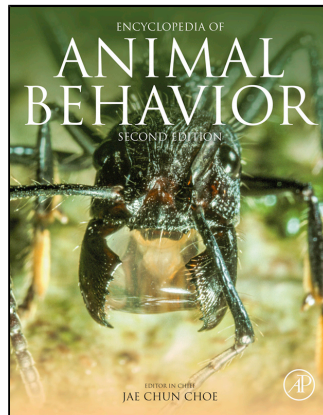


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Vibrational Signals: Sounds Transmitted Through Solids

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Glossary

Compressional wave Wave in which the particle motion is parallel to the direction of propagation. Compressional waves include body waves, also called P waves, that propagate in 3-D solids.

Cue Modification of the environment produced incidentally by an animal's behavior.

Extended phenotype External production of an organism, resulting from a specific behavior, such as a spider web or honey combs.

Frequency Number of cycles per unit of time in a signal. It is typically measured in Hz. High frequency sounds correspond to high pitched sounds; conversely, low frequency sounds are low pitched.

Shear wave Wave for which the particle motion is perpendicular to the direction of propagation. Shear waves include Rayleigh waves (in 2-D substrates), bending waves (1-D substrates), and transverse waves (1-D substrates).

Signal Modification of the environment produced by an animal's specialized behavior; i.e., behavior that has evolved under selection relating to the effect that the signal has on the behavior of receivers.

Wave Mechanical disturbance of a medium.

Abstract

Sound – A mechanical disturbance of a medium perceived by an organism – encompasses a bewildering variety of forms of communication and sensation. One of the more exotic, for the human worldview, is sound transmitted through solid substrates on which organisms stand, such as the ground or the stems and leaves of plants. Perception of substrate-borne sounds is widespread among animals, and many groups have evolved to use them in a huge variety of contexts and functions. Research on this modality of sensation and communication is revealing surprising capabilities for signal processing and cognition in animals large and small, social and solitary.

Keywords

Biotremology; Communication; Seismic signal; Sensory drive; Signal propagation; Signaling; Substrate-borne signal; Vibrational; Vibratory; Wave

Introduction

Watch an aggregation of insects on a plant for any amount of time and you will likely think that not much behavior is going on (Fig. 1). They do not seem to move a whole lot, and there are no sounds to be heard. At most there might be some chemical signaling and some feeding. These impressions would also seem to agree with the apparent simplicity of their lifestyle, their home and food right underfoot. And if they are spiny or camouflaged, their defensive strategy would also seem to rely on staying put and doing nothing. These impressions are often wrong.

Those insects are likely to be interacting in a modality of sound that is alien to us, using substrate-borne vibrations to communicate. These vibrations are a form of sound, because they constitute a mechanical disturbance of a medium (Greenfield, 2002). However, they are sounds that are transmitted through solids, rather than through a fluid such as air or water.

The medium of transmission is not the only surprising thing about substrate-borne vibrational signals. Insect vibrational signals, for instance, often present dramatic contrasts with the insect airborne sounds that are familiar to us. On a typical summer day almost anywhere near nature you may hear the comforting songs of cicadas in the distance – repetitive in structure, broad in frequency content and favoring the high frequency range. By contrast, close relatives of cicadas, such as treehoppers, produce substrate-borne signals with remarkably low and pure tones that sweep in frequency and have complex temporal patterns (Fig. 2). The world of substrate-borne sound includes simple repetitive signals, but its high end of complexity rivals the elaborate songs of birds and whales.

The diversity of substrate-borne signals in animals covers many dimensions. They are taxonomically widespread; they are used in a broad range of behavioral contexts and for multifarious functions within and between species; and they are transmitted through varied kinds of substrate as varied types of wave. Research on substrate-borne signals – a component of the growing field of biotremology (Endler, 2014; Hill and Wessel, 2016) – promotes a confluence of technological innovation, experimental creativity, and natural history exploration that offers great opportunities for discovery.



Fig. 1 Aggregation of *Antiante expansa* treehoppers (Hemiptera: Membracidae) on one of their host plants, *Acnistus arborescens* (Solanaceae). These insects communicate with plant-borne vibrational signals both as nymphs and as adults. Photo courtesy of Gerlinde Höbel.

