

Animal Signals and Communication 8

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Contents

Part I Studying Vibrational Behavior: Ideas, Concepts and History	
1 Quo Vadis, Biotremology?	3
Peggy S. M. Hill, Valerio Mazzoni, Nataša Stritih-Peljhan, Meta Virant-Doberlet, and Andreas Wessel	
2 Sound Production in True Bugs from the Families Acanthosomatidae and Pentatomidae (1958)	21
Karl H. C. Jordan, Helga Slowioczek, Hannelore Hoch, and Andreas Wessel	
Part II The State of the Field: Concepts and Frontiers in Vibrational Behavior	
3 Vibrational Behaviour and Communication in the New Zealand Weta (Orthoptera: Anostostomatidae)	37
Johannes Strauß and Daniel R. Howard	
4 Energetic Costs of Vibrational Signaling	67
Anka Kuhelj and Meta Virant-Doberlet	
5 The Hawaiian Planthoppers (Hemiptera: Auchenorrhyncha: Fulgoromorpha) and Their Courtship Songs	93
Manfred Asche, Hannelore Hoch, Caitlin O’Connell-Rodwell, and Andreas Wessel	
Part III Practical Issues in Studying Vibrational Behavior	
6 Substrate-Borne Vibrational Noise in the Anthropocene: From Land to Sea	123
Louise Roberts and Daniel R. Howard	

7	Research Approaches in Mechanosensory-Cued Hatching	157
	Karen M. Warkentin, Julie Jung, and J. Gregory McDaniel	
8	Inexpensive Methods for Detecting and Reproducing Substrate-Borne Vibrations: Advantages and Limitations	203
	Rachele Nieri, Sabrina C. J. Michael, Carlos F. Pinto, Omar N. Urquizo, Heidi M. Appel, and Reginald B. Cocroft	
Part IV Vibrational Behavior in Less Explored Contexts		
9	Sexual Selection in the Red Mason Bee: Vibrations, Population Divergence, and the Impact of Temperature	221
	Taina Conrad	
10	Vibrational Signals in Multimodal Courtship Displays of Birds . . .	237
	Nao Ota and Masayo Soma	
11	Blooms and Buzzing Bees: Bridging Buzz Pollination and Biotremology	261
	Paul Anthony De Luca and Mario Vallejo-Marín	
12	Mechanosensory Behaviour and Biotremology in Nematodes	293
	Takuma Sugi	
13	Speleotremology: Ecology and Evolution of Vibrational Communication in Cavernicolous Insects	307
	Nataša Stritih-Peljhan, Johannes Strauß, Andreas Wessel, and Hannelore Hoch	
Part V Vibrational Behavior in Some Well-Studied Taxa		
14	Ophidian Biotremology	343
	Dawei Han and Bruce A. Young	
15	Evolution of Communication Systems Underground in a Blind Mammal, <i>Spalax</i>	359
	Eviatar Nevo	
16	Vibrational Behaviour in Honeybees	387
	Wolfgang H. Kirchner, Felix A. Hager, and Kathrin Krausa	
17	Vibrational Communication Outside and Inside the Nest in Leaf-Cutting Ants	411
	Flavio Roces	
18	Biotremology of Social Wasps: The Next Step to Understand Wasps' Social Life	437
	Rachele Nieri, Alessandro Cini, Marco Valerio Rossi Stacconi, Irene Pepicciello, Valerio Mazzoni, and Rita Cervo	
19	Vibratory Sensing and Communication in Caterpillars	471
	Jayne E. Yack and Chanchal Yadav	

Part VI Applied Biotremology

20 Exploitation of Vibration Sensing for Pest Management in Longicorn Beetles 495
Takuma Takanashi and Hiroshi Nishino

21 Subterranean Arthropod Biotremology: Ecological and Economic Contexts 511
Richard Mankin

22 Vibrational Communication in Psyllids 529
Sabina Avosani, Richard W. Mankin, Thomas E. S. Sullivan, Jernej Polajnar, David Maxwell Suckling, and Valerio Mazzoni

23 Potential of Biotremology for Monitoring and Control of Stink Bugs 547
Raul Alberto Laumann, Andrej Čokl, Maria Carolina Blassioli Moraes, Aline Moreira Dias, and Miguel Borges

Chapter 19

Vibratory Sensing and Communication in Caterpillars



Jayne E. Yack and Chanchal Yadav

Abstract Over the past few decades, scientists have discovered that insects live in complex vibratory environments that they both create and exploit for their survival. Yet, this growing body of literature is focused predominantly on adults, leaving a significant knowledge gap on vibratory sensing and communication in juveniles. There is burgeoning yet scattered evidence indicating that juveniles use vibrations in a wide range of contexts. In this chapter, we endeavored to synthesize the literature on vibratory sensing and communication in caterpillars (larval Lepidoptera). Caterpillars are obligate substrate-bound insects that are exposed to a wide range of vibrations generated by biotic and abiotic sources. This chapter shows that caterpillars across diverse taxonomic groups use vibrations in a variety of contexts, including predator detection and risk assessment, detection of abiotic events such as wind and rain, recruitment and spacing, territorial defense, and maintaining relationships with ants. While it is clear that many caterpillars are capable of detecting and discriminating between vibration sources, vibration receptors have not yet been identified in caterpillars, or any other holometabolous insect larvae. We discuss potential vibration receptors in larvae based on our knowledge of adult receptors and larval morphology and physiology. The vibratory landscapes of juvenile insects, including eggs, larvae, nymphs, and pupae, remain poorly understood. Yet, most juveniles are substrate-bound, and therefore, it is likely that vibrations play an important role in their survival. We recommend further investigations on vibratory sensing and communication in juveniles, from documenting the species using vibrations to discovering the sensory organs involved in detecting and processing vibratory information.

