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REVIEW

How do animals use substrate-borne vibrations as an information source?

Peggy S. M. Hill

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Abstract Animal communication is a dynamic field that promotes cross-disciplinary study of the complex mechanisms of sending and receiving signals, the neurobiology of signal detection and processing, and the behaviors of animals creating and responding to encoded messages. Alongside visual signals, songs, or pheromones exists another major communication channel that has been rather neglected until recent decades: substrate-borne vibration. Vibrations carried in the substrate are considered to provide a very old and apparently ubiquitous communication channel that is used alone or in combination with other information channels in multimodal signaling. The substrate could be 'the ground', or a plant leaf or stem, or the surface of water, or a spider's web, or a honeybee's honeycomb. Animals moving on these substrates typically create incidental vibrations that can alert others to their presence. They also may use behaviors to create vibrational waves that are employed in the contexts of mate location and identification, courtship and mating, maternal care and sibling interactions, predation, predator avoidance, foraging, and general recruitment of family members to work. In fact, animals use substrate-borne vibrations to signal in the same contexts that they use vision, hearing, touch, taste, or smell. Study of vibrational communication across animal taxa provides more than just a more complete story. Communication through substrate-borne vibration has its own constraints and opportunities not found in other signaling modalities. Here, I review the state of our understanding of information acquisition via substrate-borne vibrations with special attention to the most recent literature.

Keywords Vibrational communication · Seismic signals · Rayleigh waves · Bending waves · Bioacoustics

Introduction

The ability of animals to detect substrate-borne vibrations predates their ability to 'hear' in the most common sense of the term. The structural and functional mechanisms required to receive and translate information carried in these vibrations appear to be ubiquitous, at least in vertebrates and arthropods. Cocroft and Rodríguez (2005) have conservatively estimated that 150,000 described species of insects use only substrate-borne vibrations to communicate with mates and family groups, and that perhaps 45,000 other insect species use vibrational signals along with other mechanical methods of signaling. If we add to this total the species of arachnids (spiders and scorpions), crustaceans, and even worms that use vibrations for information, as well as the vertebrates from mammals to fish that signal this way, the numbers alone reveal an entire world where substrate-borne vibrations are the primary mechanism employed in important and ancient communication systems that have long been overlooked and understudied (Table 1).

In this review, I present an overview of animal communication via the substrate-borne vibration channel. The scope of communication will follow Markl (1983) to mean transferring information through a specific behavior from a sender to a receiver so that the receiver's behavior is

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P. S. M. Hill (✉)
The University of Tulsa,
Tulsa, OK 74104, USA
e-mail: peggy-hill@utulsa.edu

Table 1 Species that use substrate-borne vibrations as an information source, reported in Hill (2008)

Major taxon	Order	Number of species
Mammalia	Monotremata	2
	Dasyuromorphia	1
	Diprotodontia	2
	Afrosoricida	2
	Proboscidea	2
	Primates	2
	Rodentia	12
	Soricomorpha	1
	Carnivora	2
	Artiodactyla	1
	Cetacea	1
Aves		1
Reptilia	Squamata	12
Amphibia	Urodela	2
	Anura	14
Osteichthyes		3
Insecta	Plecoptera	11
	Megaloptera	2
	Orthoptera	27
	Blattodea	2
	Isoptera	7
	Hemiptera (all)	70
	Neuroptera	16
	Coleoptera	24
	Mecoptera	3
	Diptera	8
	Hymenoptera	38
	Lepidoptera	10
Arachnida	Scorpiones	1
	Acariformes	1
	Araneae	32
Crustacea		11
Nematoda		3

modified in a predictable way that has adaptive value for the sender or receiver, or both. This definition actually allows consideration of substrate-borne waveforms that are produced inadvertently by either a predator or its prey, but which elicit behaviors from the other species that promote its fitness. Although selection pressures in predator–prey interactions are different from those that promote adaptive signaling for intraspecific communication, the same vibration detection mechanism can be used in more than one signaling context. Since a book length general review is recently available (Hill 2008), a focus of this paper is current literature on animals that signal through the ground or bodies of plants, rather than an extensive coverage of research on all taxa and all substrates. The question posed in the title asks, “How do animals use substrate-borne vibrations as an information source?” The short answer is that animals use information gathered from substrate-borne vibrations in the same contexts as they use information gathered from vision, hearing, taste, smell and touch; that most vertebrates and arthropods have the physical capability to detect such information; and that when we look for examples of animals gathering information via this modality, we tend to find it exists.

Sending and receiving information

Vibrations traveling through the atmosphere, water, or the substrate represent particle motion in a fluid or elastic body (Fig. 1). Particle motion defines the vibration, rather than vibration being defined by the medium through which it is propagated (see Hill 2008). Markl (1983) reviewed the physical properties of vibration events and classified them as contact vibrations, near-field medium motions, or boundary vibrations. Boundary vibrations are so named because they occur at the interface (boundary) between two media (solid/air, water/air, solid/water, etc.). An event that excites vibrations in a substrate may generate multiple types of boundary waves: pure longitudinal (compressional), quasi-longitudinal, transverse, torsional, or bending waves. Each of these is distinguished by the speed and direction of energy propagation, as well as attenuation properties (Markl 1983). Those of us with interests in vibrational communication tend to use ‘vibration’ to refer to substrate-borne boundary waves, whether the substrate is a plant stem or leaf, the surface of a body of water, a spider’s web, a honeycomb, or any of the myriad types of soil substrates, or soils in combination with plant debris (Hill 2008). However, we understand that vibrations pass from one medium to another at the boundary between any pair of fluids or a fluid and an elastic body in a way that adds complexity to the system, while making its study perhaps more interesting. Our documented cases of vibrational communication are almost exclusively restricted to Rayleigh waves or bending waves (Hill 2008). However, scorpions determine distance to prey using information in compressional (P) waves (Brownell 1984) and fiddler crab drumming produces Love waves, which are transverse boundary waves (Aicher and Tautz 1990).

The ‘silent’ substrate-borne vibration channel provides a rich and varied signaling environment that may also be cluttered with noise (Lewis and Narins 1985). Substrate-borne vibration communication presents opportunities and poses challenges not encountered in better-known signaling modalities. For example, inadvertent vibrations are often characteristic of the animals producing them and are

