrogge et al. 2017; Casacci et al. 2019). For example, *Scolitantides orion* (Fig. 3c) calls to ants for protection when disturbed (Riva et al. 2017; Barbero pers. comm.), and *Hypolycaena othona*, although only weakly associated with ants, signals upon disturbance (Fiedler 1992a), presumably to gain protection by ants.

Other examples of caterpillars proposed to communicate acoustically with non-predators to gain protection include early instar *D. arcuata* that signal to recruit conspecifics to build protective shelters (Yadav et al. 2017; Yadav and Yack 2018), and early instar *H. nigricans* that produce airborne sounds to coordinate a group defence (Breviglieri and Romero 2019). However, the antipredator benefits of these signals have not been experimentally validated to date.

Summary of Caterpillar Defensive Sound Production

Despite having soft bodies that limit their capabilities for producing sounds and vibrations, caterpillars have evolved an impressive variety of acoustic defence signals. These can be directed at a predator and function as warning, startle, or mimicry signals, or they can be directed at non-predators to recruit help or coordinate defences. Many of these signals are inconspicuous to humans without the assistance of specialized recording instruments, and it is expected that there are many undocumented examples.

Conclusions and Future Research

When considering caterpillar defence strategies, hearing and sound production do not immediately come to mind. Yet, evidenced by the examples discussed here, it is clear that acoustic antipredator strategies are taxonomically widespread and functionally diverse in caterpillars. Still, we have just scratched the surface in our understanding of this topic. The following lines of investigation are recommended for future studies: 1. Behavioural responses to low frequency sounds (less than 2 kHz) should be documented across different taxa and developmental stages of larval instars. Low frequency sounds simulate those of flying insect predators and parasitoids that impose significant selection pressures on caterpillars to evolve near-field sound and vibration receptors, and this form of hearing is likely to have evolved multiple times. 2. Recordings of air- and solid-borne vibrations from natural substrates (i.e. host plants, silk shelters) should be performed while videotaping predator/parasitoid and caterpillar prey interactions. 3. Sound and vibration receptor mechanisms should be identified using neurophysiological, morphological, and behavioural experiments. Given the diversity of acoustic signals and cues that are detectable by caterpillars, as well as the diversity of behavioural responses exhibited, it would not be surprising to see a diversity of sound and vibration receptors resulting from convergent evolution. 4. Hypotheses explaining the functions and evolution of defence sounds in Bombycoidea caterpillars require further testing using experiments with live predators and comparative phylogenetic analyses. Research on acoustically mediated defences is key for gaining a comprehensive understanding of the survival strategies of caterpillars, but also has some practical applications. For example, as anthropogenic noise may impair a caterpillar's ability to detect an enemy, it is important to understand what a caterpillar 'hears' for conservation purposes. On the flip side, sounds and vibrations can be implemented in pest management, as caterpillars have been shown to respond to acoustic signals and cues by ceasing movement and feeding, and dropping from host plants.

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