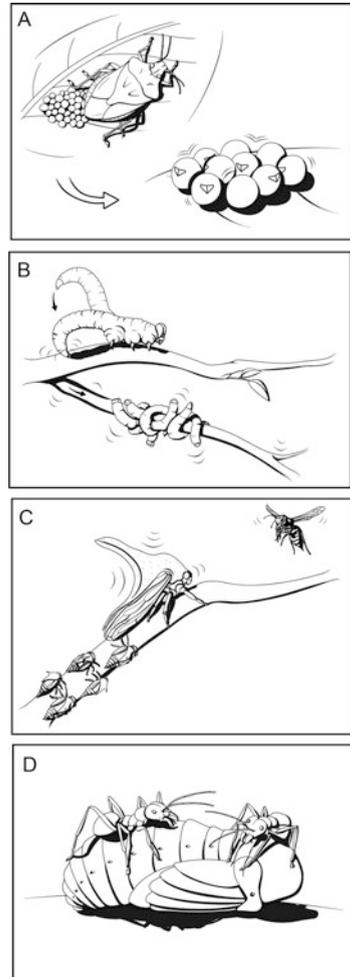
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19.1 Introduction

Vibratory sensing and communication in insects have been studied for several decades, and we are now gaining an appreciation for the ubiquity and importance of this sensory modality. At the outset, we would like to define what we mean by “vibratory.” In the broadest sense, acoustic signals and events are defined as the transmission of vibrations through an elastic medium, including air, water, or solids. Vibrations transmitted through solids such as plants or the ground are commonly referred to as “vibrations” or “substrate vibrations,” whereas air- and water-borne vibrations are commonly referred to as “sounds.” This is the terminology that we will adopt in this chapter, but for further discussion of the nomenclature and physical characteristics of vibrations and sounds, see Hill (2008, 2014) and Hill and Wessel (2016). At least 18 insect orders have been reported to include species that use vibratory communication and sensing (Cocroft and Rodriguez 2005). Vibrations are used in a wide variety of contexts, including detection of passive cues generated from biotic sources (e.g., approaching predators) or abiotic sources (e.g., wind, rain) to complex communication signals used for reproduction, territorial displays, recruitment, and other social interactions. There are many reviews on the topic of vibratory sensing and communication. Some of these focus broadly on insects or other invertebrates (e.g., Markl 1983; Gogala 1985; Virant-Doberlet and Čokl 2004; Cocroft and Rodriguez 2005; Hill 2008; Čokl and Virant-Doberlet 2009; Cocroft and Hamel 2010; Randall 2014; Yack 2016). Other reviews focus on specific taxonomic groups that use vibrations, or functions of vibrations, e.g., spiders (Barth 1997, 2002; Baurecht and Barth 1992; Elias and Mason 2010), Neuroptera (Stewart 1997; Devetak 1998), Hemiptera (Gogala et al. 1974; Claridge 1985; Cocroft and McNett 2006; Shestakov 2015), termites (Hager et al. 2019), Mantophasmatodea (Eberhard and Eberhard 2013; Eberhard and Picker 2019), predator–prey interactions (Casas and Magal 2006; Virant-Doberlet et al. 2019), courtship (Rodríguez 2019), and group-living (Cocroft 2001). Research on insect vibratory sensing and communication until now has focused on adults, and specifically, their reproductive behaviors, with little consideration to juveniles. By juveniles, we mean eggs, nymphs of hemimetabolous insects, and larvae and pupae of holometabolous insects.

There is a growing number of examples demonstrating or suggesting that juveniles belonging to several insect orders use vibrations in a variety of contexts, including but not restricted to the following: (1) egg hatching (Fig. 19.1a), e.g., Hemiptera (Mukai et al. 2014; Endo et al. 2019), Orthoptera (Nishide and Tanaka 2016; Tanaka et al. 2018); (2) coordinating social grouping activities and recruitment (Figs. 19.1b, c), e.g., Hymenoptera (Hograefe 1984; Fletcher 2007, 2008), Lepidoptera (Yadav et al. 2017), Coleoptera (Cocroft 2001), Hemiptera (Cocroft 2001; Ramaswamy and Cocroft 2009; Hamel and Cocroft 2012); (3) manipulating ants in parasitic or mutualistic interactions (Fig. 19.1d), e.g., Lepidoptera (Devries 1990; Travassos and Pierce 2000); (4) obtaining food, e.g., Hymenoptera (Ishay et al. 1974; Hograefe 1984), Diptera (McIver and Beech 1986); (5) territorial and

