

Chapter 21

Subterranean Arthropod Biotremology: Ecological and Economic Contexts



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Abstract Subterranean arthropods would be ideal candidates for biotremological studies except that soil is a heterogeneous mixture of porous and solid materials with poorly characterized mechanical properties, which makes such studies difficult in situ. However, increased awareness of the impacts of subterranean arthropod herbivory on above-ground biota and the rapid development of modern electronic sensors and computer systems have encouraged efforts to conduct subterranean arthropod biotremological studies in recent years. In addition, impetus to address economic damage caused by subterranean arthropod pests has prompted multiple studies on the intra- and interspecific vibrational communication and incidental movement activities of subterranean pests. Many of these studies have been conducted on subterranean Cicadoidean, Ensiferan, Scarabaeoid, and Curculionid species that are a focus of this chapter. Studies on Lepidoptera, social insects, and Araneae also are discussed here in economic and ecological context, particularly with respect to multimodal communication.

21.1 Introduction

Subterranean arthropods, without opportunity to easily observe their surroundings, must rely on tactile, vibratory, or chemical senses (Funaro et al. 2018) for situational awareness, predator or conspecific detection, and communication. Above- and below-ground arthropods have a long history of eavesdropping on movements of predators or prey (Cocroft and Rodríguez 2005; Virant-Doberlet et al. 2019). However, subterranean arthropods are not often considered ideal candidates for biotremological studies.

Soil, considered one of the most complicated biomaterials on earth (Young and Crawford 2004), is a composite of porous (Sabatier et al. 1990; Lo et al. 2007) and

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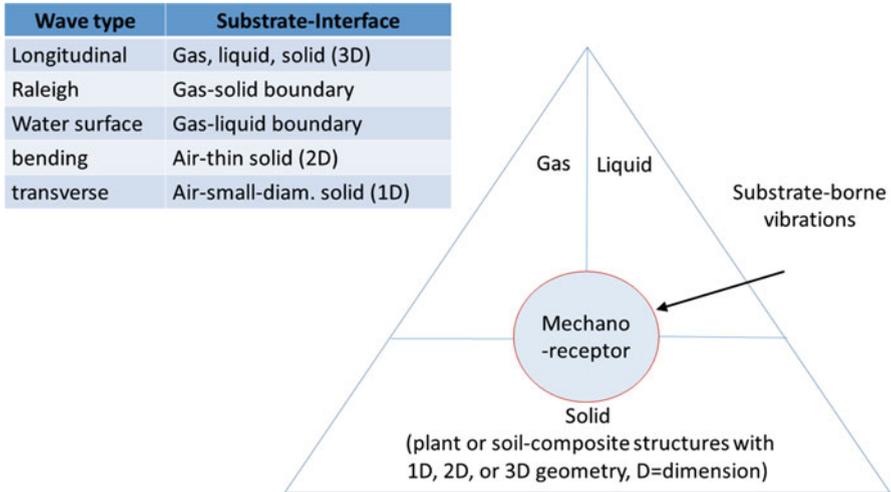


Fig. 21.1 Effects of substrate structure and geometry on the types of substrate-borne vibrational waves to which insect mechanoreceptors are exposed during biotremological communication. See Mortimer (2017) for a review of wave speeds, distortion, and attenuation of different wave types

solid (TenCate and Remillieux 2019) materials, which complicates attempts to specify the structural and mechanical characteristics that govern signal transmission within and between the different composites (Fig. 21.1). Each type of wave in Fig. 21.1 has different wave speeds and different patterns of damping at different vibration frequencies, all of which are affected by the geometry of the structure through which the waves are passing (Michelsen 2014; Mortimer 2017; TenCate and Remillieux 2019). In addition, it is difficult to precisely measure important abiotic factors such as gas exchange and temperature that affect insect behavior and survival in soil (Villani and Wright 1990; Hagedorn et al. 2019), partly because soil macrofauna actively create channels, pores, and aggregates, and transform soil nutrients in ways that directly modify the chemical, structural, and acoustic characteristics of the soil in which they live (Brussaard et al. 1997; Veen et al. 2019). Consequently, current technologies are barely in the initial stages of developing more than a fleeting awareness of the diverse environments sustaining the subterranean biota (Mammola et al. 2019). The difficulty of precisely investigating subterranean biotremology has restricted the capability and opportunity to conduct such studies. The first subterranean insect was not even reported until 1831 (Polak 2005). The arthropod biodiversity of underground environments remains largely unexplored (Ficetola et al. 2018; Rillig et al. 2019).