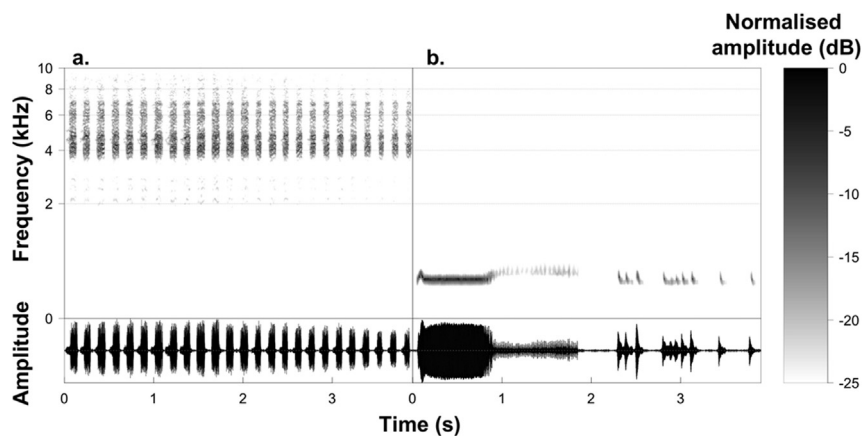


Fig. 2 Comparison of the airborne and substrate-borne signals of two insects. (a) Airborne signal of a male *Cicada orni* cicada (Hemiptera: Cicadidae) (recording courtesy of Sonotheque of the Museum national d'Histoire naturelle, <https://sonotheque.mnhn.fr/>). (b) Substrate-borne vibrational signal of a male *Enchenopa* sp. treehopper (Hemiptera: Membracidae) (recording courtesy of R. Cocroft). We show signal waveforms (bottom traces) and spectrograms (top traces). Note the much greater complexity in the frequency structure of the substrate-borne signal, and the longer span of the basic signal “unit” (in four seconds there are 26 units in the cicada signal, but only 1 on the treehopper signal).

Substrates and Waves

Animals send vibrational signals through a huge variety of substrates. Some of the best studied cases feature plant-feeding insects that communicate with plant-borne vibrational signals (Cocroft and Rodríguez, 2005). Plants are complex environments from the view point of transmission of vibrational signals. For instance, the signal frequencies that are transmitted with the least attenuation vary among plant parts (e.g., stems versus leaves) and plant species (McNett and Cocroft, 2008). Consequently, the signals of some animals may be adapted for transmission along specific substrates when most of the signaling happens on particular parts of particular plant species at particular times (McNett and Cocroft 2008), whereas the signals of others may be adapted for transmission in a variety of substrates if the individuals of the species signal on a range of sites and conditions. The noise induced by wind and rain is a major feature of a plant's "soundscape". Wind moves plant parts and strikes them against each other making a huge racket, as do the strikes of rain drops, and animals seem to deal with these noises by ceasing to signal when they reach high levels or congregating at sites where their impact is lower (Cocroft and Rodríguez, 2005; McNett *et al.*, 2010; Tishechkin, 2013; Virant-Doberlet *et al.*, 2014). Additional sources of selection on plant-borne communication systems may come from airborne sounds that are picked by plant tissues – the variety of such sounds and the fidelity with which they are imparted onto plants is remarkable (Cocroft and Rodríguez, 2005; Eriksson *et al.*, 2011; Rebar *et al.*, 2012). To a more limited extent, this is also true for sounds carried through the soil and picked up by plants (Čokl *et al.*, 2006). For animals using plant-borne communication, those sounds may represent noise, but also opportunities for detecting dangers approaching the plant from the air. For example, the flight noise of an approaching predatory wasp is perceptible to an aggregation of insects through plant tissues.