Fig. 19.1 Vibratory sensing and communication has been reported for all juvenile insect stages. Examples include the following: **(a)** Eggs/embryos. Eggs of the brown marmorated stink bug, *Halymorpha halys*, synchronize their hatching by responding to vibrations caused by egg cracking by siblings in a clutch (see Endo et al. 2019). **(b)** Nymphs. Nymphs of the treehopper, *Umbronia crassicornis* (Membracidae), produce vibrational signals to elicit their mother's protective antipredator behavior (see Crocroft 1999). **(c)** Larvae. Larvae of the sawfly, *Perga affinis*, produce vibrations by tapping and contracting to coordinate grouping (see Fletcher 2007). **(d)** Pupae. Pupae of the common imperial blue butterfly, *Jalmenus evagoras* (Lycaenidae), produce vibrations to attract and maintain the presence of attendant ants in butterfly–ant mutualism (see Travassos and Pierce 2000)



spacing behavior, e.g., Lepidoptera (Yack et al. 2001, 2014; Fletcher et al. 2006; Scott et al. 2010; Guedes et al. 2012); (6) detecting and avoiding predators and parasitoids, e.g., Lepidoptera (Djemai et al. 2001; Castellanos and Barbosa 2006; Low 2008), Coleoptera (Kojima et al. 2012), Hemiptera (Gish et al. 2012). We propose that vibratory detection and communication is widespread among juveniles. However, due to a number of factors, including the (typically) small body size of juveniles, that vibrations may be communicated at close range in small groups of juveniles, and that plant-borne vibrations of small insects may not be easily detected by human researchers without specialized instrumentation, these vibratory events may have been overlooked by scientists. Given that juveniles are flightless and substrate-bound, and purportedly require mechanisms for communication and detection of predators and parasitoids, it seems imminent that vibrations play a prominent

role in their sensory ecology. We suspect that research on vibratory communication in juveniles lags far behind that for adults, and requires further investigation. In this chapter, we explore the topic of juvenile vibratory sensing and communication by focusing on caterpillars, the larvae of Lepidoptera.

19.2 Caterpillar Sensory Ecology

As caterpillars are often viewed as the “feeding stage” of adult Lepidoptera, sometimes the complexity of their behaviors is overlooked. Caterpillars in fact exhibit highly varied and sometimes complex behaviors that require sensing and interacting with their environments. Many species must protect themselves from physical elements such as rain, light, and heat, by building shelters and finding cover (Lill and Marquis 2007; Greeney et al. 2012). They need to navigate their environments to locate and identify host plants (Fitzgerald and Peterson 1988; Zalucki et al. 2002), create leaf mines (Connor and Taverner 1997), locate pupation sites (Hagstrum and Subramanyam 2010; Grof-Tisza et al. 2015) and shelter sites (Lill and Marquis 2004; Abarca et al. 2014), and in rare cases, locate prey (Montgomery 1983). As caterpillars are prey and hosts for a variety of predators and parasitoids, they have evolved mechanisms to detect and respond behaviorally to these threats in a variety of ways (Lederhouse 1990; Wagner 2005; Greeney et al. 2012). Many species form social groups for purposes of constructing communal shelters, foraging in groups, or cooperating in defense (Despland and Le Huu 2007; Costa 2010; Despland 2019). As such, they require mechanisms to form and maintain groups, construct communal shelters, and coordinate social behaviors. Some butterfly larvae form parasitic or mutualistic relationships with ants, and have evolved mechanisms to communicate with, and manipulate their hosts (Schönrogge et al. 2017; Cassacci et al. 2019). Given these highly varied demands on their sensory systems, it is helpful to first review what is understood about the sensory modalities of caterpillars.

Sensory receptors in caterpillars used to monitor the external environment include those that detect chemical, light, tactile, and acoustic stimuli. Chemoreception is the best understood of all the sensory modalities in caterpillars. Taste and olfactory receptors occur primarily on the head (antennae and mouthparts) (Schoonhoven and Dethier 1966; Schoonhoven and van Loon 2002; Roessingh et al. 2007; Shields and Martin 2012). Gustatory receptors play a key role in food evaluation, host selection, and feeding preferences (Schoonhoven 1987; Schoonhoven and van Loon 2002; de Boer 2006). Olfactory chemoreceptors are utilized in tasks such as detecting trail pheromones (Roessingh 1989), and orientation to host plants (Piesik et al. 2009, 2013). The visual system comprises simple light receptors (stemmata) located on the head region. These can form crude images and discriminate colors (Warrant et al. 2003), potentially functioning in orienting to pupation sites (Starnecker 1996), and feeding sites (Rieske and Townsend 2005). Tactile receptors occur on different parts of the body, and function in maintaining processions (Roessingh 1989; Fitzgerald 2003), and detecting and escaping from predators (Castellanos et al. 2011). The