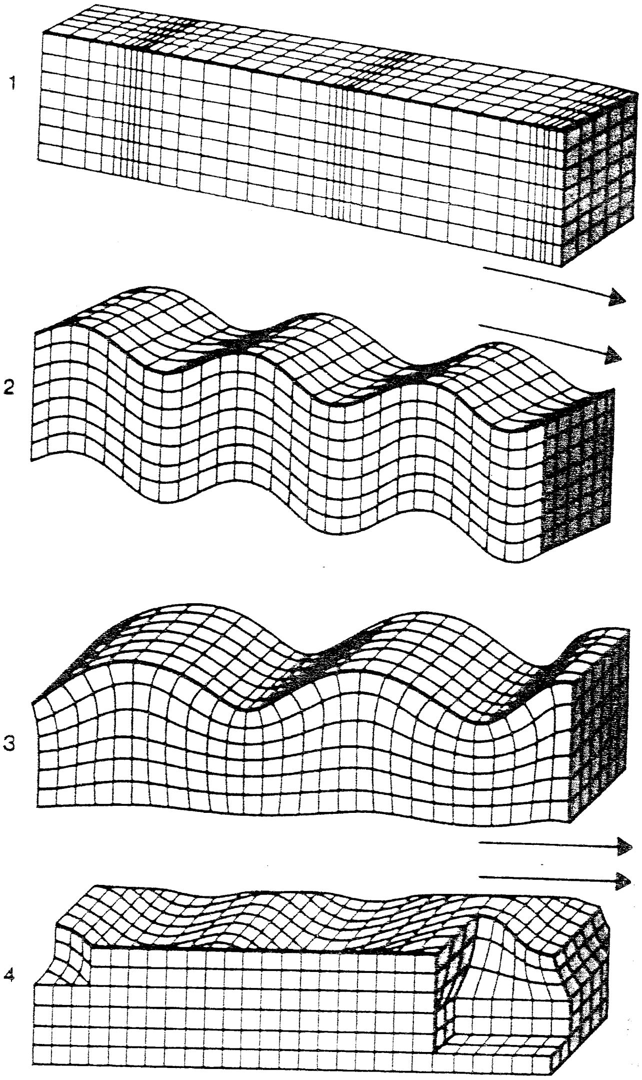

Fig. 1 Waves in elastic solids are characterized by their motion relative to the direction of energy propagation, attenuation, and speed of propagation: (1) pure longitudinal, or compressional, or P-waves; (2) transverse, or shear, or S-waves; (3) Rayleigh waves (boundary waves produced by a combination of longitudinal and transverse waves); and (4) Love waves (transverse surface waves). Reprinted with kind permission of Springer Science and Business Media and *The Journal of Comparative Physiology* from Aicher and Tautz (1990, p. 346)

difficult to avoid as individuals go about their daily lives. These vibrations can provide cues to conspecifics and others of identity, specific actions being performed as the vibrations are created, or even life stage of the individual. Moving and feeding actions produce different waveforms. Larval vibrations can be distinguished from pupal ones (e.g., see Meyhöfer et al. 1994) or adults from juveniles. Even though some species are able to conceal or mask their movements (e.g., see Tarsitano et al. 2000), substrate-borne vibrations are typically more difficult to avoid producing than airborne vibrations (sounds). The wandering spider *Cupiennius salei* is able to discriminate vibrations created by rain, wind, prey, and potential mates, even though the rare creeping grasshopper may escape predation if the vibrations it produces are enough like those of wind (Barth et al. 1988).

Benefits and costs to the signaler are more obvious once the system is examined. For social signaling, daylight and line-of-sight are not required for vibrational communication as they are for visual signaling. Likewise, flightless individuals may spend less time locating a potential mate by following the most direct route defined by substrate-borne vibrations, rather than by following sound or chemicals deposited on the path. For the male tok-tok beetle *Psammodes striatus*, drumming an alternating sexual advertisement signal and then searching for a responding female is ten times more energy efficient as a mate location strategy than searching an equivalent area with no vibration cues (Lighton 1987).

An understanding of the ubiquitous nature of vibrations in the natural world, and even that animals might be able to detect such particle motion, does not obviously support the conclusion that animals communicate via the vibration channel. A communication system requires an individual action to encode information, whether incidental or intentional, which is then propagated through a medium to another individual. The second individual's receivers detect and decode the information, and the receiving animal ultimately acts based on the message received. Confirmation of this pathway is required to establish that a communication system exists.

Up through the 1970s, the conventional wisdom held that substrate-borne vibrations could not serve as signals among animals, especially the very small, except as a generalized alerting mechanism that something had happened nearby (Schwartzkopff 1974). It was generally thought that natural solids were neither uniform nor elastic, the wavelengths were too large to be detected, and conduction velocities were too great. Then, Brownell and Farley (Brownell 1977; Brownell and Farley 1979a, b, c) provided empirical evidence supporting arguments that scorpions hunting on sand actually extract information on distance and direction of prey from vibrations produced by activities of the prey. They found that sand, rather than damping low-frequency vibrations or scattering high-frequency ones, was a good conductor of both compressional (P) and Rayleigh waves, and that waves actually travel more slowly in sand than theory had predicted. Thus, scorpions, at least, could detect and act on information encoded in substrate-borne vibrations created by their prey. When Ehrenberg's mole-rat *Spalax ehrenbergi* was observed banging its flat head against its underground tunnel walls, the action could have been interpreted as part of the blind animal's tunnel building behavior. Yet, when individuals responded in a repeatable way to playback stimuli that simulated the head banging of neighbors (Heth et al. 1987) and when individuals responded to these simulations in artificial tunnels as well as in a natural setting (Rado et al. 1987), vibrational communication in a terrestrial mammal was confirmed for the first time.

Sending signals

Mechanisms animals use to send information via vibrations are as variable as animal life itself. For example, very large mammals produce vibrations in the substrate as they vocalize (O'Connell-Rodwell et al. 2001). Some reptiles initiate substrate-borne vibrations as they vibrate their bodies on a leaf (Barnett et al. 1999) or the soil (Young 2003). Neither vocalization nor body vibration has been extensively studied as vibrational signal mechanisms in vertebrate animals, perhaps because the airborne or visual aspects of the behavior are a more obvious component. However, drumming (percussive) behavior is common in vertebrates and much better documented as a sending mechanism in vibrational communication. Individuals bang heads, rap trunks or tails, stamp or drum with front feet or hind feet or teeth, thump a gular pouch, and basically employ available appendages to create vibrations on the substrates where they live (Hill 2008). Signaling in mammals by drumming some body part against the substrate is known from at least 32 species in 11 families. The contexts in which this drumming is initiated include predator defense, territory maintenance and individual spacing, male–male competition, reproductive behavior, and alarm calling. We do not know in each case, however, whether substrate-borne vibrations encode the signal, or whether the sound alone or sound plus visual stimuli provide the essential stimulus of the signal (Randall 1993, 1994, 2001).

Invertebrate sending mechanisms are really only known from arthropods, where the hard exoskeleton provides opportunities not available to vertebrate animals (see Hill 2008). Individuals do drum with one or more appendages (i.e., legs, chelae, pedipalps, mandibles, antennae, and wings), the head, or abdomen. They also send a variety of substrate-borne signals by body vibrations, or tremulations, which have been described across taxa with a number of names (i.e., bobbing, rocking, female abdominal vibration, dorsoventral abdominal movement, opisthosomal vibration, vibration dance, and flight muscle contraction with or without accompanying wing flicks). Arthropods also stridulate as they rub one body part against another, most often with some sort of morphological modifications to serve as a file and scraper (i.e., leg–leg, leg–body, leg–head, wing–wing, wing–body, adjacent surfaces between body segments or legs, and proboscis–body). Cicadas and their relatives, as well as a few other bugs in the Hemiptera, and some tiger moths (see Claridge 1985) produce vibrations by buckling tymbals. Tymbals are usually thin membranes in the exoskeleton of the dorsal or dorsolateral first abdominal segment that overlay resonant air sacs. While cicadas are known for their loud airborne calls, most of the other species with tymbals have long been considered 'silent'. Recent work by Hoch and others, however, has provided evidence that tymbal vibration, drumming, and stridulation had already evolved by 230 million years ago in insects (Hoch et al. 2006).

Some generalizations can be drawn from our current understanding of the mechanisms used to create vibrations. Drumming produces broadband, noisy signals that may also have an airborne component. Information on identity and quality of the sender can be contained in temporal characteristics such as drumming rate, duration, and pattern of elements, as well as amplitude (intensity) of the signal. Stridulation also produces airborne and substrate-borne vibration components simultaneously. However, details of the file and scraper morphology may allow information to be encoded by variation in frequency of the signal components, as well as in their temporal patterns. Tremulations tend to produce low-frequency vibration signals in a narrow range that varies with the morphology of the sender, as well as with the body motions that create the signals. Signals produced by tymbal buckling are tuned by the underlying abdominal air sacs. This allows for production of broad frequency signals in some species, while others produce more pure tones at the tymbal's natural frequency (see Hill 2008).