Other animals communicate with substrate-borne signals on soil, rocks, sand, or leaf litter, as well as on animal-constructed extended phenotypes, such as honeybee combs and spider webs (Hill, 2008). Some species specialize on only one or a few kinds of substrates. For example, a web spider that courts with web vibrations will only ever signal on the highly-predictable and stereotyped substrate constituted by the web of its potential mate. Other species have occasion to use multiple substrates. Males of some spiders, for example, signal on different types of substrate (e.g., rocks, sand, and leaf litter for *Habronattus dossenus* jumping spiders, or leaf litter, pine litter, and clay for *Schizocosa retrorsa* wolf spiders), performing the same courtship behaviors across substrates; however, the signal-transmission properties of the substrates vary considerably, and courtship success varies across them (Elias *et al.*, 2004; Hebets *et al.*, 2008). This suggests that even such "generalists" may be selected to specialize on a subset of the substrates available; alternatively, they may be selected to use signals that perform well across substrates, which may involve the incorporation of signal components in other modalities (e.g., visual) (Elias and Mason, 2014). Environmental sources of noise such as wind and rain are also important features of all of these soundscapes – not only as sources of selection on communication, but also as potential masks for approaching predators, which may evolve to exploit such opportunities (Wignall *et al.*, 2011) or even mimic the noises (Tarsitano *et al.*, 2000). Some of these substrates (e.g., leaf litter) also pick up airborne sounds that influence vibrational communication; e.g., by delaying the onset of courtship (Gordon and Uetz, 2012).

The variety of substrates on which vibrational signals are transmitted is matched by the variety of wave types that constitute the signals (Greenfield, 2002; Hill, 2008; Mortimer, 2017). Roughly speaking, animals that produce vibrational signals from inside the substrate (say, from below the soil) produce "body waves" (also termed "compressional waves" or "P waves") that propagate spherically from the source. Animals that signal on a surface (e.g., a fiddler crab on wet sand) produce Rayleigh waves that propagate radially on a two-dimensional plane from the source. And animals on plate-like or rod-like structures such as plant leaves and stems produce bending waves that propagate longitudinally away from the source.

The geometry and heterogeneous composition of the substrates, and the different wave types involved, constitute different selective environments for signaling. For example, for signals that propagate in two or three dimensions (e.g., Rayleigh waves and P waves), signal energy content decreases in proportion with the distance from the source, whereas such decrease is weaker or absent for bending waves (Mortimer, 2017). On the other hand, bending waves exhibit "dispersion", whereby different frequencies propagate at different speeds along the substrate (higher frequencies propagate faster), whereas other wave types do not show dispersion or do so only in particular conditions and types of substrate (Mortimer, 2017). Additionally, in many substrates, signalers produce – and receivers need to process – multiple wave types (Casas *et al.*, 2007; Elias and Mason, 2014; Mortimer, 2017).

Regardless of the types of substrate and wave involved, there are some common functions and challenges to vibrational communication. For instance, most if not all cases entail localizing specific individuals and distinguishing friend from foe, or preferred from disliked individuals (and all those from noise). Given the complexity of the environments and the wave forms involved, it is astonishing that animals would be able to accomplish this, and yet accomplish it they do (Virant-Doberlet *et al.*, 2006; Guedes *et al.*, 2012). How they manage is a flourishing area of research (Gibson and Cocroft, 2018) with the potential to bring great insight into the field of auditory scene analysis (Miller and Bee, 2011; Bee and Miller, 2016). In the vibrational realm, this field is in its early days, in part because of the recency of the rise to attention of this modality (Ossiannilsson, 1949; Michelsen *et al.*, 1982; Henry, 1994; Čokl and Virant-Doberlet, 2003; Virant-Doberlet and Čokl, 2004; Cocroft and Rodríguez, 2005; Hill, 2008); and because some key questions in vibrational communication present substantial methodological challenges (McNett *et al.*, 2006; Cocroft *et al.*, 2014; Elias and Mason, 2014; Gibson and Cocroft, 2018).