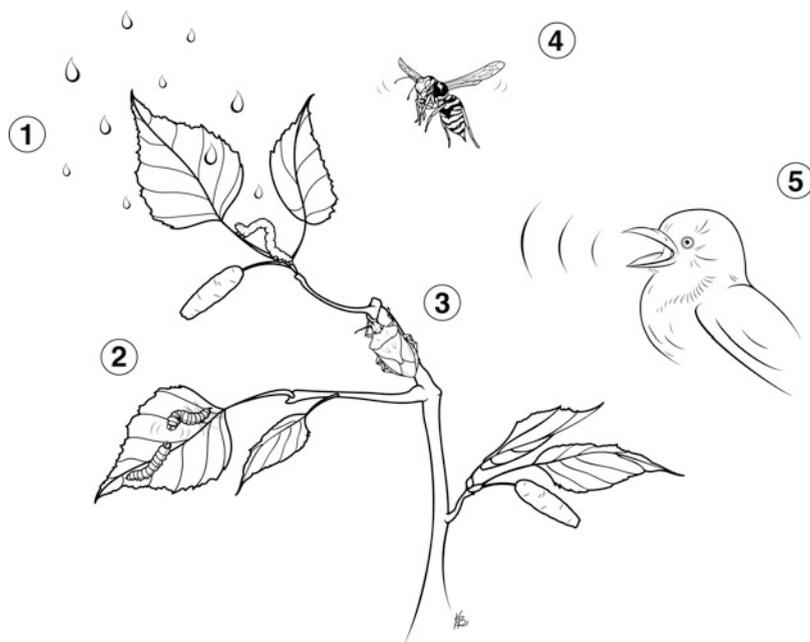


Fig. 19.2 Potential sources of vibrational information for a caterpillar. (1) Abiotic sources including rain droplets and wind could inform caterpillars of weather conditions, or mask important vibratory information. (2) Other caterpillars may produce incidental vibrations by locomotion (e.g., crawling) or chewing, or by actively signaling (e.g., for recruitment or advertising territory). (3) Caterpillars that are prey or hosts may detect incidental cues produced by an approaching predator or parasitoid directly through the substrate. (4, 5) Vibrations may be transmitted to the plant indirectly from air-borne sounds produced by a flying predator, such as a wasp, or a calling predator, such as an insectivorous bird singing in the vicinity

acoustic sensory modalities, including mechanoreceptors that detect both air- or solid-borne vibrations, are poorly understood in caterpillars. In some species, long hairs called trichoid sensilla have been shown to detect near-field sounds and function in detecting flying insect predators and parasitoids (Markl and Tautz 1975; Tautz 1977, 1978; Tautz and Markl 1978; Taylor and Yack 2019). There is increasing evidence that many caterpillar species use solid-borne vibrations. Being substrate-bound, either living on or inside plant material, vibratory sensing and communication may be an important mechanism for communication and risk assessment. Vibrations that are potentially relevant to caterpillars could be transmitted through three routes: from solid to solid, from solid to air to solid, or from air to solid (Fig. 19.2). Vibrations have been noted or proposed to function in a number of different contexts including territorial behavior, recruitment and social interactions, mutualistic or parasitic relationships with ants, and predator detection. The remainder of this chapter focuses on what we know, and what we do not know, about vibratory detection and communication in caterpillars.

19.3 Vibratory Detection and Communication in Caterpillars

19.3.1 Territorial Behavior

Several species of Lepidoptera larvae use substrate-borne vibrations in territorial contests over a resource, such as a feeding site or leaf shelter. Leaf shelters are commonly observed in larval Lepidoptera, providing benefits such as protection from enemies, improved microclimate, and feeding sites (e.g., Hunter and Willmer 1989; Sagers 1992; Berenbaum et al. 1993; Eubanks et al. 1997; Fukui 2001; Lill and Marquis 2007; Abarca et al. 2014). Given the benefits and energetic costs associated with shelters, caterpillars exhibit competition to defend them from intruders (Sigmon 2015). Vibrations have been shown to function in both detecting intruders and generating signals to defend territories. At present, vibratory-mediated territoriality has been most thoroughly studied in species belonging to the superfamily Drepanoidea.

Vibratory-mediated territoriality is widespread in larvae belonging to the superfamily Drepanoidea, and specifically, those in the family Drepanidae (Bowen et al. 2008; Scott et al. 2010; Scott and Yack 2012). The species that has been most thoroughly studied is the masked birch caterpillar (*Drepana arcuata*). Late instar masked birch caterpillars construct and occupy silken leaf shelters on birch (*Betula papyrifera*). Shelters can take more than 3 hours to construct, consuming valuable time and energy. When approached by a conspecific intruder, resident larvae produce a combination of three distinct vibrations by drumming and scraping their mandibles and scraping specialized anal “oars” against the leaf’s surface. In staged interactions between residents and intruders, Yack et al. (2001) demonstrated that resident larvae won territorial acoustic disputes 86.8% of the time. A resident larva confronted with an intruding conspecific typically stops feeding, backs into its leaf shelter, and begins signaling. Residents were observed to increase the rate of signaling and varied the use of particular signals in relation to its distance between itself and the intruder (Yack et al. 2001). Signaling rates increased with the amount of time a caterpillar spent on a leaf, as well as with silk accumulation (Yack et al. 2014). Conversely signal rates decreased with shelter removal (Yack et al. 2014). Residents use vibrations to detect approaching intruders, and can distinguish among vibrations caused by a conspecific intruder, wind, and rain (Guedes et al. 2012). Comparative studies show that vibratory-mediated territoriality is taxonomically widespread within the Drepanidae, and it is proposed that the types and intensity of signals vary among species depending on the amount of energy investment in shelters (Scott et al. 2010). A phylogenetic study showed that vibratory-mediated territoriality is a derived trait in species belonging to the subfamilies Drepaninae and Thyatirinae, but is absent in the ancestral Cyclidiinae (Scott et al. 2010). Phylogenetic mapping showed that vibratory signaling evolved as a form of ritualized aggression, and that movements associated with physical fighting (crawling, biting)

evolved into ritualized signals to avoid damage incurred by physical fighting (Scott et al. 2010).