Receiving signals

A signal is received by a message 'decoder' that allows both detection and analysis at the central nervous system level. The detection process involves a receptor that serves as both a filter and a transducer to convert information from energy carried by vibrations through the substrate into action potentials in the animal's nervous system (see Hill 2008). Animals that communicate via substrate-borne vibrations typically employ receivers that detect particle motion perpendicular to the direction of propagation and often involve a form of inertial motion sensor (see Lewis 1984). Skin vibration detectors in vertebrates, of course, are essentially displacement sensors. However, the mass (inertia) of the body helps them to operate by providing something for the substrate to push.

In vertebrate animals (McIntyre 1980), these may be distributed somatosensory receivers (Pacinian corpuscles in placental mammals: Calne and Pallis 1966; similar lamellated corpuscles in marsupials: Gregory et al. 1986; Herbst corpuscles in birds: Dorward and McIntyre 1971; and a variety of encapsulated or naked nerve endings in other taxa: Proske 1969a, b). Such receivers detect vibrational events in the skin and joints, from which they are typically carried as action potentials to and through spinal nerves to the spinal cord and then the brain. While vibrations under the head of snakes, for example, could generate action potentials carried through cranial nerves, the somatosensory receivers in the head appear to be activated only at very high stimulus amplitudes (Hartline 1971). Alternatively, receivers may be centralized in the cochlea of the inner ear. Vibrations are carried from the substrate to the cochlea through the body (bones, fluids, cartilage, etc.) in an ‘extratympanic’ pathway that bypasses the eardrum, and sometimes, even the middle ear. Vibrations then project to the brain along with information from airborne sound received via the eardrum. Very little work has been focused on centralized processing of vibrational signals in vertebrates, but we do know the story is more complicated than simply that somatic receivers project to the primary somatosensory cortex of the cerebrum while bone-conducted information is carried via the VIIIth cranial nerve to the auditory cortex (see Hill 2008).

Levänen et al. (1998) reported that a congenitally deaf human subject could discriminate frequency differences between two vibrotactile stimuli delivered to the left hand. In addition to the typical activation of the right primary somatosensory cortex of the cerebrum, the auditory cortex on either side of the brain was activated in this individual much as would be expected in a hearing subject exposed to audible tones of different frequencies. In humans (Foxe et al. 2002) and macaque monkeys (Schroeder et al. 2001), both auditory and somatosensory information received as vibrational events project to a multisensory subregion of the auditory cortex. In snakes, Hartline (1971) found that projections from bone (ground to mandible to quadrate to columella) to the VIIIth cranial nerve pathway led to a region of the midbrain totally contained within the area to which information from the somatic receivers was projected. The empirical results from even these few cases are cause for us to reconsider our previous segregation of communication channels into sound and vibration.

Specialized skeletal features in some vertebrates allow efficient conduction of vibrations from the soil to the inner ear, while perhaps limiting simultaneous ‘hearing’ of airborne events (Hill 2008): the opercularis system in amphibians (Hetherington 1988; Jaslow et al. 1988), a pseudofossa just posterior to the temporomandibular (T-M) joint in blind mole-rats (Rado et al. 1989, 1998), and massive ear ossicles in elephants (Reuter et al. 1998) and golden moles (Mason 2001; 2003; Mason and Narins 2002). The Cape golden mole, however, has a middle ear morphology that appears to allow detection of both airborne and substrate-borne signals (Willi et al. 2006). Blanco and Rinderknecht (2008) examined the ear ossicles of two extinct ground sloth species, adults of which had estimated body masses of 1,500 and 4,100 kg, respectively, to study their potential hearing sensitivity. Their results suggest that ground sloth ossicles (>500 mg) are among the largest found in terrestrial animals, extant or extinct, and that the size approaches that of elephants. These species appear to have a morphology that would support their being able to detect substrate-borne vibrations, but more study is required before any position on a potential communication pathway can be taken. Unresolved theoretical issues continue to drive research efforts to better understand the mechanisms and importance of the extratympanic pathway to vibration reception.

Another area of promising research is the apparent ‘acoustic fat’ in elephant feet that may promote better coupling with the substrate while receiving substrate-borne vibrations. The weight-bearing foot increases in circumference up to 10% in the region just above the toenails as this fatty cushion is compressed. Individuals lean forward, increasing the weight on their front feet in such a way that the ears are in direct alignment with the feet and legs. This appears to occur when substrate-borne stimuli are greatest, such as just before the arrival of a new group to the water hole (O’Connell-Rodwell et al. 2001). Furthermore, the Indian elephant has large clusters of Pacinian corpuscles in the dermis of the feet, especially on the forward side of the front feet and posterior part of the hindfeet (Bouley et al. 2007). Confirmation of a role for acoustic fat in vibrational communication by terrestrial vertebrates and its presence in animals other than the elephant awaits further research.

Invertebrate receivers of a variety of types have been well described in previous reviews (i.e., Barth 1982; Hutchings and Lewis 1983; Kalmring 1985; Popper et al. 2001; Devetak et al. 2004). These receivers may or may not reflect homology within and among taxa. The subgenual organ found inside the legs of insects takes on many forms, as do the slit sense organs in the exoskeletons of arachnids. For example, the wandering spider *C. salei* has a pair of single slits, which is sensitive to substrate-borne vibration, on either side of the tarsus of each leg, just behind the claw. However, this spider has as many as 3,300 slits in its exoskeleton, including one reported to be sensitive to far-field sound (Barth 1982). The basitarsal compound slit sensilla (BCSS) are the primary substrate-borne vibration receivers in scorpions, and the metatarsal lyriform slit organs in spiders are homologous to the BCSS (Brownell and Farley 1979a). However, other types of sensory adaptations allow invertebrate animals to gather vibrational cues, including a variety of hairlike projections, chordotonal organs (of which subgenual, Barth’s and Johnston’s organs are specialized types), the mid-coxal protuberance (a putative vibration receiver in flies: Kanmiya 2006), and slit sense organs not organized as a BCSS or lyriform organ

(Hill 2008). In many cases, these vibration receivers have long been recognized as specialized features for detecting substrate-borne vibration, but an investigation into any roles they might play in an adaptive context has not always followed.

Importance of properties of the substrate

Animals generate a large number of potential signals through substrate-borne vibrations created, intentionally or not, as they move (Hill 2008). Signals that are produced by percussive events, or drumming some body part against the substrate, are broadband and ubiquitous among many animal groups that communicate via substrate-borne vibration. The signals are not matched to any microhabitat, and thus will propagate through a variety of substrate types, regardless of composition. However, the characteristics of the substrate do serve as a filter, and frequencies attenuate differentially across substrate types, including with distance (Hebets et al. 2008). The wolf spider *Schizocosa retrorsa* can court via drumming on leaf litter, where the species is not typically found; however, greatest mating frequency is on the natural substrate of pine litter or clay. Female receptivity, measured as copulation frequency, is linked to the natural substrate for the species and may provide evidence that receiver behavior is adapted to the habitat, irrespective of efficiency of propagation of the sender's signal (Hebets et al. 2008). These findings support and extend earlier work (Elias et al. 2004) that found the jumping spider *Habronattus dossenus* could court on the sand, rock, or leaf litter substrates that it would encounter on a daily basis; however, most successful courtship was on a leaf, which was also the most favorable substrate in terms of signal transmission. Substrate characteristics thus may influence evolution of signaling via drumming events, whether selection is on sender or receiver behavior (Hebets et al. 2008).