The Features of Substrate-Borne Signals

Above we referred to the sound of cicadas as agreeable from a distance, but up close they are ear-splittingly loud. High energy content is a major feature of animal airborne sounds. It is quite common for airborne acoustic signals to have sound pressure levels of 80–100 dB SPL (for reference, quiet conversation occurs at 70 dB SPL, and note that this is a logarithmic scale). This reflects selection on signals to reach a wide range of receivers, and presents the challenge to small animals (such as insects) of maximizing the energy they radiate onto a large volume of air (Bennet-Clark, 1998; Gerhardt and Huber, 2002). There are exceptions, with some airborne signals having remarkably low amplitudes, as the advertisement signals of whispering moths (Nakano *et al.*, 2009), or some forms of aggressive song in birds (Searcy *et al.*, 2014). But airborne signals are largely selected to have high amplitude and radiate broadly.

By contrast, substrate-borne signals are often very low in energy, commonly involving minute movements of the surface of plant stems that propagate at low speeds (Cocroft and Rodríguez, 2005). This observation is often juxtaposed with another: the space occupied by potential receivers of substrate-borne signals is frequently small, restricted for example to the insects on a bush (Cocroft and Rodríguez, 2005). There are of course exceptions, as with the exceptional reach of potential vibrational signals in elephants (O'Connell-Rodwell *et al.*, 2000, 2001), but such cases seem to be rare. A third common feature is that substrate-borne signals often exhibit remarkable complexity, as noted above (Fig. 2). This is all the more striking when it involves small animals with small brains, as it often does.

Are these juxtapositions a coincidence? Or is there something about the relative lack of selection for large-volume radiation that frees animals to realize the behavioral complexity of which they are capable? Imagine that the repetitiveness of airborne insect signals, for instance, is designed to optimize transmission and detection in large noisy spaces (Guilford and Dawkins, 1991) rather than reflect constraints on cognitive abilities and behavioral complexity. This is not to ignore the high levels of noise in the substrate channel (see above). But perhaps there may be different dynamics, given common communication distances and noise patterns (Cocroft and Rodríguez, 2005), that explain the differences in energy levels and complexity.

Another potential connection with the complexity of substrate-borne signals may lie in their often having low, near-pure tone frequency composition (Cocroft and Rodríguez, 2005) (see for example Fig. 3). This is associated with a considerable lowering of the intercept of the relationship between body size and signal frequency that occurs in the substrate-borne channel, possibly from the lack of necessity to radiate sounds broadly (Cocroft and Rodríguez, 2005; Cocroft and De Luca, 2006; Lubanga *et al.*, 2016). The explanation is probably more complex, but the basic observation is that many animals that signal with substrate vibrations have very fine control of signal frequency and are able to generate high structure complexity.

The Taxonomic Distribution of Substrate-Borne Signals

Substrate-borne signals are widespread in animals. They are probably ancestral to many groups within insects and spiders, if not to each of those classes (Čokl and Virant-Doberlet, 2003; Virant-Doberlet and Čokl, 2004; Cocroft and Rodríguez, 2005; Drosopoulos and Claridge, 2006; Hill, 2008). Other invertebrate groups have been less well sampled, but there are documented cases of substrate-borne vibrational signals in fiddler crabs (Hill, 2008) and scorpions (Briceño and Bonilla, 2009), and there are potential cases in annelids and chaetognaths (Hill, 2008). In vertebrates, too, there are varied examples: mole rats, kangaroo rats, elephants,