In addition to the abovementioned Drepanoidea species, the use of vibrations during competition for resources has been reported for species in the superfamilies Gracillarioidea, Gelechioidea, and Tortricoidea. The cherry leaf roller, *Caloptilia serotinella* (Gracillariidae, Gracillarioidea), produces three distinct vibratory signals: scraping, plucking, and vibrating in response to a conspecific intruder entering a resident's leaf shelter (Fletcher et al. 2006). Scraping, a form of stridulation, is produced by lateral head movements, while the mandibles are held open and scraped against the leaf surface. Vertical movements of the head and thorax produce the plucking signal; either the mandibles or the thorax pulling up on the leaf are thought to produce the signal. "Vibrating" is produced when the larva remains in a fixed position on the leaf and oscillates the thorax horizontally, and while doing so, the thoracic legs scrape the leaf. The "vibrating" signal is presumed to be a combination of tremulation and stridulation. The signals differed in usage when interacting with a conspecific: the most frequently used is scraping followed by plucking and vibrating. The distance between the resident and the intruder also determined which signal was used; at farther distances vibrating was observed, while at closer distances scraping was observed. Vibrational signaling in *Diurnea fagella* (Oecophoridae) larvae has been suggested to play a role in defending resources (Hunter 1987). These larvae occupy leaf shelters where they feed and reside. When disturbed, they scrape a "hook," located on the distal end of a modified third thoracic leg, back and forth on the leaf's surface. Although the signals were recorded as airborne sounds with microphones, it is most likely they are transmitted as vibrations through the leaf. Further research is required to ascertain the precise functional significance of signaling in *D. fagella* larvae, but it has been proposed to function primarily in territorial contests with conspecifics. Another example of vibration-mediated territorial defense was reported for *Sparganothis pilleriana* (Tortricoidea) (Russ 1969). Caterpillars form a leaf shelter on grape leaves and defend them against conspecifics and heterospecifics by rearing up and striking (drumming) the webbing on the leaf repeatedly. Vibration signals were recorded by placing a microphone directly on the substrate. Signals increased in intensity when conspecific intruders remained near the leaf shelter. Fighting ensued until one of the contestants fled. In another study of territorial encounters in shelter building Gelechiidae and Oecophoridae caterpillars (Sigmon 2015) "audible sounds" were noted during territorial encounters when a caterpillar repeatedly tapped (drummed) its head on the leaf surface. However, vibration recordings were not conducted and the role of vibratory communication was not formally tested. Vibratory-mediated territorial disputes may be widespread among the many lepidopteran larvae that invest time and energy in building and maintaining shelters, and should be further investigated.

19.3.2 *Group Formation and Maintenance*

Several caterpillars form groups at different stages of their development (Costa and Pierce 1997; Fitzgerald and Costa 1999; Zalucki et al. 2002; Costa 2006) for purposes of collective predator defense, thermoregulation, and feeding (e.g., Costa and Pierce 1997; Prokopy and Roitberg 2001; Reader and Hochuli 2003; Costa 2006; Despland 2019). The sensory mechanisms used to form, maintain, and coordinate activities within these groups, however, are not well understood. There are some examples of chemical-mediated recruitment in processionary species (e.g., Costa 2006; Matthews and Matthews 2009; Pescador-Rubio et al. 2011). Vibration-mediated recruitment and group formation would seem to be an optimal means of communication, as signals are short and therefore more difficult for predators to detect than chemical signals. At present, there is one example in larval Lepidoptera. Early instar caterpillars of the hooktip moth caterpillar, *Drepana arcuata*, live in small groups of 2–5 on birch leaves (Yadav and Yack 2018). Upon hatching, neonates begin shelter construction on the edge of a birch leaf, and generate vibratory signals while feeding using specialized oar-like structures, called anal oars, located on the last abdominal segment. These vibratory signals are used by early instars for recruitment by advertising feeding sites and shelter locations to conspecifics (Yadav et al. 2017). To the best of our knowledge, there are no other examples of vibratory recruitment and group maintenance in caterpillars, but there are examples in other holometabolous larvae including sawflies (Hograefe 1984; Fletcher 2007, 2008) and beetles (Greenfield 2002; Cocroft and Hamel 2010). Given the importance of social groups in caterpillars, we recommend that more species be investigated for the role of vibrations in forming and maintaining groups.

19.3.3 *Myrmecophilous Larvae*

One of the most fascinating examples of vibratory communication in caterpillars occurs in myrmecophilic (ant loving) species belonging to the butterfly families Lycaenidae and Riodinidae. Myrmecophilous larvae “break the codes” of their ant host’s communication system to gain access to rich resources, as well as shelter and protection offered by the ant colony. Communication with ants is multimodal, involving chemical, tactile, and vibroacoustic sensory modalities. General reviews on the ecology and evolution of caterpillar–ant interactions include those by Hinton (1951), Fiedler (1991), Pierce et al. (2002), and Casacci et al. (2019). Reviews focusing more specifically on the role of vibratory communication include those by Devries (1991), Travassos and Pierce (2000), Riva et al. (2016), and Schönrogge et al. (2017). Specific, and non-mutually exclusive, examples of caterpillar–ant interactions involve vibroacoustic signals that include the following: (1) attracting ants to be carried into the chamber; (2) begging for food; (3) signaling to strengthen the social status with the colony, and (4) mimicking queen signals. Although

riodinid and lycaenid larvae independently evolved the capacity to produce vibratory signals, vibroacoustic signals in larvae of both families have evolved in the context of establishing or enhancing ant symbioses (DeVries 1991). Here, we briefly summarize vibratory-mediated myrmecophilia in larvae of Riodinidae and Lycaenidae.