Some plant-dwelling insects are restricted to a single host plant, while others are found living and communicating on a variety of plant species. A continuing and fruitful line of research is concerned with the interaction of animal and plant, including selection on signal properties linked to variation in physical properties of the plant tissue. Michelsen et al. (1982) set the standard for thinking about signals propagated through plants by studying communication of non-cicada Hemiptera (planthoppers and leafhoppers) and cydnid bugs along with physical properties of a variety of plant material. They found that wild and domesticated herbaceous plants, as well as fresh and dry tree leaves, all filtered plant-borne vibrations in similar ways. Further, vibrations could be propagated over distances of 1–2 m in green plant stems with similar signal velocities and little loss of energy with distance at the dominant frequency.

The green stinkbug *Nezara viridula* is a crop pest that has been able to disperse throughout much of the world in the last 100 years, in part because of its ability to feed and reproduce on a number of host plants. Even though the propagation of its rather pure-tone signals through green bean is significantly more efficient than through soybean or pea plants, *N. viridula* is able to use these three legumes and others as hosts (Virant-Doberlet and Čokl 2004). The harlequin stinkbug *Murgantia histrionica* also lives on a variety of host plants, but individuals produce signals with broader band spectra and utilize these signals only at close range (Čokl et al. 2004). A comparison of communication in these two species led Čokl et al. (2007) to the conclusion that low-frequency signals with narrow frequency peaks are attenuated less than the higher components of broader band signals and are thus well suited for transmission through green plant tissues, which act as low pass filters.

The treehopper *Umbonia crassicornis* also produces a rather pure-tone call and lives and signals from a variety of host plants. Even though signals recorded from host and non-host plants showed differences in spectral and temporal characteristics of the call with distance, the effects were small, and individual singers could be recognized (Cocroft et al. 2006).

Bell (1980) found differences in transmission curves of vibrational waves in Canadian plants used as perches by tree crickets in the genus *Oecanthus* when he compared them with plants in the same habitats not used as perches. However, Henry and Wells (2004) found that songs of one species of green lacewing in the *Chrysoperla carnea* group, which is associated primarily with conifers, and one that sings from grass plants propagated equally well in either substrate with no changes in the frequency spectrum of either. They concluded that natural selection appeared to play no role in selection for a match between song and substrate in this rapidly diverging group. Yet, these conclusions were not supported as a general model for characterizing potential selection by plant tissue on substrate-borne signals when the animal species were strict host specialists.

McNett and Cocroft (2008) tested hypotheses on signal divergence in the *Enchenopa binotata* complex of treehoppers that signal with a rather pure tone, each species linked to a different host plant. Signal frequency is critical for mate recognition in members of this complex where males duet with, and search for, sedentary females (Hunt 1994). Females from *Viburnum* that were presented with signals from males of their own and five other species in the complex responded only to their own males and to the black walnut males, which are distantly related and thought to be basal in the clade. No females responded to the signals of the more closely related bittersweet and black locust males (Rodríguez et al. 2004) which, under natural conditions, would then cease to search for the female. McNett and Cocroft (2008) determined that species found on redbud and wafer ash each use a signal frequency that transmits with the least attenuation through their own host plant, which suggests that shifts in the host plant can impose natural selection on the mating signals of these host-specialist species. Patterns are thus still emerging as research continues on specialist and generalist species, as well as those calling with relatively pure tones versus those producing broader frequency calls.

Another finding from Michelsen et al. (1982) was that vibrations travel through plant stems as bending waves, which they suggested might provide cues to a receiving animal that could be used in estimating distance to the sender. Dispersive bending waves are defined by different frequencies within a signal traveling at different velocities. Songs with different functions analyzed from their ‘small cicadas’ and cydnid bugs all contained energy in broad frequency bands that would thus propagate through the stems at a different velocity per frequency.

Multimodal signaling

When the animal’s signals are multimodal, the story becomes even more complicated. Recent work with jumping spiders pushes us to reconsider interpretations of known bodies of work, even as we strive to continue bringing unstudied systems into the story. Jumping spiders typically have image forming principal eyes, which provide resolution at an unusually high level for the taxon, and color perception. Their use of ornamented colored appendages and complex movement in species recognition, species isolation, and female choice have steered us toward the interpretation that communication among potential mates is driven by sexual selection, but primarily through visual signals. However, *H. dossenus* males also produce multiple substrate-borne vibration signals through stridulation, drumming, and tremulation (Elias et al. 2003). We have considered that elaborate signaling behaviors and sexually dimorphic ornamentation are the result of specialization for communication in one sensory modality (Elias et al. 2005). However, when male *H. dossenus* were tested in experimental groups (muted and non-muted) where both could continue to display via visual signals, the males that could also produce vibrational signals in a multimodal display were three times more likely to successfully copulate. The question then becomes, is the information conveyed through substrate-borne vibrations truly redundant with that carried in other modalities? One hypothesis is that this suite of vibrational signals may provide very different bits of information to the female on male condition than she obtains via vision or even other vibrational signals (Elias et al. 2003). The use of signals from multiple sensory pathways, and their potential for synergistic effects, may allow individuals to make faster, safer choices of a robust conspecific mate in a complex environment. Of interest is that in species groups of *Habronattus* with the most complex ornamentation and visual displays we also find the most evidence of increased speciation through sexual selection, as well as the greatest diversity of substrate-borne vibrational signals (Elias et al. 2005).

In addition, VanderSal and Hebets (2007) have shown that in *H. dossenus* the presence of an essentially non-informative vibrational stimulus improves color discrimination and learning. Spiders were tested for learning using heat-aversion, and those individuals stimulated by a substrate-borne vibration jumped on the heated color significantly less often than those not exposed to a vibration stimulus. This was the first demonstration of learning under the influence of cross-modal stimuli by an invertebrate animal. The strong implication is that some invertebrates integrate cross-modal cues in a complex way, just as vertebrates are known to do.

Wolf spiders in the genus *Schizocosa* have a stridulatory apparatus with which they produce substrate-borne vibration signals in mating. All known species of *Schizocosa* stridulate, while some also produce visual displays simultaneously with the vibrations, and some even have decorated forelimbs (Hebets and Uetz 1999). A pair of sibling species, *Schizocosa ocreata* and *Schizocosa rovneri*, are reproductively isolated by courtship behavior. Male vibration alone will elicit a female response in *S. rovneri*, while visual cues alone will not (Stratton and Uetz 1983). *S. ocreata* males have tufts of hairs on the tibia, and they wave their legs during courtship in addition to signaling via the substrate. *S. rovneri* males do not have the tufts of hair and mostly depend on vibrational signaling (stridulation and a percussive body bounce). Four species of *Schizocosa* (*Schizocosa duplex*, *Schizocosa uetzi*, *Schizocosa stridulans*, and *Schizocosa crassipes*) representing a range of display from mostly vibrational to mostly visual were chosen to test female detection and receptivity to isolated visual or vibrational cues. Details from *S. rovneri* and *S. ocreata* were also considered in the analysis, and the general trend was for female receptivity to visual signals to increase with the degree of visual signaling by the male. Likewise, ornamented males used visual signals more than vibrational ones. However, female receptivity responses by the six species were never higher to visual-only cues than to vibration-only cues (Hebets and Uetz 1999). When *S. stridulans* was tested for actual mating success, the vibration cue alone was sufficient for copulation success, while the visual cue alone was not even necessary. Even though males tap ornamented legs during courtship, presence/absence of the visual cue did not influence mating success, suggesting it was not part of a backup system (Hebets 2008).