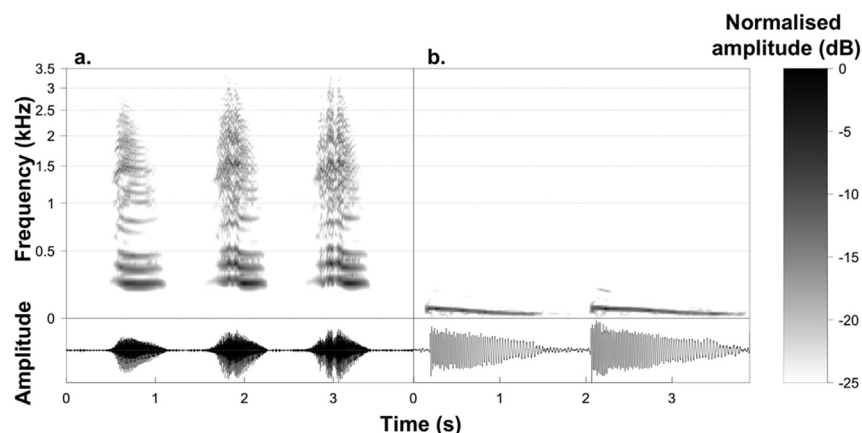


Fig. 3 Comparison of the airborne signal of a frog and the substrate-borne signal of an insect. (a) Airborne signal of a male *Rana catesbeiana* bullfrog (Anura: Ranidae) (recording courtesy of Mark Bee). (b) Substrate-borne vibrational signals of a male *Chrysoperla zastrowi* subsp. *sillemi* lacewing (Neuroptera: Chrysopidae) (recording courtesy of Charles Henry). We show signal waveforms (bottom traces) and spectrograms (top traces). Note the lower frequency of the lacewing signal in spite of their being orders of magnitude less massive than the bullfrogs.

moles, and frogs (Hill, 2008; Caldwell *et al.*, 2010a,b; Randall, 2014), as well as suggestive evidence for various other large mammals (O'Connell-Rodwell *et al.*, 2000, 2001), chameleons (Barnett *et al.*, 1999), and sculpins (Whang and Janssen, 1994).

There is also a great variety of mechanisms of production of substrate-borne signals. Some animals drum, stamp, scrape or head-bang, while others stridulate, click tymbals, tremulate, or resonate their abdomen with muscle contractions (Uetz and Stratton, 1982; Čokl and Virant-Doberlet, 2003; Hill, 2008; Henry and Wells, 2015; Miles *et al.*, 2017).

There exists also great variety of perception mechanisms, with virtually any body part being involved across animals. In vertebrates, the most likely organs involved in the perception of vibrations are the ear (with substrate vibrations reaching the ear through the bones), and tactile perception (Hill, 2008). For instance, naked mole rats have a bony bridge between the lower jaw and the middle ear. When listening for neighbours' head bangs, naked moles will de-articulate their jaw and press it against the walls of their burrows (Rado *et al.*, 1989). Another striking example is the fat padding on elephant feet which are thought to play a role in the reception of vibrations. These pads may function as impedance matching structures, reducing the sudden change in density between the soil and the elephant's skin and bones that would result in an intense loss of amplitude (O'Connell-Rodwell *et al.*, 2001). In arthropods, a variety of hair sensilla throughout the body may be involved in the perception of vibrations (Barth, 2002; Čokl and Virant-Doberlet, 2003; Hill, 2008). Additionally, insects and spiders have specifically dedicated perception organs such as the subgenual organs on insect legs (Gogala *et al.*, 1974) or the metatarsal lyriform organ in spiders (Barth, 1982, 2002). This variety is suggestive of multiple origins between clades (and perhaps within some clades too), but the observation that some animals use several of these mechanisms simultaneously complicates the picture (Barth, 2002; Čokl and Virant-Doberlet, 2003; Hill, 2008).

The above diversity of examples indicates widespread sensibility to substrate vibrations and widespread use of such vibrations in communication. There remain, however, many unexplored groups, and there is yet much to be discovered about the phylogenetic distribution and density of species that use substrate-borne vibrational communication.

The Functions of Substrate-Borne Signals

Animals use substrate-borne vibrational signals for a wide diversity of communication purposes, and in a variety of within-species and between-species interactions. Some species have multiple signals, each with its own function and context.

