

Chapter 2

Stretching the Paradigm or Building a New? Development of a Cohesive Language for Vibrational Communication

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Abstract Before we can recruit the broader community to share our conviction of substrate-borne communication in animals as ancient, important, widely employed in vertebrates, and perhaps exclusively employed in a broad range of arthropod taxa, we first must assess our current status within the animal communication paradigm and plot a course with that focused goal in sight. We must agree on the words we use to unambiguously communicate research findings among ourselves. We can do this rapidly through consensus, or allow terminology and protocols to slowly evolve to cohesion over an extended period of time through inaction. This chapter briefly explores the current position of shared core concepts on vibrational communication within the framework of Thomas Kuhn's *Structure of Scientific Revolutions* and suggests that the study of substrate-borne vibrational communication really can be accommodated within the dominant paradigm of animal communication. We require a reinterpretation of what 'everyone knows to be true' in some cases where empirical studies now have falsified previous widely held assumptions. A first step might be to develop a concerted, coordinated strategy that is widely employed by those currently studying vibrational communication. The paradigm can be stretched without being replaced, or we can forge a separate paradigm for vibrational communication. It is simply time to collectively decide on a course of action.

2.1 A Revolution in Progress?

In his theoretical framework to explain the history of scientific revolutions, Kuhn (1996) described a series of events that typically define the stages in establishing a new scientific discipline. At first, there is a period of observing and gathering facts,

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using existing tools and vocabulary from other established disciplines. Then, schools of thought are formed by like-minded individuals who seek to establish a paradigm, or shared methodology, that helps to answer the greatest number of questions of interest to the group. Competing schools of thought gradually disappear as evidence accumulates to support the paradigm of one group, and scholarly discourse moves away from general texts that are broadly read to journal articles that are accessible primarily to those who share the emerging paradigm. The school then may become an established discipline with its own societies, journals, and academic departments. Ultimately, the new discipline develops its own research technology and vocabulary, and finally its own textbooks.

2.1.1 *Fact Gathering*

The period of observations of vibrational communication among arthropods and other animals is centuries old (see Anderson 1973; Tributsch 1982; Snarr 2005; Hill 2008). Before there was a sense of the channel being employed, interested observers described what we now know to be substrate-borne vibrational signaling (e.g., book lice: Pearman 1928; termites: Emerson and Simpson 1929; Howse 1964). Even when the interactions among individuals were attributed to some other communication modality, sufficient evidence was included in the descriptions for us to now recognize them as classic vibrational communication systems.

Ossiannilsson (1949) produced an extensive treatise on leafhoppers where he described male alternation of calls, chorusing, male–female duets, and pitch variation with temperature. He suggested that vibrations produced by the tymbals of hoppers were conducted to receivers through the substrate. Working with bugs in the Cydnidae in the early 1970s, Gogala and his colleagues confirmed that the silent substrate-borne vibrations produced in signaling, rather than the airborne component audible to humans, was the adequate and essential stimulus used in mating interactions. They further described differences in signal frequency before there was much interest in more than the temporal component of vibrational signals (Gogala et al. 1974).

This period of fact gathering continues on at least two fronts. Those who have studied vibrational communication in one taxon are continuing to provide empirical data to fill knowledge gaps and are then often branching out to explore its use in unstudied groups. For example, Wignall and Herberstein (2013) described for the first time the repertoire of web-borne courtship vibrations of the well-studied model species *Argiope keyserlingi*. Mello and Dos Reis (1994) described a new species of phalangopsid cricket, but also included observations of foreleg drumming behavior and the substrate-borne vibrations produced that were required for successful mating. At the same time, those who have not yet been enlightened are still describing signaling that is highly likely due to substrate-borne vibrations, but ascribing the signals to visual or sound displays. Bringing this second group into the fold is a challenge that must be addressed.