In Riodinidae larvae at least 19 species have been reported to produce vibratory calls and all of these species are associated with ants (Devries 1991). Most species that produce vibrations do so using a stridulatory mechanism comprising two structures: vibratory papillae and epicranial granulations (Devries 1990, 1991). The vibratory papillae consist of a pair of rod-like appendages on the prothorax. The papillae strike against the head (on various types of textured surfaces referred to as epicranial granulations) through oscillations of the head. The resulting substrate vibrations appear to communicate with ants as demonstrated by DeVries (1990). Larvae that had their papillae removed lost their ability to call and failed to attract ant attendants. After molting, they regained the structures as well as their ability to call.

In Lycaenidae, at least 30 species of larvae have been reported to produce vibratory calls, and all are associated with ants (Devries 1991), but it is proposed that the ability to produce vibrations may be universal in larvae of this family (Riva et al. 2016). A variety of different vibration signals characterized as pulses, drumming, grunts, and hisses have been noted (Travassos and Pierce 2000; Schönrogge et al. 2017). However, the specific mechanisms of signal generation in Lycaenidae larvae are not well understood. One mechanism of call production in Lycaenidae suggested by Hill (1993) involves a file of teeth on the posterior side of the fifth abdominal segment grating against an opposing stridulatory plate on the posterior side of the sixth segment. In other species, sound production is thought to occur through a forced air mechanism (Schurian and Fiedler 1991). Travassos and Pierce (2000) characterized three types of vibrational signals in the Australian lycaenid, *Jalmenus evagoras*. Grunts, hisses, and drums occurred in different contexts and are proposed to play specific roles in communicating with ants. One of the best studied myrmecophilic larvae are *Maculinea* species that are obligate parasites of *Myrmica* ants. *Maculinea* species mimic vibrations of their hosts to attract ants, exploit nest resources, and elevate their social status by mimicking vibration signals of queens (reviewed in Sala et al. 2014; Casacci et al. 2019).

Vibratory-mediated relationships between caterpillars and ants are highly complex and there is much left to learn. Vibration signals should be recorded and characterized for more species, although such studies are difficult to perform inside ant colonies. The mechanisms of vibration production remain unknown for most of the Lycaenidae species. Another challenge is to disentangle the contributions of multiple modes of communication, including chemical and tactile, from vibratory signals. Finally, like for other holometabolous larvae, there is nothing known about how signals are received by the caterpillars.

19.3.4 *Avoiding Predators and Parasitoids*

Caterpillars are attacked by a wide variety of enemies, including vertebrate predators (e.g., birds, lizards, rodents, frogs) and invertebrate predators and parasitoids (e.g., wasps, flies, mantids, dragonflies) (Jennings et al. 1991; Heinrich 1993; Montllor and Bernays 1993; Greeney et al. 2012) (Fig. 19.2). Sources of vibrations produced by predators or parasitoids that could be used by caterpillars include the following: (1) incidental vibration cues transmitted directly through a plant from the predator to prey, e.g., adult Japanese sawyer beetles (*Monochamus alternatus*) exhibit antipredator behaviors in response to low-frequency vibrations simulating a predator (Takanashi et al. 2016) and adult termites (*Coptotermes acinaciformis*) avoid predatory ants by eavesdropping on their walking vibrations (Oberst et al. 2017); (2) incidental vibration cues transmitted indirectly through the plant from the flight sounds of an approaching vertebrate or invertebrate predator (Caldwell 2014); (3) incidental vibrations transmitted indirectly to the prey from the calling songs of predators such as birds (Caldwell 2014; Yack 2016); and (4) drumming vibration echolocation signals of parasitoids used to locate their hosts (Henaut 1990; Broad and Quicke 2000). All of the abovementioned vibrations could be used by caterpillars to assess predation risk. Currently, however, there are only a few experimental examples showing this. Larvae of the apple leaf miner *Phyllonorycter malella* (Gracillariidae) were shown to detect and respond to vibrations produced by a parasitic wasp *Sympiesis sericeicornis* (Hymenoptera: Eulophidae) (Meyhöfer et al. 1997). During a foraging bout on a mine, *S. sericeicornis* produces characteristic vibrations during the insertion of its ovipositor into the mine. Vibrations are detected by the leaf miner larvae, which stop feeding upon detecting vibrations and resume only after the parasitoid has left the mine (Meyhöfer et al. 1997). Late instar larvae of the masked birch caterpillar (*Drepana arcuata*) detect the low-frequency crawling vibrations of predatory stink bugs (*Podisus sp.*) and are capable of discriminating among vibrations of biotic and abiotic factors, and different types of intruders (Guedes et al. 2012). Larvae of *Semiothisa aemulataria* (Geometridae) responded differently to vibrations produced by various predators and abiotic factors (Castellanos and Barbosa 2006). Larvae responded differentially to different invertebrate predators (stink bugs, wasps) by producing silk escape threads of different lengths, and it was suggested that this could be a result of the differing amplitude of high-frequency components (Castellanos and Barbosa 2006).