In within-species communication, substrate-borne vibrational signals are used in a broad range of contexts. These include activities as varied as cooperative foraging, recruitment of parental care, alarm signaling, coordinating group defense, sustaining group cohesion, resource defense, and even caste determination in social insects (Cocroft and Rodríguez, 2005; Hill, 2008; Morales *et al.*, 2008; Ramaswamy and Cocroft, 2009; Caldwell *et al.*, 2010b; Gilbert *et al.*, 2011; Suryanarayanan *et al.*, 2011; Pielström and Roces, 2012; Hager and Kirchner, 2013; Yadav *et al.*, 2017). In the context of sexual interaction, they are used in aggressive signaling, pair formation, pre- and post-copulatory courtship and mate choice (Cocroft and Rodríguez, 2005; Rodríguez *et al.*, 2006; Hill, 2008; Shamble *et al.*, 2009; Noh and Henry, 2010; Sivalingham *et al.*, 2010; Wignall and Herberstein, 2013). These lists cannot do justice to the richness of the variety entailed in these interactions. Consider, for instance, the case of the rhinoceros beetle in which pupae produce vibratory signals that induce freezing startle responses in approaching larvae (aimed mainly at conspecifics and but effective with larvae of other species too) to avoid being damaged by their passing too closely by in the soil (Kojima *et al.*, 2012a,b). Or the cases where a back-and-forth between the alarm signals of juveniles and the calming signals of their mom guides maternal defense behavior while modulating the risk of false positives and retaining brood cohesion (Cocroft, 1996, 1999; Hamel and Cocroft, 2012); or when maternal signals help synchronize egg hatching (Mukai *et al.*, 2012). Each of the above mentioned functions and contexts includes dozens of examples of similar appeal and interest.

Some of these signal functions involve spectacularly complex individual interactions. Both in cooperative synchronized signaling and in competitive duetting and chorusing, for instance, there is sophisticated modification of signal placement relative to the signals of other individuals (Cocroft, 1996, 2005; Kotiaho *et al.*, 2004; Legendre *et al.*, 2012; Rodríguez *et al.*, 2018) (Fig. 4). We also commonly observe back-and-forth male-female signal exchanges whereby females selectively indicate their presence to mate-searching males, expressing their mate preferences for signal traits in ways that give feedback to males regarding the likely success of their courtship efforts (e.g., Figs. 4 and 5(d)) (Henry and Wells, 2006; Rodríguez and Cocroft, 2006; Rodríguez *et al.*, 2006, 2012; Sullivan-Beckers and Hebets, 2011, 2014; de Groot *et al.*, 2012; Polajnar *et al.*, 2014; Rodríguez and Barbosa, 2014; Rodríguez, 2015; Kuhelj *et al.*, 2016). Substrate-borne signals are part of what may be the most complex communication systems known in animals, at least in terms of the sheer number and arrangement of the elements in the signals (Girard *et al.*, 2011; Elias *et al.*, 2012).

Substrate-borne signaling used in between-species communication is no less sophisticated. Most commonly, perhaps, animals produce defensive startle signals, but more specialized functions include signaling to recruit care from mutualists, or mimicking the signals of social species to parasitize their care behavior (Cocroft and Rodríguez, 2005; Hill, 2008; Barbero *et al.*, 2009; Di Giulio *et al.*, 2015).

Some species use substrate-borne signals throughout their lives in a variety of interactions and for different functions. In some species, for example, juveniles use specialized signals as they coordinate cooperative foraging efforts and adults use different sets of signals as they search for mates. This may add up to quite considerable signal repertoires, remarkable especially when considering the small brain sizes of many of the species involved (e.g., Fig. 5).