For these reasons, when investigations are conducted on *Scaptocoris* burrower bugs (Čokl et al. 2006a) or *Melolontha* beetle larvae (Görres and Chesmore 2019), they typically must deal with heterogeneous substrate–mechanosensor interfaces (Akent'eva 2012; Eilers et al. 2012) that are less understood than, e.g., the interface between a stink bug subgenital organ and a plant stem (Čokl et al. 2006b; Prešern

et al. 2018). Investigators must deal with information transfer processes (Michelsen 2014; Hill and Wessel 2016; Mortimer 2017) that are less well defined than processes characterized above ground, such as the transmission of information between duetting *Homalodisca vitripennis* (Germar) (Hemiptera: Cicadellidae) in grapevines (Gordon et al. 2019).

Nevertheless, there are fundamentally important reasons to study communication and the incidental movement and feeding vibrations of arthropods in soil, given the ecological importance of subterranean herbivory (Hunter 2001; Lavelle et al. 2006; van Dam 2009; Adhikari and Hartemink 2016; Veen et al. 2019) and the evolutionary processes (Camacho et al. 1992) leading to a high diversity of known subterranean arthropod lineages (Mammola et al. 2019). Subterranean arthropods interact with the environment over a much smaller spatial scale than above-ground arthropods (Veen et al. 2019), and subterranean species sometimes are restricted to small areas such as isolated mountain valleys (van Tol et al. 2004). Population growth often is small because energy-limited and stable environments have selected for long-lived species with low metabolism and fecundity (Mammola et al. 2019). Consequently, needs for conservation efforts to protect endemic subterranean arthropods are reported often (Harvey et al. 2011), especially in view of recently reported trends of reduced biomass of flying insects in protected areas (Hallmann et al. 2017). There also are highly practical reasons to address economic damage caused by root-feeding pests (Jackson et al. 2000; Keller and Zimmermann 2006; Johnson and Murray 2008) and invasive species that directly cause damage or vector plant diseases (Fei et al. 2019).

Several examples of insect vibrational signals and eavesdropping cues in soil are considered in ecological and agro-economic contexts in this chapter. As in above-ground arthropods, stridulation (Görres and Chesmore 2019), scraping, drumming, and tapping (Hayashi et al. 2018), tremulation (Ohmura et al. 2009), and other vibratory behaviors (Funaro et al. 2018) are known to be widely employed for communication by subterranean arthropods.

21.2 Cicadoidean and Ensiferan Communication and Eavesdropping Cues

Considerable knowledge about above-ground biotremological processes has been obtained from studies in the Cicadoidea and Ensifera, where tymbals (Wessel et al. 2014) and the first stridulatory organs (Senter 2008; Strauß and Stumpner 2015) likely evolved. Tymbals are exoskeletal organs with resonant cavities and plate structures that buckle and vibrate when pulled by muscles (Wessel et al. 2014). Stridulatory organs consist of a plectrum (with a sharp large ridge) and a pars stridens (with finer parallel ribs) that move past each other while in direct contact (Senter 2008). The stridulations frequently occur as pairs when the plectrum

protracts over the pars stridens, pauses, and then retracts to its original position (Mankin et al. 2009a; Görres and Chesmore 2019).

Ensiferan species are useful models for studying vibrations but more commonly are used for studies of airborne sound communication (Prešern et al. 2018). There has long been awareness of the mating calls of crickets, mole crickets, and katydids (bush crickets), several species of which produce signals with both vibrational and acoustic components (Morris et al. 1994; Gogala et al. 1996). Cicadas produce both vibrational and acoustic components during their communications, as well (Stölting et al. 2002). Bennet-Clark's (1970) investigation of the mechanism of mole cricket sound production commented that males of several mole cricket spp. had been known for centuries to produce loud mating calls that attracted females to their burrows (Howard et al. 2011; Pollack 2017). Thus, it is not surprising that two South American, *Neoscapteriscus* (Orthoptera: Gryllotalpidae) mole cricket species with loud mating calls, inadvertently introduced to Florida in the late 1800s, were among the first insects to be targeted with acoustic trapping technology after their damage to the root systems of turfgrass began causing noticeable economic damage (Ulagaraj and Walker 1973, 1975; Walker 1988). In this case, the hornlike burrows themselves were not duplicated, but loud synthetic or recorded mating call stridulations were broadcast to attract females to a swimming pool trap (Walker 1982).