Use of multimodal cues to allow flexibility of response based on context is surely much more important than we often recognize. Thus, even in groups where the mechanisms of stimulus and response have been well-documented, other possibilities, including use of the vibrational channel, might be considered as a context-related option. For example, soil-dwelling nematodes that are lethal parasites of insects have long been known to locate their hosts while in the non-feeding infective larval stage by using chemical cues. Torr et al. (2004) questioned the efficacy of communication via chemical cues for host finding at any distance in soils with high organic content, which should absorb the chemical stimulus. When they tested larvae of three nematode species with chemical and vibrational stimuli in both sand and peat, they found that members of all three species moved toward the vibrational, but not the chemical, stimulus in peat, while two of the species were attracted to the chemical stimulus in sand. One of the species failed to move toward the chemical stimulus in either sand or peat (Torr et al. 2004). Thus, just as with the visual displays of wolf spiders, empirical tests revealed that the obvious chemical cues were less important information sources for the nematode larvae than the previously untested ones carried as vibrations.

Context

Some of the earliest observations of potential signaling via substrate-borne vibration did not invoke the possibility of vibrational communication nor did they even test to confirm that the observed audible events served as a sufficient stimulus to evoke a response in the species. Pearman (1928) reported that female booklice in the Psocoptera produce a faintly audible sound with tapping that was thought to be a sexual advertisement. We now understand that the tapping would also send out vibrations through the substrate, but whether or not the booklouse responded to the airborne or substrate-borne component as an essential stimulus was not investigated at the time. Emerson and Simpson (1929) reported that head drumming by soldier termites after a disturbance produced an airborne signal described as audible if amplified; however, experimental evidence indicated that termites are not very sensitive to airborne sounds but are highly sensitive to substrate-borne vibrations.

The deathwatch beetle *Xestobium rufovillosum* was given its common name for the 'tick, tick' sound produced as males drum their foreheads on the substrate (Birch and Keenlyside 1991), but we now know that the airborne vibration is an artifact of the behavior and does not elicit a drumming response in return from a female. The substrate-borne vibrations produced by the drumming male serve as the actual signal and are sufficient to elicit a response from the female, while the airborne vibrations alone are not. Males search for drumming females but require repeated reciprocal signaling, possibly because their small body dimensions make it difficult for them to extract directional cues from the arrival time differences in the substrate-borne vibrations (Goulson et al. 1994).

The Gogala group knew by 1974 that bugs in the Cydnidae produce both audible airborne and silent substrate-borne vibrations but that the substrate-borne vibrations are the component that carries the communication signals. They also recognized variations in frequency of these substrate-borne signals at a time when frequency had not been considered to transmit information in the way that temporal pattern or amplitude of the signal was thought to do (Gogala et al. 1974). Once this door was opened, evidence on a number of songs in contexts of courtship, disturbance, and aggression was rapidly accumulated from species in the Cydnidae (Gogala 1985).

One of the most extensive early works on substrate-borne signaling was Ossiannilsson's (1949) treatise on the 'silent' mating songs produced by tymbal buckling in the 'little cicadas' of the Hemiptera. Ossiannilsson was a musician, and at a time that predated easy access to recording devices, he placed tiny leafhoppers on blades of grass in a test tube and then used musical notation to describe the amplified songs he could hear by holding his ear to the opening of the tube. He asserted toward the end of his manuscript his suspicion that the animals were sending and receiving signals through the substrate, but he suggested that whether or not one called this 'hearing' was merely a matter of taste. One statement rings prophetic across the space of 60 years:

> This discussion has been made more complicated by many workers having felt obliged to separate a perception of air-born vibration by a specific auditory sense from a perception of the vibrations by the tactile sense. This presentation of the problem will, in my opinion, very easily turn into a battle of words (Ossiannilsson 1949, p. 136).

Thus, humans have observed and documented instances of animals using information from substrate-borne vibrations in a variety of contexts since the earliest years of the twentieth century. Perhaps the best-documented cases are found in studies of predator–prey, mating, and family group interactions.

Predator–prey interactions

Predators may depend on substrate-borne vibrations to detect and capture prey. The Namib Desert golden mole *Eremitalpa granti namibensis* is a blind mammal that actively forages on insects at night by dipping its head and shoulders into the sand in a sequence with 'sand swimming' as it navigates in search of prey (Narins et al. 1997). The eyelids of *E. g. namibensis* fuse early in development, and the ear lacks a pinna. The reduced ear opening is hidden under fur. Individuals do, however, have enlarged middle ear bones, or ossicles, that appear to act as inertial sensing masses that could detect substrate-borne vibrations. The organization of the middle ear and the behavior of dipping the head into the sand would allow these golden moles to locate prey from information carried by Rayleigh waves created by any motion of the prey (Mason and Narins 2002; Mason 2003). Experimental evidence supports the hypothesis that substrate-borne vibrations produced as wind blows through grassy hummocks influence these predators as they forage on termites associated with the grassy mounds, which are spaced at distances of 20–25 m. The exact mechanism of extracting directional information from the vibrations has not been confirmed (Narins et al. 1997; Lewis et al. 2006).

Snakes have long been thought to use cues primarily from odor or body heat or their vision to locate and capture prey. Young and Morain (2002) provided experimental evidence that substrate-borne vibrations are not only an important source of information for some snakes in stalking prey but that temporarily blinded sand vipers (*Cerastes cerastes*) that have had their olfactory and vomeronasal organs denervated are still able to locate and capture living prey. They do better in localizing prey if they can use cues from both substrate-borne vibrations and vision, but our long-held belief that chemosensory input provides the primary cues used in foraging, especially for vipers, is no longer supported (Young and Morain 2002).

Stance is known to be important in the ability to accurately orient toward prey in some species of spiders and scorpions (Hill 2008). The sand scorpion *Paruroctonus mesaensis* is able to integrate information from vibrations to locate prey when it assumes a characteristic stance in which all eight legs are arranged in a circle with each tarsus positioned perpendicular to the substrate (Brownell and van Hemmen 2001). This scorpion uses vibration cues to determine distance and direction, and it does a better job of resolving these fine spatial variables than do predatory insects that use cues from vibrations in the air or water surface (Brownell and Farley 1979b, c).

Larvae of the antlion *Myrmeleon formicarius* can detect a common prey species *Formica rufa* from as far away as 6 cm simply by detecting substrate-borne vibrations produced by the ants (Kirchner 1997), and detection distance correlates well with the mass of the prey (Devetak 1985). The larval antlion's environment is quite different, however, from the sand scorpion's. Antlion larvae at the end of a funnel-shaped pit constructed in sand are able to orient to the direction of prey sliding down the slope to their position. They attempt to grasp prey with their mandibles, and they throw sand with their heads at prey that manage to scramble up the slope toward the funnel entrance. Fertin and Casas (2007), using a mechanical shaker to simulate vibrational cues generated by prey, learned that the larvae are not capable of gauging distance to prey, even though they are clearly able to extract directional information from substrate-borne vibrations created as the prey struggle. Fertin and Casas (2007) did not determine which substrate-borne waveforms were actually used by the antlion larvae from those generated by the shaker, but the thorax of the larva is the area of the body most sensitive to vibrational cues (Devetak 1985). The particle motion (perpendicular to the direction of propagation) of Rayleigh waves would make those a strong candidate to stimulate a thorax in contact with the soil. Perhaps vision, which was of no use in evaluating the shaker-generated cues, provides a supplementary sensory pathway to determine distance when the real prey is present.