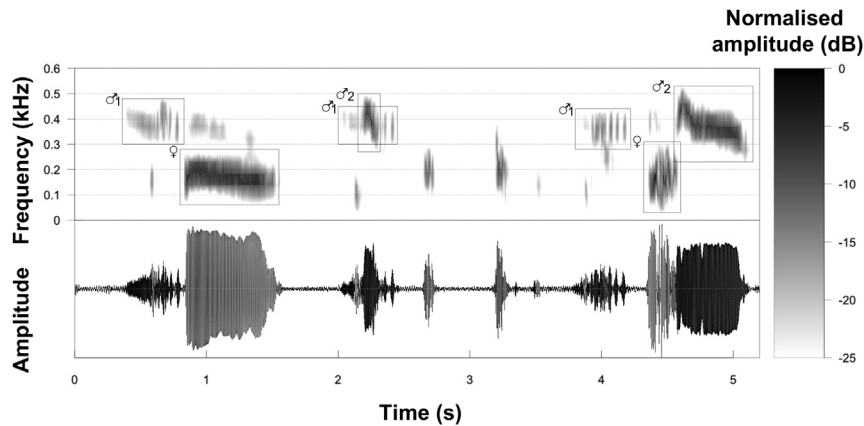


Fig. 4 Example of competitive signal placement in a vibrational insect, a member of the *Enchenopa binotata* complex of treehoppers (Hemiptera: Membracidae) (recording courtesy of Laura Sullivan-Beckers). We show signal waveforms (bottom traces) and spectrograms (top traces). The recording shows an interaction between two males and one female. At the beginning, a male and a female are engaged in a duetting interaction – he produces his advertisement signal and she produces her response signal to encourage him to approach her. However, on his second and third signals, the male is overlapped by a jamming signal produced by another male, and at the end of the recording the response signal by the female is jammed by the other male.

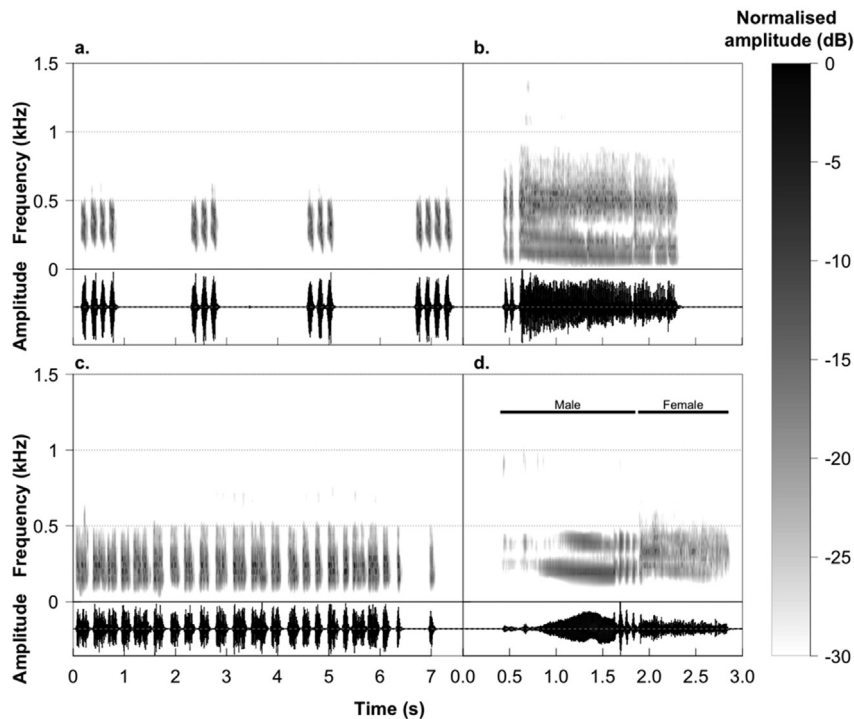


Fig. 5 Partial signal repertoire of one species in the *Enchenopa binotata* complex (Hemiptera: Membracidae). (a-c) Different signal types used by nymphs. (d) Adult male-female duetting signals. We show signal waveforms (bottom traces) and spectrograms (top traces).

Evolutionary Origins

It is extraordinarily difficult for an animal to move without generating substrate vibrations, which are therefore ubiquitous cues about the presence and behavior of animals in the vicinity of other animals. It is not surprising, then, to see that a great variety of species attend to substrate vibrations to obtain information about multifarious features of their surroundings, including the presence of prey or natural enemies (Hill, 2008; Cocroft, 2011). Termites, for instance, eavesdrop on substrate vibrations to detect and avoid conspecific competitors (Evans *et al.*, 2009), while frogs attend to substrate vibrations to detect and escape predators, and can distinguish the patterns made by their approach from those made by the rain (Warkentin, 2005; Warkentin *et al.*, 2007; Caldwell *et al.*, 2010a). General sensitivity to substrate vibrations is much more widespread than their use for communication: It seems to be basal for vertebrates, and probably is so for many if not all groups of invertebrates as well (Barth, 2002; Čokl and Virant-Doberlet

2003; Coccoft and Rodríguez, 2005; Hill, 2008). Even some plants are sensitive to the vibrations induced by the insects that feed on them – specifically monitoring the vibrations and not merely the damage of feeding – and modulate their chemical defenses accordingly (Appel and Coccoft, 2014).