Bennet-Clark (1970) reported also that some mole cricket species were very sensitive to ground vibrations; however, Hill and Shadley (1997) were first to suggest a bimodal communication mechanism in mole crickets where the airborne component of stridulation was a sexual advertisement call directed toward flying females, and the substrate-borne component influenced spacing of male burrows. Later, Hill and Shadley (2001) and Hill (2009) reported that *Gryllotalpa major* Saussure mole cricket males responded to calls played back alone through a vibration exciter without the accompanying acoustic signal. This suggests that some species of mole cricket can communicate through both acoustic and vibrational signals, as is frequently observed also in hemipterans, e.g., Schilman et al. (2001). Acoustic trapping of *Neoscapteriscus* remains an effective monitoring tool (Dillman et al. 2014; Rohde et al. 2019) but the potential for mole cricket management (Mankin and Lapointe 2003) using vibrations has not yet been investigated extensively.

21.3 Scarabaeoid Stridulatory Communication and Eavesdropping Cues

Stridulation has been reported from adults, larvae, and pupae of numerous species of soil-dwelling Scarabaeoids (Wessel 2006; Kojima et al. 2012; Barbero et al. 2012), including economically important dynastids (Bedford 1980), the near-threatened *Lucanus cervus* (L.) (Coleoptera: Lucanidae) (Harvey et al. 2011), and white grubs (Merchant et al. 2004; Wagenhoff et al. 2014) several species of which live

in grassland systems where more than 70% of the invertebrate biomass is estimated to occur below ground (Seastedt and Murray 2007). Pupal vibrations are produced by rotating the abdomen and beating the pronotum against the pupal cell wall (Kojima et al. 2012). In many cases, the vibrations are powerful enough to produce audible signals (Takanashi et al. 2019) and are examples of multimodal signaling similar to those observed with mole crickets (see Sect. 21.2). In adults, stridulations often are associated with defensive (Palestrini et al. 1990) or mating behavior (Harvey et al. 2011), and in larvae and pupae, stridulations, and other vibrational cues usually are associated with defensive behaviors (Kojima et al. 2012) or avoidance of predators (Hill 2009) or cannibalism (Kočárek 2009), which occurs in *Melolontha* (Görres and Chesmore 2019). Alexander et al. (1963) described general aspects of evolutionary differentiation of stridulatory signals in Coleoptera.

It has been proposed that stridulations characterized in particular species can be monitored in field environments to acoustically identify the species presence for conservation or pest management purposes (Mankin et al. 2009a; Harvey et al. 2011; Görres and Chesmore 2019). In the absence of a stridulatory organ, subterranean insect larvae may also produce relatively stereotyped abdominal, proleg, and mandibular movements (Villani et al. 1999), which produce vibrational pulse trains (bursts) (Mankin et al. 2009b) that are useful as a means of distinguishing vibrations produced by hidden insects from background noise (Mankin et al. 2011; Jalinas et al. 2019). The types of vibrations produced depend on the friction of the interface between the insect and substrate surface. Interfaces with two dry surfaces, such as an insect integument sliding over dry soil with small asperities produce short, broadband vibration pulses similar to those produced by human footsteps on a dry surface (Ekimov and Sabatier 2006). Slip-stick friction between two wet surfaces, like wet skin on glass or brakes on a wet road (Patitsas 2010), can produce squeal vibrations with loud harmonics. Knowledge of these interfacial interactions has been used previously to help identify the species of insect that had produced the vibrations (Jalinas et al. 2019).