Prey species are also capable of using vibrational cues to avoid, or even challenge, predators. Males and females of the banner-tailed kangaroo rat *Dipodomys spectabilis* will drum their feet toward a snake after an initial interaction with the snake, in a manner distinct from social signals (Randall and Matocq 1997). Snakes not motivated by hunger will modify their behavior in response to this footdrumming to avoid the kangaroo rat and will reduce stalking following an increased rate of drumming. The congeneric *Dipodomys deserti* drums and even kicks sand at snakes, while *Dipodomys ingens*' drumming will drive away a kit fox (Randall 2001).

Young of the red-eyed tree frog *Agalychnis callidryas* develop in a gelatinous clump on leaves that overhang pools of water from the Yucatan of Mexico to Panama. Undisturbed clutches hatch gradually between 5 and 10 days after being laid, and embryos (tadpoles) drop into the water below the leaf from which the clutch is suspended. However, if an arboreal predator, such as a snake or wasp, attacks the clutch, the young exhibit a predator-induced rapid hatching response that does not occur with wind, rain, or earthquakes (Warkentin 1995). Clutches attacked by snakes hatch up to 30% earlier than undisturbed clutches, and most embryos escape (Warkentin 2005). If a wasp attacks the clutch, only the individual being grasped and its nearest neighbors hatch rapidly, while more distant young are not affected (Warkentin 2000). Embryos in the egg clutch are subject to attacks by arboreal predators, but aquatic predators also prey on new hatchlings in the pool. Thus, an ability to assess vibrational cues from the predator (propagating through the substrate of the leaf and/or the gel of the clutch), and to balance risk of being eaten by a snake (before hatching) with the risk of being eaten after falling into the pool in a more vulnerable early stage, would provide a distinct advantage to an embryo. Red-eyed tree frog embryos have a surprisingly complex vibration-based strategy that uses multiple vibration properties to assess risk (Warkentin et al. 2006; Caldwell et al. 2009).

Larvae of the spotted tentiform leaf miner *Phyllonorycter malella* also assess risk by using vibrational cues as they live and feed inside apple leaf tissue. These larvae serve as the host of the parasitoid *Sympiesis sericeicornis*, a wasp that lands on the surface of the apple leaf, pierces it with its ovipositor, and attempts to lay an egg on the leaf miner larva it has detected from vibrational cues created as the larva feeds inside (Meyhöfer et al. 1994). Larvae tend to cease any motion when a vibration characteristic of the wasp's probing behavior is detected (Djemai et al. 2001). Vibrations created by wind and rain events are similar to those associated with takeoff and landing of the wasp, and larvae do respond to non-parasitoid-related vibrations, suggesting that response to a non-threat is less costly than failing to respond to a real threat (Casas et al. 1998).

Caterpillars of the common angle moth *Semiothisa aemulataria* also appear able to assess predation risk from cues carried in substrate-borne vibrations. Individuals can distinguish among vibrations created by bird predators, invertebrate predators, invertebrate herbivores (non-predators), and abiotic factors. Caterpillars feeding on a leaf respond to vibrations from invertebrate predators by suspending themselves from the leaf on a silk thread that varies in length with predator species. The caterpillars never suspended themselves by a thread when bird predators were the source of the vibration (Castellanos and Barbosa 2006).

Prey species are thus able to respond with evasive actions appropriate to the risk of predation. Depending on the size discrepancy between predator and prey, and agility of the prey species, they may also aggressively confront the predator. Predators use vibrations created by prey to locate a meal, even if they ineffectively mask their own presence. Prey may then use the vibrations created by the predator to avoid becoming the meal.

Mating

Communication in the context of mating involves signaling between individuals of a potential mating pair, but it also frequently involves an aspect of intraspecific competition from either males or females that intercept the signal. Lewis and Narins (1985) gave us one of the earliest reports of vertebrate signaling via substrate-borne vibrations as they described a bimodal system in the sexual advertisement of the white-lipped frog *Leptodactylus albilabris* in Puerto Rico. Males on the ground sing airborne advertisement songs that target receptive females, but instead of supporting themselves on their front limbs as other frogs often do, they partially bury themselves in soft soil. As they inflate their vocal sacs to produce the airborne call, the gular pouch impacts the soil as a 'thump' that sets up Rayleigh waves that propagate 3–6 m through the substrate. Advertising males space themselves at distances of 1–2 m, thus, the nearest neighbor males are able to receive and respond to substrate-borne vibrations created by other males. A simulated substrate-borne stimulus is sufficient (in the absence of the airborne component) to elicit sounds associated with male–male interactions (Lewis et al. 2001). Males thus use the simultaneously produced airborne and substrate-borne signals to solicit females with the airborne component and to space themselves in an aggregation of displaying males with the substrate-borne component.

The prairie mole cricket *Gryllotalpa major* employs a similar bimodal communication strategy. Individual males aggregate in mating choruses, each constructing an 'acoustic' chamber in the grassland soil from which he signals by wing–wing stridulation. Males produce loud (mean= 96.1 dB sound pressure level, with 0 dB re 20 μPa: see Hill 1998) airborne calling songs that target flying females (Fig. 2). With the same stridulating movement that creates this airborne component, males generate substrate-borne vibrations that are carried as Rayleigh waves (Fig. 3). The substrate-borne vibrations provide a sufficient stimulus to elicit responses from competitors at distances of 3 m or more in a variety of ways characteristic of male–male competition, while males fail to respond to the airborne component alone (Hill and Shadley 1997, 2001).

The vast majority of our documented evidence of vibrational signaling during mating comes from the study of arthropods, including fiddler and ghost crabs, members of several orders of insects, and spiders that live and signal on the soil surface or on leaves and stems of plants. Signals

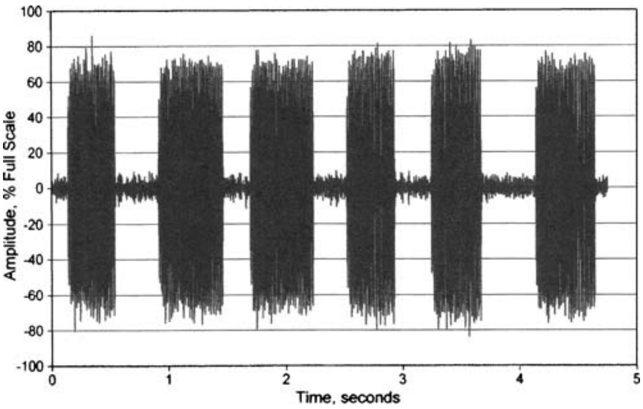

Fig. 2 Relative sound pressure amplitude versus time of the airborne component of the calling song of *Gryllotalpa major* Saussure recorded 1 m from the burrow opening. Reprinted with kind permission of the Society of Integrative and Comparative Biology and the authors from Hill and Shadley (2001, p. 1202)