Sophisticated behavioral adaptations and counter-adaptations have evolved around the sensitivity to substrate vibrations. Earthworms, for example, were discovered by Darwin to be sensitive to vibrations propagated through the soil, and he proposed that they use them to detect the approach of burrowing predators such as moles and escape them by rising to the surface (Darwin, 1881; Costa, 2017). In turn, other predators, such as gulls and turtles, have evolved to exploit this response by stomping the ground to induce the worms to surface in order to catch them, to say nothing of the humans that also exploit this defense to gather them for fishbait (Catania, 2008; Mitra *et al.*, 2009).

Similarly remarkable is the case of “seismic echolocation” by blind mole-rats, which strike their head against the substrate inside their tunnels and navigate by the reflections they receive (Kimchi *et al.*, 2005). And termites can attend to the resonant features of the wood on which they are feeding to select blocks of preferred sizes (Evans *et al.*, 2005). Consider also “vibrational sounding” by some parasitoid wasps (Broad and Quicke, 2000; Laurenne *et al.*, 2009). The insect larvae that these wasps seek out as hosts for their brood often conceal themselves inside plant tissues or in the soil. Some parasitoid wasps detect the incidental vibrations produced by their hosts to locate them (Djemai *et al.*, 2004). Further, several species within two families of parasitoid wasp have repeatedly evolved a form of echolocation whereby they tap the substrate with their antennae, which are modified especially for the purpose, and sense the returning echoes through the subgenual organ in their legs – the mechanism of perception of vibrational signals in many other insects (Čokl and Virant-Doberlet 2003; Coccoft and Rodríguez, 2005) – to locate the site to insert their ovipositor.

The widespread sensitivity to substrate vibrations among animals of all sorts sets the stage for the evolution of signaling in this channel through the cue-to-signal pathway (Greenfield, 2002). In other words, given the ubiquity of substrate-vibration cues about the presence and behavior of other individuals in the environment, animals have very often been selected to attend to those vibrations to gain information about their surroundings. In turn, some of the animals that produce such cues have been selected to modify their behavior according to the effect they have on those attending to their cues, thereby exerting selection on receivers to modify their responses and eventually yielding specialized signals and receiver responses in communication systems. A beautifully worked example of these transitions is the evolution of ritualized vibrational signaling by anal scraping from modified locomotory behavior in masked birch caterpillars (Scott *et al.*, 2010).

As a consequence of the above evolutionary pathway, there are many species that both communicate with substrate-borne signals and attend more broadly to disturbances in the substrate for threat detection and prey localization – spiders, scorpions, and stink bugs offer examples of this, but it is probably much more widespread than currently appreciated (Hill, 2008; Coccoft, 2011). The evolutionary twists and turns may continue even further when predators sensitive to substrate vibrations are selected to eavesdrop on the signals of their species prey to locate them (Coccoft and Rodríguez, 2005; Coccoft, 2011; Laumann *et al.*, 2007, 2011; Virant-Doberlet *et al.*, 2011), or to aggressively mimic the prey species' prey to lure and approach them (Jackson and Brassington, 1987; Wignall and Taylor, 2011), or even to aggressively mimic the prey species' courtship signals (Jackson and Wilcox, 1990).

Conclusion

Reports of communication with substrate-borne signals date back at least two centuries (Smeathman, 1781), but only in the last two decades did the pace of research pick up as researchers have become increasingly aware of this channel of sensation and communication. Along this history, careful observation of the natural behavior of animals and technical innovation have been twin keys for progress in our knowledge. With the increasing availability of methods and techniques for monitoring and experimenting with substrate borne signals (Coccoft *et al.*, 2014; Elias and Mason, 2014) huge opportunities for discovery are opening for students of animal behavior.

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See also: Communication: Signal Modality: Acoustical Signals – in air and water. **Neurons and Senses:** Vibration Perception: Vertebrates.

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