Other examples where the signal characteristics of incidental movements of scarabaeoids have been used to distinguish vibrations of underground larvae or adults from background noise include Mankin et al. (2000, 2007, 2009a, b), Brandhorst-Hubbard et al. (2001), Zhang et al. (2003a, b), Johnson et al. (2007), and Mankin and Moore (2010). Various instruments, including microphones, accelerometers, geophones, and piezoelectric probes, have been employed for detection (Mankin et al. 2008, 2011), as well as laser vibrometers (Zorović and Čokl 2015). A recently developed vibroacoustic device for detection of insects in trees (Potamitis et al. 2019) also provides an inexpensive method to detect subterranean arthropod vibrations, and it can be expected that even more sensitive, less expensive instrumentation will be commercialized during the next decade (e.g., Bayrakdar 2019; Rillig et al. 2019). Improved signal processing analyses have enabled better discrimination of insect-produced vibrations from background noise and nontarget arthropods (Ganchev et al. 2007; Mankin et al. 2011, 2018; Lampson et al. 2013; Korinšek et al. 2016; Hetzroni et al. 2016; Rathore et al. 2019) but there is considerable opportunity for improvements in instruments and computer analyses

that automate the detection and analysis of arthropod vibrations and distinguish them from background noise. In many crops, because subterranean insect pests often occur in aggregations (Mankin et al. 2007; Inyang et al. 2019), timely use of such instrumentation can enable effective detection and targeting of infestations before above-ground damage is detected.

21.4 Curculionid and Silphid Stridulatory Communication and Eavesdropping Cues

Stridulatory organs and stridulatory behavior have been reported in adults of numerous curculionids (e.g., Mampe and Neunzig 1966; Gibson 1967; Wilson et al. 1993; Rudinsky 2009; Pureswaran et al. 2016) and silphid species (Hall et al. 2013). Curculionid stridulations may be produced by either or both sexes, depending on the species, and can be involved in mating or defense (Webb et al. 1980). Many curculionids that exhibit stridulatory behaviors are important both ecologically and economically, particularly in forests (Marini et al. 2017), and some spend part of their life cycle in the soil, including *Conotrachelus nenuphar* (Herbst), which pupates underground, mates on the ground underneath host trees, and hibernates under the orchard litter (Lafleur et al. 1987). Soil-dwelling curculionids that do not stridulate can be detected by their incidental movement and feeding sounds, including *Otiorhynchus sulcatus* (Fabricius) (Coleoptera: Curculionidae), which has been the subject of tests to detect larvae in container crops (Mankin and Fisher 2002, 2007). *Otiorhynchus sulcatus* has a broad host range and reproduces by parthenogenesis (van Tol et al. 2004); consequently, a single, unmated female can rapidly infest a variety of different plants in a nursery and the larvae can cause unseen damage to the root systems. Another economically important curculionid that has not been reported to stridulate is *Diaprepes abbreviatus* (L.). Acoustic methods have been developed to detect *D. abbreviatus* larvae feeding in roots of citrus trees and distinguish their movement and feeding activity from background noise (Mankin et al. 2001; Mankin and Lapointe 2003).

As in the Ensifera (see Sect. 21.2), the communication signals of Nicrophorine burying beetles in the Silphidae have been documented for centuries (Landois 1869; Darwin 1871). Mating stridulations of the eight North American Nicrophorine species have been characterized (Hall et al. 2013) and were found to have differences that could be used over short distances to discriminate among species, but likely are involved also in competition for resources. The genus *Nicrophorus* is unusual in that both males and females take care of the brood (Smiseth and Parker 2008).

21.5 Vibrational Communication and Eavesdropping Cues in Other Arthropod Orders

Lepidopteran adults, larvae, and pupae (Chapman 1998), some of which spend a portion of their life cycles underground, have been reported to stridulate in different contexts. Stridulations of myrmecophilous butterfly larvae (Barbero et al. 2009, 2012; Casacci et al. 2019) in *Myrmica* ant nests mimic host ant stridulations (Spangler 1967) and their cuticular hydrocarbons also mimic those of their hosts, an example of multimodal mimicry. Similar mimicry has been reported by the myrmecophilous butterfly, *Spindasis lohita* (Fruhstorfer) (Lepidoptera: Lycaenidae) in *Crematogaster rogenhoferi* Mayr (Hymenoptera: Formicidae) nests (Lin et al. 2019).