Caterpillars have also been reported to generate vibrations in response to enemies. Larvae of the Tupelo leafminer, *Antispila nysaefoliella*, emit vibratory signals when disturbed (Low 2008). Two signals produced by the larvae are referred to as the “tick” and the “rattle.” Ticks are produced by rhythmic back and forth movements of the abdomen that are likened to movements of a clock pendulum. Rattles are produced by shorter, more rapid movements of the abdomen likened to a rattle of a rattlesnake, which vibrate the abdomen rapidly, resembling a tremulatory mechanism. Ticks are described as being slow and rhythmic and rattles are very rapid and occur in bursts that punctuate the ticking. Modified sclerotized structures, referred to

as ridges and bumps, occur on the dorsal surface of the abdomen and are proposed to contribute to generating these vibrations. However, the study did not identify whether these structures impact the leaf surface, or whether vibrations were generated by stridulation or tremulation. These signals are proposed to disrupt foraging in parasitic wasps. Another example of signaling in the presence of a predator was reported in late instars of the masked birch caterpillar, *Drepana arcuata* (Drepanidae). When approached by a stink bug predator (*Podisus sp.*), larvae residing inside silk shelters remain still when first detecting the predator, but when pursued, the caterpillar initiates rapid drumming and scraping signals that appeared to thwart the impending attack (Guedes et al. 2012).

19.3.5 Other Potential Functions

In addition to using vibrations for the abovementioned functions, caterpillars have been reported to distinguish between biologically relevant signals or cues and background vibratory noise caused by abiotic factors such as wind and rain (Castellanos and Barbosa 2006; Guedes et al. 2012). Other proposed functions include using vibrations in coordinating group activities such as taking turns feeding and advertising when a caterpillar is about to move in the shelter (Yack lab, unpublished), and identifying individuals for purposes of leadership or task roles. Other possible functions include coordinated molting, navigation (e.g., echolocation), and synchronizing hatching times in neonates.

19.4 Vibration-Sensitive Sensilla and Sensory Organs

While there are many examples of caterpillars demonstrating behavioral evidence of vibratory sensing, vibration-sensitive sensory organs have not yet been identified in any larval insect to the best of our knowledge. Before speculating on the types and locations of putative receptors in larvae, we provide a brief overview of what is currently known for vibratory sensilla in adults (see also Field and Matheson 1998; Yack 2004, 2016; Lakes-Harlan and Strauss 2014; Strauss et al. 2019). In adult insects, mechanosensitive sensilla associated with vibration detection include scolopidia, sensory hairs (i.e., trichoid sensilla), and campaniform sensilla. These sensilla may function as vibration receptors, individually, or may be grouped into sensory organs. Scolopidia are internal mechanoreceptive sensilla that occur throughout the body of Insecta and Crustacea. Scolopidia can be very sensitive to vibratory stimuli and, depending on their position in the body and association with peripheral structures, have been shown to function as proprioceptors (detecting self-induced movements) or exteroceptors (detecting gravitational forces, air- or water-borne sounds, or solid-borne vibrations) (Field and Matheson 1998; Yack 2004).

Groups of scolopidia are called chordotonal organs. Chordotonal organs identified as being specialized for vibration reception in adult insects include subgenual organs, Johnston's organs, and femoral chordotonal organs. Subgenual organs are the best known vibration receptors in insects and occur in the proximal region of the leg tibia. Johnston's organs occur in the second antennal segment (pedicel) and in some insects function as a vibration receptor when the antennae are placed in direct contact with the substrate. Femoral chordotonal organs occur in the proximal region of the femur and have been shown to detect vibrations in some stick insects and beetles. Trichoid sensilla are long hair-like mechanoreceptors that are widely dispersed over the insect body, and have been proposed or shown to function as vibration receptors in some adult insects, spiders, and scorpions (Keil 1997; Barth 1998; Lakes-Harlan and Strauss 2014). Campaniform sensilla are dome-like structures embedded in the cuticle of insects and respond to stress on the cuticle. There is neurophysiological evidence that they respond to vibrations in the legs of locusts (Kühne 1982), but at present their function as vibration receptors has not been confirmed in any insect. In summary, all vibration-sensitive sensilla confirmed to date in adult insects are either scolopidia or trichoid sensillae, and these can be organized into different vibration sensory organs that vary in their complexity and location on the body. All share a common feature in that they are in direct or indirect contact with the substrate, usually via the legs (Lakes-Harlan and Strauss 2014; Yack 2016). Based on this information, we can speculate on putative vibration receptors in larval insects. A few structures have been proposed based primarily on morphological evidence. These are described below in this section, according to body location.

The antennae have been suggested to detect vibrations in caterpillars based on morphological features and neurophysiological responses (Dethier 1941). The antennae of larval Lepidoptera are located on the ventral surface of the head near the base of the mandibles; each antenna is three-segmented and possesses different mechanoreceptors, including trichoid and campaniform sensilla (Dethier 1941). The antennae from several different lepidopteran species were observed to move in their sockets and respond neurophysiologically when stimulated with a glass probe, and it was proposed that they are capable of detecting both tactile and vibratory stimuli. Therefore, if the antennae are in contact with the substrate during vibratory communication, they might function as vibration receptors.

Structures associated with the thorax and abdomen in caterpillars that have been suggested to function in vibration reception include setae and scolopidia located on the thorax, abdomen, and prolegs. Larvae belonging to the superfamilies Pyraloidea and Gelechioidea possess individual setae, which are connected to internal chordotonal organs via an apodeme, on various locations on the thorax and abdomen (Hasenfuss 1992). The setae and the apodemum are proposed to function as a system of levers transmitting substrate-borne vibrations to the chordotonal organ. Larvae of these two families usually construct tubular silk webs; when the larvae are inside the webs the setae are bent and remain in contact with the threads of silk in the wall (Hasenfuss 1992). The function of the setal-apodemum system has yet to be tested experimentally. Another location to look for vibration receptors in larval insects are