2.1.2 *Taking Control of the Terminology*

While much of the work that has advanced our understanding of vibrational communication in arthropods has been carried out in relative isolation, the theoretical framework for this study composes a set of shared core concepts that have been elaborated in chapters of this volume and in earlier reviews for both arthropods and vertebrates (e.g., Kalmring and Elsner 1985; Devetak 1998; Virant-Doberlet and Čokl 2004; Cocroft and Rodríguez 2005; Drosopoulos and Claridge 2006; Hill 2008; O’Connell-Rodwell 2010). For example, we recognize that the term vibration as defined in engineering and physics encompasses all particle motion in a fluid medium, whether that medium is air, water, or a substrate such as the Earth or a plant body. Thus, our concept of sound is simply a subset of the larger category of vibrations that specifies a hearing organ as the receiver mechanism. We also recognize that at the boundary between two media, such as air/soil, water/soil, air/spider web, etc., energy being propagated as a vibration in one medium is always transferred to energy propagated in the other. So, even as one event can produce both airborne and substrate-borne vibrations, at the boundary between the air and substrate, we see exchange taking place between the two media that renders the entire distinction between sound and vibration a complex tangle. Ossiannilsson (1949) suggested long ago that whether we called something sound or vibration was simply a matter of taste.

Further, even though we recognize a range of vibrations that can be introduced to a substrate by a single event, not all of these appear to be used by animals as signals (see Markl 1983; Gogala 1985). In almost all cases, substrate-borne vibration signals travel as either Rayleigh waves (through the Earth) or bending waves (in plants). With both of these waveforms, particle motion is perpendicular to the direction of propagation or surface of the solid through which it is traveling (Gogala 1985), at least in part, and detection of the wave typically involves an inertial motion sensor that makes the animal’s stance with respect to direction of wave propagation important (see Lewis 1984; Hill 2008). Animals, thus, may experience Rayleigh waves as a pushing up from the surface on which they stand, but those on a plant surface experience bending waves as a whirling motion that pushes both up and to the side (McNett et al. 2006, see Cocroft et al. Chap. 13, this volume). As we continue to use newly developed tools and protocols in our investigations, we will continue to reassess prior interpretations of complex waveform interactions within a substrate. For example, while we have held for some time that the substrate on which animals perch must be continuous for individuals to successfully signal to each other (see Hill 2008), we have recently learned that this does not hold true always for leafhoppers (Eriksson et al. 2011). We may also need to rethink conventional wisdom on substrate continuity for other taxa, as well as to consider the role of some of the waveforms created by an event that have previously been discarded as likely not important to vibrational communication (see Hill 2008) as we learn more about the dynamics of substrate-borne waveforms.

Table 2.1 Examples of terms that could be assigned to a larger functional category

| Recommended Term | Synonym from Literature | Example of use by source |
|------------------|--|---|
| Drumming | Rapping | Clayton (2005) |
| – | Thumping | Salmon and Horch (1972) |
| – | Sounding | Broad and Quicke (2000) |
| – | Tapping | Pearman (1928), Zeigler and Stewart (1977) |
| Tremulation | Vibration | Fletcher et al. (2006) |
| – | Vibration signal | Lewis and Schneider (2000) |
| – | Dorsoventral abdominal vibration (DAV) | Rupprecht (1974) |
| – | Opisthosomal oscillation | Rovner and Barth (1981) |
| – | Body jerking | Henry (1979) |
| – | Thoracic muscle contraction | Kanmiya (2006a) |
| – | Tremble dance | Seeley (1992) |
| – | Begging signal | Esch (1961) |
| – | Stop signal | Nieh (1993) |
| – | Shaking signal | Seeley et al. (1998) |
| – | Spirit-tap | Milum (1955) |
| – | Queen piping: tooting, quacking | Michelsen et al. (1986) |

We also recognize common features among the mechanisms animals employ to generate substrate-borne vibrations in signal production. However, our historical literature is filled with terminology borrowed from physics and engineering and further refined to describe vibrational communication behaviors before we became aware of the size and scope of this communication modality. A range of jargon also was used to describe specific behaviors not reported before in the taxa being studied. This is part of the normal pattern during fact gathering in a scientific revolution before a more cohesive language has been developed. Still, some currently submitted manuscripts and grant proposals continue to use terms that have become ambiguous now that we have gathered enough data across taxa to see the commonalities in signaling mechanisms. This use of highly specific terms when describing behaviors that could be fit into a more generalized framework inhibits progress in pursuing both proximate and ultimate questions by limiting study to a novel behavior restricted to a single taxon.