The function of ant stridulations is not well understood in general (see Golden and Hill 2016), but stridulations often are produced by ants under stress and attract workers into aggregations that can provide assistance or produce nest-wide activity (Rauth and Vinson 2006; Chiu et al. 2011; Barbero et al. 2012). Ant stridulations and termite headbanging (Howse 1965; Evans et al. 2005; Inta et al. 2009; Hager and Kirchner 2013) may play somewhat similar functional roles, and they both have been observed together, e.g., when a colony of subterranean termites, *Drepanotermes* sp., was attacked by *Camponotus denticulatus* Kirby ants (Mankin and Benshemesh 2006). Termites have been shown to assess incidental vibrations produced in wood to estimate the size of a termite colony and they use resonant frequencies to assess the volume of food to which they have access (Evans et al. 2005).

Ultrasound receptor organs have evolved in many lepidopteran species in response to predation by insectivorous bats (Connor 1999) and, given the opportunity of a new communication channel, several species have employed ultrasonic signals for courtship (Spangler et al. 1984). However, because ultrasound attenuates more rapidly in soil than in air (Mankin et al. 2011), ultrasonic communication in soil is possible usually only over distances of a few centimeters; although, ultrasonic vibrations produced by termites in wood can be detected up to 2.2 m (Scheffrahn et al. 1993). Non-ultrasonic, 2000–10,000 Hz, vibrations produced by individual *Vitacea polistiformis* Harris (Lepidoptera: Sesiidae) larvae feeding on grapevine roots (Sanders et al. 2011; Inyang et al. 2019) can be detected with vibration sensors in soil over distances of about 20 cm, similar to detection distances observed in sand (Devetak 2014). Large colonies of *Coptotermes formosanus* Shiraki (Isoptera: Rhinotermitidae) in soil underneath trees can be detected with non-ultrasonic sensors over distances of 50 cm or more (Mankin et al. 2002), and can be detected over several meter distances within large hardwood trees (Osbrink and Cornelius 2013). Also, colonies of termites can extend the communication distance of headbanging in soil by responding to detected headbanging with their own signals, serving as relays to extend an alarm several meters across a large-sized colony (Hager and Kirchner 2013). Active spaces of vibrational signals, i.e., their effective detection ranges

(Mazzoni et al. 2014), are discussed by Virant-Doberlet et al. (2019) for a variety of different above-ground insects.

Subterranean arthropods are known to use vibrational cues to catch prey, including several species of antlion larva (Neuroptera: Myrmeleontidae), who wait for ants and other prey in the sand at the bottom of a funnel-shaped pit (Devetak 2014; Podlesnik et al. 2019) and grasp what falls in, or toss sand at the prey to cause a landslide that brings it within grasping distance. Araneae, some of which spin webs and identify prey by their vibrations (Parry 1965), or become prey when they seek out a predatory reduviid (Wignall and Taylor 2011), are studied above ground primarily, but many also live below ground (Läska et al. 2011; Abrams et al. 2019) and, along with Collembola, Diptera, and Oniscidea, are among the most numerous taxa reported in soil (Läska et al. 2011; Inyang et al. 2019). Many underground spiders stridulate during courtship (Quirici and Costa 2005) or tremulate (Carballo et al. 2017), in addition to using vibrations for prey capture.

21.6 Biotremology in Multimodal Communication

The examples (see Sects. 21.2–21.5) of vibrational communication by subterranean arthropods that also involved acoustic (mole crickets: Hill and Shadley 1997, 2001, Hill 2009; Hemiptera and Coleoptera: Takanashi et al. 2019) or chemosensory communication (butterfly larvae: Barbero et al. 2012; Casacci et al. 2019) are from several of numerous reports where multimodal communication has been identified in arthropods. Various driving forces have been proposed to explain the evolution of multimodal insect communication, including variation in localization and ranging of signal sources, “multiple message” redundancy that serves as a backup signal (Halfwerk et al. 2019), and context-dependent shifts in signal structure when one of the communication modes becomes dangerous, costly, or ineffective (Higham and Hebets 2013; Caldwell 2014). One commonality between acoustic and vibratory modes of communication is that the vibration sensors used for detection of airborne sound have evolved similarly to those used for detection of vibrations (Strauß and Stumpner 2015). It is thus not a surprise that pseudophylline katydids in neotropical rain forests have been reported to combine ultrasonic signalling in calling songs with vibrational tremulation signals, possibly to avoid bats; although, spider predation increases as a result (Morris et al. 1994). Multimodal use of pheromone and acoustic cues in pine beetles (Pureswaran et al. 2016) may be involved in species isolation between *Dendroctonus brevicomis* LeConte and *D. frontalis* Zimmerman. The extent to which multimodal signals provide additional range, redundancy, species isolation, or safety to subterranean insects has not been investigated widely, but spiders that detect insect movement and stridulation vibrations are commonly found near where subterranean insects are present (Sanders et al. 2011; Inyang et al. 2019). More often, such studies are conducted with above-ground insects. Rajamaran et al. (2018), for example, reported that female *Onomarchus uninotatus* (Serville) katydids tremulate when calling males are less than 4 m away, but perform phonotaxis