the prolegs, as they are usually in direct contact with the substrate. Cuticular hairs (trichoid sensilla) occur on the prolegs of many caterpillar species (Stehr 1987), but the functions of these setae are not well understood. Prolegs of the masked birch caterpillar, *Drepana arcuata* (Drepanoidea), previously described (See Sect. 19.3.4) to use complex vibratory signals for territorial communication, predator detection, and recruitment, possess setae and scolopidia in their prolegs (Rosi-Denadai 2018; Yack lab, unpublished). One particularly prominent thick and rather stiff seta that is innervated by a bipolar sensory neuron is in direct contact with the leaf substrate. Preliminary neurophysiological recordings from the proleg peripheral nerve indicate that these structures are capable of detecting solid-borne vibrations (Rosi-Denadai 2018; Yack lab, unpublished). Another possible location for vibration receptors is on the abdominal body wall. In larvae of cerambycid beetles groups of scolopidia are oriented in ray-like structures (called pleural discs) in the abdominal region and are thought to play a role in orientation by detecting vibrations (Hess 1917; Saliba 1972). In Saliba's study (1972), beetle larvae were observed to re-orient themselves when exposed to the vibrations produced by conspecifics gnawing on wood. Whether the re-orientation was in response to vibration detection by scolopidia of the pleural discs was not confirmed.

Given the wide range of vibrations that caterpillars and other larval insects are capable of detecting, and the (sometimes) complex behaviors associated with vibratory detection and communication, we expect to see corresponding anatomical and physiological complexity mirrored in their vibratory sensory organs. The next steps toward identifying vibratory receptors in caterpillars and other larval insects should include physical or neuropharmacological ablations of putative receptors, coupled with behavioral testing and neurophysiological recordings.

19.5 Conclusion and Future Directions

While the importance of vibrational communication and sensing is well established in adult insects, we are only beginning to appreciate this sensory modality in juveniles. In this chapter, we narrowed our focus to the vibratory “world” of caterpillars. Larval Lepidoptera are important insects both ecologically and economically. Far from being merely the “feeding stages” of adult moths and butterflies, these larvae exhibit complex behaviors associated with feeding, social interactions, defense, and shelter acquisition. However, little is known about their sensory ecology, and particularly how they use sounds and vibrations for their survival. As substrate-bound organisms, it is likely that plant-borne vibrations play a crucial role in their livelihood. In this chapter we have identified a wide range of contexts whereby caterpillars use vibratory signals and events. The best documented examples are those of vibratory-mediated territorial interactions and mutualistic or parasitic relationships with ants. Vibrations have also been confirmed to function in discriminating between different types of predators and recruiting members to social

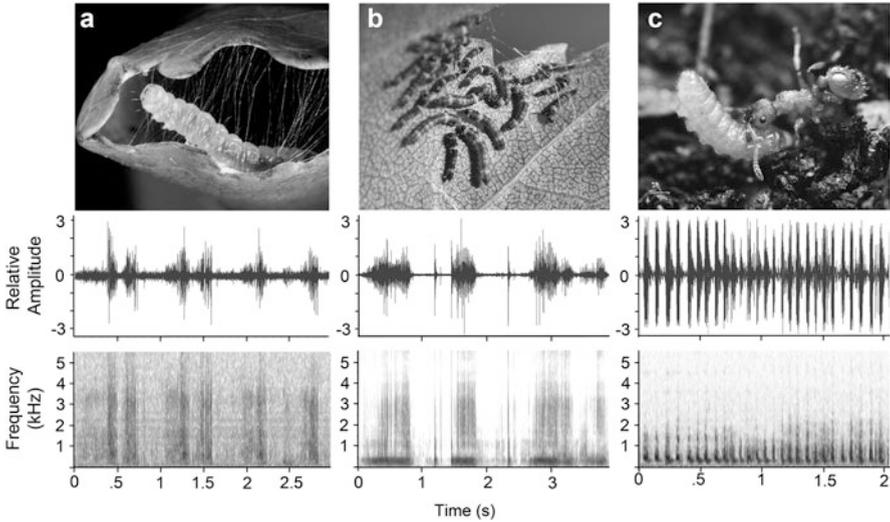


Fig. 19.3 Caterpillars communicate using vibrations in a variety of contexts, as shown in the following examples. **(a)** Territoriality. The cherry leaf roller, *Caloptilia serotinella* (Gracillariidae), defends its leaf shelter by scraping its mandibles on the leaf, plucking, and vibrating (see Fletcher et al. 2006). **(b)** Social recruitment and coordination. Social (early instar) caterpillars of the hook tip moth, *Drepana arcuata* (Drepanidae), generate complex vibrations including mandible scraping, mandible drumming, buzz scraping, and anal scraping on birch leaves to recruit conspecifics to a social group, and possibly to coordinate social activities such as feeding and shelter building within the group (see Yadav et al. 2017). **(c)** Social parasitism. Parasitic larvae of the butterfly *Maculinea alcom* uses vibrations to call to its ant host, *Myrmica scabrinotus*, prior to being adopted into the ant colony (see Sala et al. 2014)

groups, and have been implicated in assessing physical conditions. Despite our increased awareness that caterpillars engage in complex vibratory interactions, we know virtually nothing about how they detect and process vibrations. Also, there is a lack of research on the physical characteristics of their natural vibratory landscapes. Further investigations on the vibratory sensory modalities of caterpillars will no doubt lead to novel insights into the complex vibratory environments of other substrate-bound organisms, and may have practical applications for monitoring and managing pests, and inspiring biomimetic devices.

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