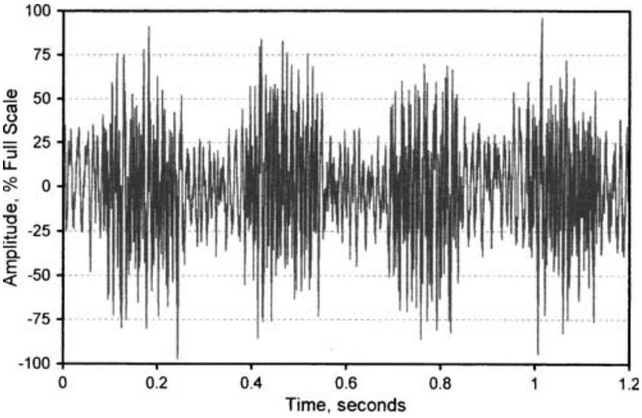

Fig. 3 Substrate-borne component of the male calling song of *Gryllotalpa major* Saussure recorded with a geophone 1 m from the burrow opening and expressed as relative velocity amplitude versus time. Reprinted with kind permission of the Society of Integrative and Comparative Biology and the authors from Hill and Shadley (2001, p. 1204)

used in long-range advertisement, as well as shorter-range mate location and courtship, are produced in various taxa by drumming, stridulation, tremulation, or tymbal buckling. Some taxa produce vibrational signals using more than one of these mechanisms, and vibrational signals can be a component of multimodal mating displays that include vision or pheromones. Male–male competition (rivalry) or aggressive signals are known, and the mating pairs of some species signal in complex duets (see Hill 2008). Female choice based on a component of the male's vibrational signal has been documented in the meadow katydid *Conocephalus nigropleurum* (DeLuca and Morris 1998). The treehopper *Ennya chrysura* produces as many as eight distinct substrate-borne vibrations signals: five male, two female, one used by both sexes (Miranda 2006). Hoch and Wessel (2006) described mating signals used by a highly specialized group of planthoppers: cave-dwelling species that live and signal on roots of surface plants that hang down within lava tubes in Hawaii, Australia, and the Canary Islands. The calling songs are mostly simple, with little variation in tempo or amplitude, and very little variation between male and female calls. Once a potential mate is recognized, individuals display no coyness. Since the most closely related surface dwelling species are not well studied, it is premature to speculate on whether these cave-dwelling species exhibit a reduction in call complexity that parallels reductions in body pigment, eyes, and wings in these taxa, where vibrations sent through the root tissue may be the only component of the mate location and recognition systems.

Communication within a group

Animals great and small live in groups with varying degrees of social complexity, and just as group members communicate via airborne sounds, visual cues, pheromones, and direct touch, we also find communication among group members via substrate-borne vibrations. In the case of social insects, we already know a great deal about how information is transferred within many groups. For example, Markl (1967) described four decades ago the alarm signal of a leaf-cutter ant *Atta sexdens* when a worker was buried in a cave-in. Individuals recruit help from nestmates by stridulation, and since their bodies are surrounded by the substrate, vibrations are transferred to the soil to be picked up by relatives that hurry to free the buried ant. Members of this species also produce vibrations via stridulation that serve as a warning when attacked or disturbed. Even though the stridulation also produces an airborne component, it is the substrate-borne vibration that signals nestmates (Masters et al. 1983). Likewise, the damp-wood termite *Zootermopsis angusticollis* produces an alarm signal that attracts nestmates for help, but in the presence of pathogenic fungal spores, the vibrations produced serve to repel nestmates. Exposed individuals remain in place and begin to signal, while nestmates that receive the vibrational cue flee the area (Rosengaus et al. 1999). Other social insects such as bees and wasps, as well as other termites and ants, use vibrational signals to communicate a variety of conditions or simply to motivate nestmates to increase their level of activity and work harder (Hill 2008).

Footdrumming is well studied in kangaroo rats of the genus *Dipodomys*. Production of substrate-borne signal patterns can be simple or complex but generally communicate an individual's position to its neighbors as a mechanism to avoid conflicts over territory. *D. spectabilis* produces individually distinct drumming signatures, while others in the genus exhibit species-specific patterns but no currently recognized individual variation in signaling (Randall 1997).

Humans have long been fascinated by the herding behaviors of large mammals, such as the shared protection of young and complex social relationships, especially in very long-lived species such as elephants. Further, large herbivores of the African savannah actually produce species-specific vibrations in the substrate as they move about, because they each exhibit a species-specific gait (O'Connell-Rodwell et al. 2001; Wood et al. 2005). It makes intuitive sense that predators may be able to use information contained in these substrate-borne vibrations, but we are beginning to generate empirical evidence that members of the species communicate via this channel, as well. For example, elephants live in family groups that fragment into smaller ones, often separated by great distances, and re-form at a later time. We know that they are able to detect distant thunder and to move toward it to find water after a rain. Elephants create Rayleigh waves as they move and vocalize (O'Connell et al. 1997; Gűnther et al. 2004) and geophones in the soil can measure these waves at 120 m from the source (Arnason et al. 1998). African elephants stimulated by substrate-borne vibrations for which the airborne component had been masked became more vigilant in their behavior, herding together and orienting themselves perpendicular to the direction of the stimulus (O'Connell-Rodwell et al. 2006). When wild herds were played familiar and unfamiliar alarm calls via the substrate, they also exhibited more vigilance and decreased spacing with familiar alarms, but they did not respond to the unfamiliar alarms or controlled stimuli (O'Connell-Rodwell et al. 2007).

If we switch scales from elephants to a tiny treehopper, *U. crassicornis*, we find a 'silent' species where maternal care and sibling interactions employ substrate-borne vibration signals. As many as 80 nymphs are found in an aggregation on a plant stem, attended by their mother. The female can successfully defend her clutch of young from 77% of predatory attacks by fanning her wings and kicking at the predator. A major predictor of offspring risk is when the mother is absent from the group, but they are also at greater risk when located further from her or toward the edge of the sibling group (Cocroft 2002). Young participate in a group signal to which the mother responds, even though she and they tend to ignore individual sibling signals (Cocroft 1996, 1999a). The female signals to the young at a low level throughout the day, and they continue to signal her even after a wasp has been successfully repelled. Although an understanding of the full context of this family group signaling continues to be revealed, the role of the signal is clearly more than just an alerting mechanism to inform the mother of a predator attack (Cocroft 1999b).

Conclusions and future directions

Many scientists have worked for decades to reveal the fascinating details described here from their studies across animal taxa, sometimes almost in isolation. Earlier work has been primarily accomplished as side projects to some other, sponsored research. In many instances, we only know one or two details of an observed behavior that might indicate vibrational communication, or we have a description of a morphological feature or sensory structure that is similar to one in members of a related taxon that signals via the vibration channel (Hill 2008). We continue to add to our list of species of interest as investigations reveal the role of substrate-borne vibration in their lives (i.e., Sandberg and Stewart 2006; Virant-Doberlet and Žežlina 2007), or we add to our understanding of the signals produced once use of the signal has been confirmed (Kroder et al. 2007; Quirici and Costa 2007). In other cases, more extensive empirical testing has given us sufficient knowledge of a communication system to actually use information coded in substrate-borne vibrations much as researchers use cues from any other communication system. Polajnar and Čokl (2008) have worked at this level to study disturbance of reproduction in a pest species of stinkbug and Elias et al. (2008) have used the body of knowledge on vibrational communication in jumping spiders to test game theoretical models of contests. More work is needed even on well-studied taxa in order to fully reveal the roles of substrate-borne vibration in animal communication.