In arthropods, we can distinguish at least four primary categories of signaling mechanisms that subdivide the general pool, based on shared signal parameters, into four rough functional groups: drumming, tremulation, stridulation, and tymbal buckling (Hill 2008, 2009, 2010). Yet, a range of terms, especially notable in describing drumming and tremulation events (Table 2.1), can be found in the past and current literature. Standardizing these terms is perhaps a very good point of focus for a concerted strategy.

2.1.2.1 Drumming

Drumming is the term used more frequently than others in recent years to describe the production of substrate-borne vibrations using some body part to strike the substrate in a percussive event. The body parts could be the abdomen, one or more legs, one or two feet, tails, teeth, antennae, various parts of the head (including an elephant's trunk), or other specialized structures. Basically, any body part that can be used to strike the surface is likely being used by some animal group, had we only time and resources sufficient to survey every one. Sometimes, the body part is modified, but often there is little to hint at its role in vibrational signaling. Ossianilsson (1949) used the term drumming to describe a very different phenomenon, and this has led to some confusion and proliferation of use of other terms.

Drumming on a substrate produces broadband, noisy signals that theoretically represent all frequencies produced by the event at equal intensity at the source of the signal. Spectral differences in the signal at the receiving end are due to filtering by the substrate through which the signal is propagated, and the temporal patterns are thus more important than spectral details to the individuals receiving drummed signals. Drummed signals often have both an airborne and a substrate-borne component and appear to be associated with habitats that are more heterogenous in substrate composition (Elias and Mason 2010). In the arthropoda, fiddler crabs (Aicher and Tautz 1990) and ghost crabs (Clayton 2005) signal via drumming, as do alderflies (Rupprecht 1975), ants (Kirchner 1997), Jerusalem crickets (Weismann 2001), wasps (Pratte and Jeanne 1984), gryllacrids (Field and Bailey 1997), heel-walkers (Eberhard and Picker 2008), and a vast number of spiders (Rovner 1975; Barth 1982; Uetz and Stratton 1982; Quirici and Costa 2005; Elias and Mason 2010), among others. Recently, Kojima et al. (2011) determined that pupae of a group-living beetle were able to signal via drumming to their larval family members that share the same soil space.

Vertebrate animals, especially mammals, are known to drum appendages as they signal (see Randall 2010). The first documented use of vibrational signaling in terrestrial mammals was for the Israeli mole rat (Heth et al. 1987; Rado et al. 1987), but drumming is known from at least 32 species in 11 families of mammals (Randall 2001). Drumming is the best known mechanism that mammals employ to produce substrate-borne vibrational signals, which are known almost exclusively as seismic signals that propagate through the Earth (Hill 2008).

2.1.2.2 Tremulation

Morris (1980) first used the term tremulation to describe body motion without any percussive impact with the substrate, and since then, a broad range of behaviors have been recognized that would fit within the set of criteria that define tremulation. The term was coined to describe a trembling, shaking, sometimes jerking, body motion in katydids (bush crickets) that introduced substrate-borne vibrations into the plants on which the animals were perched. Substrate-borne tremulations

are still known almost exclusively for animals that live and signal from plants. Typically, the vibrations pass to the substrate via appendages that couple with the surface (almost always legs/tarsi), but any body part (e.g., thorax) conceivably could be employed. Although animals across taxa produce non-percussive motions in communication that are distinctive, species specific and even context specific, thus arguably warranting a definitive descriptive term of their own, there are commonalities among the signals produced that allow us to group these into the single category of tremulation (Hill 2008).