when males are further than 9 m. Gordon and Uetz (2011) reported that male *Schizocosa ocreata* (Hentz) wolf spiders, which use visual and seismic signals in courtship, could use either or both modalities depending on environmental conditions.

One of the environmental conditions of interest is temperature. The effects of temperature on acoustic/vibrational/visual multimodal signals have been a topic of interest in studies of ectotherm behavior. It has been reported that temperature changes affect the timing of mating in arthropods that employ multimodal signalling (Brandt et al. 2018) but have little effect on species recognition (Greenfield and Medlock 2007).

The role of learning in vibrational and multimodal communication is largely neglected in subterranean arthropod biotremology; although, it is becoming an area of considerable research interest in studies of above-ground arthropod courtship. Several different insects and spiders have been reported to learn from acoustic, vibratory, or multimodal signals in different contexts (Dion et al. 2019). De Simone et al. (2019) reported that male *Allocosa senex* (Mello-Leitão) (Araneae: Lycosidae) wolf spiders that use multimodal chemical and vibratory communication enlarged their burrows after rejection by females. Also, burrows were shorter when constructed in fine sand, where digging is more difficult than in coarse sand, which suggests they may have learned to adapt their digging behavior to maximize reproductive success while minimizing digging effort.

21.7 Conclusions

This chapter considers twenty-first-century biotremological and related research on subterranean arthropods in relation to above-ground arthropods in ecological and economic contexts. As has been found above ground, stridulatory, scraping, drumming, tapping, and tremulation behaviors are frequently employed for courtship and defense. Vibrational eavesdropping on conspecifics, predators, and prey is widely used to enhance survival. In spider burrows, ant colonies, and termite colonies, vibrational and chemical senses frequently serve as a replacement for vision, even though the high attenuation of vibrations in soil reduces the range of detection to a few decimeters. Vibration detection methods have been developed over the last 30 years that enable the sounds of subterranean pests to be detected and discriminated from background noise, and further improvements are expected.

Present-day vibration detection instrumentation has been applied with economic benefits for early detection of crop damage by subterranean insect pests that are rarely detected in time for effective control measures using above-ground surveillance. In addition, acoustic targeting of subterranean pest aggregations enables reduction of pesticide usage in crops and forages. There is increasing concern about subterranean larvae that can injure plant root systems and predispose them to infection, as has occurred with the curculionid, *D. abbreviatus*, predisposing citrus to damage from *Phytophthora* spp. (Graham et al. 2003). Other plant diseases

such as *Fusarium* wilt tropical race 4 may soon devastate the South American banana industry (Galvis 2019). It is not yet well investigated whether *Fusarium* wilt or Port Oxford Cedar root disease in North America (Fei et al. 2019) is significantly exacerbated by subterranean insects.

There also is room for expanded usage of vibration detection instrumentation in conservation research, especially because many subterranean arthropod species have limited geographic ranges. Recent alarming decreases of flying insects in protected areas (Hallmann et al. 2017) suggest that subterranean arthropod biodiversity may be in decline as well, but confirmatory studies remain to be conducted (Mammola et al. 2019). Finally, there are some areas such as the role of learning and the role of multimodal communication in subterranean arthropod courtship that has been severely neglected but beg for further consideration. Biotremological research on subterranean arthropods is likely to expand in the future as its ecological and economic relevance become more prominent and the sustainability of agriculture and forestry are threatened by increased rates of expansion of human populations and concomitant reductions in the quality and availability of water and other resources.

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