A limited number of taxa have been studied extensively enough to examine how vibrational signals are used across a clade of related species. The decades-spanning body of work on the broad range of stonefly mating signals, framed in a phylogenetic context, from K. W. Stewart and colleagues (i.e. Szczytko and Stewart 1979; Sandberg and Stewart 2006; reviewed also in Hill 2008) provides a notable exception. Friedrich Barth and his colleagues have done the same with spiders, especially in the genus *Cupiennius* (i.e., Barth 1982; reviewed also in Hill 2008). DeVries (1990) studied a predation-avoidance symbiosis between a species of butterfly caterpillar (*Thisbe irenea*) and local ants. The larvae secrete nutritive substances that feed ants, and create substrate-borne vibrations with specialized papillae to attract them, while the ants protect the larvae from predators. Larvae not associated with ants are not able to survive predator attacks. When DeVries looked for evidence of such an association in related species, he found the same sort of vibratory papillae on 13 other species of riodinid larvae, which also lived in association with ants and produced substrate-borne vibrations to attract them. Of 19 species in this group from the same region that did not live with ants, DeVries (1990) found that none of them produced vibrations or secretions. Further work by additional research groups with taxa closely related to their own focal species might yield the same sort of rich data set for others.

A wealth of examples can be found in the behavioral ecology literature for taxa that exhibit behaviors suggestive of those in other groups that are known to produce substrate-borne vibrations. Looking where we have not sought to find substrate-borne vibrations before may yield important examples of ecological systems where vibrational communication is a critical component. Recently, Barbero et al. (2009) found another ant association where the larvae and pupae of a parasitic butterfly mimic the distinctive signals produced by the ant colony's queen. Unlike DeVries' mutualistic example, these larvae appear to be providing no benefits to the ants, which afford them a high status. Even though the authors did not suggest substrate-borne vibration as a potential mechanism used in the mimicry, they also did not test the acoustical pathway to eliminate vibrational signals from consideration. A similar situation exists with the wingless New Zealand tree weta in the genus *Hemideina*

(Field and Rind 1992; Field 1993; McVean and Field 1996), which exhibit dorsoventral abdominal vibrations typical of tremulation in other taxa (Supplementary Fig. 4). Males may stridulate to produce defensive signals, but what are assumed to be social signals are produced by abdominal oscillations produced while all six legs are on the substrate. No vibrational component has been identified for the social signals, even though McVean and Field (1996) proposed a hypothesis for communication via the dorsoventral abdominal movements.

The historical literature, as well as the results of experiments with related taxa, may provide us with interesting hypotheses to be tested. Darwin (1911) actually provided the background observations to motivate Mitra et al. (2009) and Catania (2008) to independently seek and find empirical evidence that confirmed for the first time that members of the Phylum Annelida respond to substrate-borne vibrations from a predator. Darwin noted as early as 1881 that earthworms emerge from the soil in response to pounding a shovel on the earth, and he speculated that the worms might be escaping predaceous moles. In the recent studies, vibrations could come either from foraging moles or from humans collecting the worms for fishing baits (worm grunting), suggesting that humans are exploiting the worm's innate response to predation pressure for economic gain.

One emerging trend seen when placing vibrational communication into a phylogenetic perspective is that even closely related taxa may utilize a range of signals and signaling mechanisms in a number of different contexts. Morris and colleagues studying bush crickets (katydids) in the neotropics (Morris 1980; Morris et al. 1994) found that species produced vibrational signals via tremulation, stridulation, and drumming in their communication systems (Table 2). The general pattern was for substrate-borne vibrations to be generated by males and to be made from

Table 2 Substrate-borne signaling in ensiferan Orthoptera

Species	Signal mechanism	Context	Males/females
Data extracted from Morris 1980			
Miogryllus sp.	Tremulation	Copulation	Male
Teleogryllus sp.	Tremulation	Copulation	Male
Gryllopsis sp.	Tremulation	Courtship	?
Orocharis (two species)	Drum (maxillary palps)	Courtship	Male
Nemobius sp.	Tremulation	Courtship	?
Oecanthus sp.	Tremulation	Courtship	Male
Conocephalus nigropleurum	Tremulation	Courtship/aggression	Male
Orchelimum sp.	None		
Copiphora rhinoceros	Tremulation/stridulation	Advertisement/courtship	Male
Neoconocephalus melanorhinus	Tremulation/stridulation	Advertisement	Male
Neoconocephalus retusus	Tremulation/stridulation	Advertisement/courtship	Male
Neoconocephalus triops	Tremulation/stridulation	Advertisement	Male
Neoconocephalus caudellianus	None		
Neoconocephalus exciliscanorus	None		
Neoconocephalus robustus	None		
Ephippiger sp.	Tremulation	Courtship	Both
Meconema thalassinium	Drumming (hindleg on leaf)	Advertisement	Male
Cocconotus insularis	Drumming (abdomen tip)	Courtship	Both
Data extracted from Morris et al. 1994			
Eschatoceras sp.	Tremulation	?	?
Cestrophorus sp.	Tremulation	?	?
Copiphora brevirostris	Tremulation/stridulation	Advertisement	Male
Docidocercus gigliotosi	Tremulation/stridulation	Advertisement	Male
Schedocentrus differens	Tremulation/drumming (abdomen)	Advertisement	Male
Myopophyllum speciosum	Short/long tremulation	Distant/close courtship	Both
Haenschiella sp.	Tremulation	Advertisement	Male
Choeroparnops gigliotosi	Tremulation/drumming (abdomen)	Advertisement	Male
Balboa tibialis	Tremulation/drumming	Advertisement	Male
Acanthodis curvidens	Tremulation/drumming	Advertisement	Male

and carried through plants. However, even within a single genus (*Neoconocephalus*), three species were found to signal with both tremulation and stridulation, while three species produced no observed vibrational signals. Current work with many animal groups continues to explore the potential use of vibrational pathways by taxa closely related to a species known to communicate this way. Fertile ground is found when researchers shift research foci to include studies from behavior to phylogenetics to neurophysiology to evolution.

New young scientists are now being funded by government agencies specifically to do research in vibrational communication; whereas, individuals labored early on just to obtain empirical support that such communication actually existed. Newer technology allows for more detailed analysis than was available in the 1980s, and the possibilities for other scenarios are expanding. For example, McNett et al. (2006) used two perpendicularly positioned transducers to characterize a plant stem in two-dimensions. This allows examination of the signaling environment of a six- to eight-legged animal perched on a plant, which can likely integrate sensory input from all its legs. Casas et al. (2007), using two laser Doppler vibrometers and wavelet analysis, have shown that a rush stem can transmit both dispersive (those with different component frequencies traveling at different velocities) and non-dispersive bending waves. In larger diameter stems, they found that propagation speed is independent of the stem diameter, and propagation speed is independent of frequency when frequencies are higher. Animals could thus produce non-dispersive bending waves by either signaling at higher frequencies or signaling on larger stems. In fact, Casas et al. suggest that the larger the stem, the harder it is to distinguish bending waves from surface waves such as Rayleigh waves that are known to be the primary waveform carrying vibrational signals from animals that signal on soil.

Work continues in a number of laboratories around the world to further illuminate the complex interactions among animals that signal via substrate-borne vibrations and the substrates upon which they signal. Perhaps an appropriate closing for this review would be to challenge others on several fronts: (1) to expand our number of known species that signal via substrate-borne vibrations by revisiting anomalies in the species we best know; (2) to be alert for historical examples we encounter in the literature (e.g., Darwin) of behavior that might indicate vibrational communication is being employed; (3) to examine related taxa when vibrational communication is confirmed in a species, especially in groups where phylogenetic relationships are known; (4) to search for additional communication contexts in which vibrational communication might be used once it has been confirmed in a species (i.e., predation, mating, and parental care); (5) to seek out alliances with colleagues in other disciplines with specific skills sets (i.e., engineering, technology, and historical perspective of a taxon) required to ask and answer vibration related questions; and (6) to allow ourselves to be skeptical, curious, and deliberate as we think about this heretofore ‘silent’ and ‘hidden’ world of animal communication.

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