Unlike drumming signals, tremulation produces substrate-borne vibrations in frequencies that are more pure tone, narrowbanded, and low in frequency. For example, in spiders, we find tremulation signals in the range of 1–300 Hz, and even very small oscillations of the body are sufficient to introduce vibrational signals into the substrate (Elias and Mason 2010). Arthropods that signal via tremulation have often been considered to be silent, due to the inability of humans to detect the low frequencies of their calls. Tremulation is a more effective strategy in environments with rather homogenous substrates, where low frequencies are not filtered or distorted as they are propagated (Elias and Mason 2010). Other than in katydids (Morris 1980; De Souza et al. 2011), tremulation is known, for example, from spiders (Rovner 1980; Dierkes and Barth 1995) and a variety of insects, among them planthoppers (Ichikawa 1976; Claridge 1985), whiteflies (Kanmiya 2006b), wetas (McVean and Field 1996), cave crickets (Stritih and Čokl 2012), groundhoppers (Kočárek 2010), lacewings (Devetak 1998), and bees (Sandeman et al. 1996; Kirchner 1997). There are surely others, including those with behaviors described in the literature that appear to be tremulations, but where the experimental design of a study did not include testing for possible use of vibrational signals.

We have also found production of tremulations in vertebrate animals that live and signal on plants (see Caldwell, Chap. 6, this volume). Caldwell et al. (2010) argue that arboreal vertebrates likely use substrate-borne vibrational signals to a much greater degree than is currently known, especially since almost all their movements excite the substrate. In the case of the red-eyed tree frog, all known signaling behavior produces stereotypical vibrational waveforms. Other modalities, especially visual displays, have been assumed in the past to be the mechanism of information transfer in tremulating vertebrates. However, in the red-eyed tree frog, which has been so well studied for its predator-induced rapid hatching response, experimental evidence confirms that substrate-borne tremulation vibrations provide the necessary and sufficient stimulus to elicit a tremulation response from other male competitors (Caldwell et al. 2010).

Tremulation by vertebrate animals that signal through the soil has not been described, but neither have we actually looked for this. It would take a very large animal to induce substrate-borne vibrations with a tremulation, but what about the rumbling vibrations that elephants produce with vocalizations (Hill 2010)? We may need to develop consensus after a dialog to consider a fifth category for vertebrates, vocalizations, but perhaps we can also manage to fit our examples into one of the four groups suggested here and consider whether these elephant vibrations are functionally close enough to plant-borne tremulations to warrant that label.

2.1.2.3 Stridulation

Animals produce both airborne and substrate-borne vibrations as they rub one body part against another, generating friction. Stridulation is rather common in the Arthropoda, but in most cases, we do not yet know whether both the airborne and substrate-borne vibrations produced are actual signals used by the animals. Typically, a specialized file and scraper mechanism can be identified, and at least eight different types of these are known in spiders (Uetz and Stratton 1982). A variety of possibilities exist for the body components used (wing–wing, leg–wing, two body segments, etc.; see Wessel 2006), and signal characteristics vary with the body parts used (Hill 2008).

The substrate-borne vibrations produced by stridulation are generally higher in frequency than those produced by tremulation (Elias and Mason 2010), and they may include harmonics, unlike the broadband noisy signals produced by drumming (see Hill and Shadley 2001). Stridulation is known from ghost crabs (Clayton 2005), spiders (Hebets and Uetz 1999; Elias and Mason 2010), and a large number of insect groups (e.g., ants: Kirchner 1997; beetles: reviewed by Wessel 2006; dung beetles: Kasper and Hirschberger 2005; cerambycid beetles: Breidbach 1986; psyllid bugs: Tishechkin 2006; water bugs: Theiß 1982, etc.).

An interesting interpretation has been suggested by Kenneth Stewart that a rubbing of a body part against the substrate is ‘actually a body-substrate stridulation’ (Stewart 2008, 4103). A ‘scraping’ with the mandibles has been described for larvae of hornets (Ishay and Landau 1972; Ishay and Schwartz 1973; Ishay et al. 1974), and both scraping and plucking are known in cherry leaf-roller caterpillars (Fletcher et al. 2006). In addition, caterpillars of the Lepidopteran genus *Drepana* exhibit mandibular and/or anal scraping behaviors (Yack et al. 2001). These substrate-borne vibrational signal-producing behaviors were classified under ‘other mechanisms’ in Hill (2008), but in keeping with the theme of this chapter, stretching the current definition to include rubbing a body part against the substrate seems logical, as well as provocative, in anticipation of the possibilities for additional uses of the label.

2.1.2.4 Tymbal Buckling

Tymbals are specialized features of the exoskeleton of the lateral first one or two abdominal segments in cicadas, their non-cicada relatives in the Auchenorrhyncha, other bugs in the Hemiptera, and some tiger moths (Shaw et al. 1974; Shaw and Carlson 1979; Claridge 1985). Hoch et al. (2006) described substrate-borne vibration production via a putative simple tymbal by a member of the ancient Coleorrhyncha now found in Australia. Although the exact mechanism of signal generation has not been confirmed, physical characteristics of the first two abdominal segments and properties of the signal itself are consistent with tymbal-generated signals in cicadas and others. These observations support the argument that communication via tymbal vibrations, as well as drumming and stridulation, is at least 230 million years old in insects (Hoch et al. 2006).

Tymbal structures may be thinner walled or thicker regions of the exoskeleton, but vibrations are produced as muscles attached to the inner surface of the membrane contract to distort or buckle the tymbal in an in-and-out clicking motion (Hill 2008). In addition to his observations of behavior, Ossiannilsson (1949) described tymbal anatomy for 79 species and signals produced by tymbal buckling for 96 species of Auchenorrhyncha. Animals that possess tymbals may also produce substrate-borne vibrations through tremulation (Shaw and Carlson 1979) or stridulation (Gogala 1985); however, Ossiannilsson (1949) commented on the lack of information available on the tymbals and songs of the non-cicada relatives, especially when considered in light of the wealth of details available for cicadas. Work continues in a number of laboratories to document mechanisms of communication in species that possess tymbals.

2.1.3 Schools of Thought, Publications, and a New Sub-discipline: Increasing Accessibility and Broadening the Scope of Study

While some researchers who are new to the study of vibrational communication, or who are exploring the possible use of this modality in an unstudied group, are still gathering facts, for the most part, the community has moved beyond the school of thought to a functioning paradigm-based entity that communicates through scholarly articles and interactions at professional meetings. Yet, we have not become a discipline, even a sub-discipline, in the biological sciences with dedicated journals and academic departments or exclusive professional societies. I would suggest that individual working groups have not completely abandoned a degree of isolation in our scholarship, even though we are in clear agreement on basic core principles of animal communication via substrate-borne vibration. This is not to trivialize the practice. How does one make that leap? How do you define your peer group, and who is the audience of focus to whom you report research findings, when your questions are all interdisciplinary or cross-disciplinary in nature? How do you design experiments to test hypotheses of evolution of communication in your taxon of interest when no phylogeny exists, or when you observe a behavior but know nothing of the underlying morphology, or when the most closely related species and genera are just as poorly studied as the one that becomes your passion? How do you go back to the sloggish efforts of descriptive studies after you have experienced the freedom to test models in your previous work? Fortunately, the synergistic effects of collaboration in interdisciplinary investigations can be just as rewarding. Seeking collaborations and forming alliances outside our own expertise helps to broaden the scope of study and may open unexpected doorways to new possibilities.

Even as we have studied signals and continue to document the array of sending mechanisms employed by the arthropoda, receiving mechanisms are still poorly

known for many major groups, with a few exceptions. An array of invertebrate mechanoreceptors (reviewed in Hill 2008, Lakes-Harlan and Strauß, Chap. 14, this volume) are known: scolopale joint receptor, campaniform sensilla, hair sensilla, Johnston's organ, subgenual organ, tarsal scolopidial organ, mid-coxal protuberance, trichobothria, slit sensilla (BCSS in scorpions and lyriform organ in spiders), and Barth's organ. However, receivers have been fully described only in the legs of two species of green lacewings (Neuroptera) (Devetak and Amon 1997; Devetak et al. 2004) and two species of heelwalkers (Mantophasmatodea) (Eberhard et al. 2010).

Studies of the complex tibial organ (a complex of the subgenual and intermediate organs and a crista acoustica homolog) in the Ensiferan Orthoptera are underway and yielding a wealth of data with far-ranging consequences for our collective progress (Strauß and Lakes-Harlan 2008a, b, 2009, 2010, 2013, see also Chap. 14, this volume). The research initiative that has so far described the neuroanatomy and physiology of this complex in the legs of raspy crickets (Gryllacrididae), Jerusalem crickets (Stenopelmaticidae), splay-footed crickets (Schizodactylidae), and stick insects (in the sister group of Orthoptera, the Phasmida) has yielded sufficient data to map this character onto existing phylogenetic trees to generate or support hypotheses on relatedness and evolution of communication systems in the Ensifera. In so many other groups where substrate-borne vibration signaling is well documented for a small taxon, or for one behavioral context in a larger group, insufficient comparative data are available to do more than speculate on evolution of the signal strategy. Therefore, being able to work across sub-discipline boundaries provides us with the opportunity to explore substantive questions once the low-hanging fruit has already been harvested from the safety of the mainstream, but at the same time, we face the challenges of working within methodologies and terminology that are less familiar, which can be daunting.

Taking up these challenges, Michelsen et al. (1982), in turn, challenged conventional wisdom on propagation of substrate-borne vibrations through plant tissue by actually testing a variety of insect species signaling on a variety of plant materials and producing a variety of context-specific signals. In the history of studies of animal communication via this channel, it still amazes that what everyone knew/knows to be true is sometimes based on little to no empirical evidence. Data from studies of other groups have been extrapolated to draw conclusions without confirmation. Actual experiments designed to falsify these established facts often have indeed falsified them. Michelsen's group thus set the bar for research on vibrational communication when the substrate is plant tissue. They were able to confirm, among other things, that plant-borne vibrations were filtered by the substrate in similar ways by both fresh and dry leaves and that vibrations could travel 1–2 m through a green stem without much loss of energy at the dominant frequency, even traveling up and down a stem several times at detectable levels. Since then, data continue to accumulate with the use of new technology to support our understanding of the signaling environment of a three-dimensional plant stem. McNett et al. (2006) used two transducers, rather than the single one used in prior studies, and placed them in position perpendicular to each other to more accurately model the world an animal encounters as it perches with

all its legs in contact with (and gathering input from) a plant stem. Challenges continue to be addressed with creativity and effort.

One rich area for further study is to use newer technology or techniques from other sub-disciplines to examine substrate-borne vibration use by animals across contexts in groups for which signals in one context have already been confirmed. Virant-Doberlet et al. (2011) used molecular tools to examine predation of leaf-hoppers in the genus *Aphrodes* for which both male and female calling signals are known. The experimental evidence they obtained from PCR analysis of gut contents, along with playback and microcosm trials, was able to confirm for the first time that arthropod predators could not only use substrate-borne vibrations produced by prey to locate and capture them, but that they could use information in male mating signals to assess prey abundance, rather than randomly foraging on males, females, and nymphs.

My interest in vibrational communication sprang from necessity, as the male mole crickets I was studying in hopes of gathering data that could be used in making conservation decisions failed to respond to simulations of the loud air-borne calling songs of other males. They did, however, respond with maddening consistency to the vibrations produced in the substrate by ceasing to call when one tried to approach them (Hill 2008). I was interested in revealing details of population ecology, life history, and mating behavior in order to construct quantitative models, but only two papers on the species existed at the beginning of my work. In the end, our research group needed expertise in mechanical engineering and bioacoustics, molecular genetics and phylogenetics, neurophysiology, soil science, biostatistics, and more. Yet, we have not really suffered as behavioral ecologists from the lack of an exclusive disciplinary home for vibrational communication studies as much as we have from the lack of field-worthy equipment that is not prohibitively expensive. This represents a related, but separate and ongoing challenge.

2.1.4 A New Paradigm, or a Challenge of the Common Ground?

The question then remains, do we really require a new and different paradigm that is separate from that employed by those who study communication via sound signals, or even from the general methodology important to studying communication in general? If not, then how do we best provide our ‘silent singers’ with a voice, at last? At this stage, and without a strong argument for increased isolation, making a place for ourselves within the dominant communication paradigm seems the best option. A concise vocabulary is essential for us to, at minimum, communicate efficiently with each other. We simply must agree upon the definitions of terms that we use. Most with research interests in substrate-borne vibration have already done so, but I suggest that we must rigorously require this of others as we

share ideas in person and through peer reviews of manuscripts and funding proposals. For any 'new' ideas to be taken seriously by the extended community, they must first be defended seriously and consistently by those who require the dominant paradigm to be stretched to include them.

Once we examine our shared core concepts of substrate-borne vibrational communication, whether from vertebrates or invertebrates, none of them really is in conflict with traditional components of the dominant paradigm in animal communication. For example, the definitions for unidirectional and bidirectional airborne communication (Gerhardt and Huber 2002) could be slightly modified to accommodate a single individual of either sex searching for a silent sedentary mate, as well as the full range of mating strategies we know from substrate-borne vibrational dueting (Hill 2008). Does it really matter whether the female searches for a sedentary male, or the male searches for the female? Or, does it matter whether only one sex calls instead of both calling in an alternating sequence? Perhaps what is more important is how these communication systems might have evolved across taxa within the constraints of calling and mating investment strategies (de Groot et al. 2011). Our search for commonalities and standardization of terminology in communication simply requires that some established truisms be re-examined now that our technology is sufficiently advanced to make testing for substrate-borne vibrations accessible when anomalies persist in any body of work. We can be thankful to those whose curiosity and efforts provided adequate observational details upon which we can build evidence for vibrational communication, even as we appreciate the challenges of working in a climate that in some ways inhibited looking for the vibrational signals in the first place. When we first confirmed that leaf-cutter ants stridulate to produce signals that recruit help when a nest mate is buried (Masters et al. 1983), why would we have considered that the airborne component of this signal was not all that was produced, or that it would be in any way ineffective in recruitment? Yet, 10 years later, we learned that recruits respond to the substrate-borne component produced by stridulation when it is presented alone, but not to the airborne component alone (Roces et al. 1993). Likewise, wolf spiders exhibit clear visual mate-attraction displays as they wave their ornamented legs, but the substrate-borne vibrations produced by drumming are both sufficient and essential to elicit female response in a courting pair when the pair is not in visual contact (Gibson and Uetz 2008). Anyone who hears a calling cicada experiences a very clear signal that is impossible to ignore; however, Claridge et al. (1999) explained that this loud airborne vibration is derived from a substrate-borne vibration system still being used by their silent Auchenorrhyncha relatives. Adult cicadas have thousands of sensory cells that converge on only a few interneurons that carry hearing information to the brain for processing. The presence of so many receivers suggests that cicadas are capable of very fine-tuned discrimination in hearing, but our inability to find more interneurons suggests to Lakes-Harlan and Strauß (2006) that these thousands of cells must have had a different function in the cicada's evolutionary history. They propose that larval cicadas in the soil have substrate-borne vibration-sensitive scolopidial organs that are merely retained in the adult, even if they have no

function in adult hearing. Since this hypothesis was proposed, Chuche et al. (2011) have looked for, but been unable to confirm, use of vibrational communication in nymphs of the grapevine leafhopper. They found no vibrations in the substrate other than those that could be attributed to incidental movements, and nymphs did not respond to playback stimuli, nor did they respond to substrate-borne vibrations produced in the presence of actual predators. Still, this hypothesis opens a huge portal, not just a window of opportunity, for further research into the evolution of communication through substrate-borne vibration in the cicadas and their relatives, as well as other groups, with only a bit of stretching of the dominant paradigm.

When Philip Brownell was a PhD student working with Roger Farley to tease out the details of how sand scorpions were able to locate and capture their prey so quickly and efficiently, he worked within a paradigm where conventional wisdom held that vibrations in a natural substrate could not carry biologically meaningful information in a signal because of the inelastic medium and the propagation speed of the waveforms. The best that could be hoped for was some sort of alerting mechanism that a disturbance had occurred (see Schwartzkopff 1974). However, when Brownell falsified every hypothesis that did not involve vibrational signaling, he was forced to test and then challenge this conventional wisdom. He found that instead of damping low-frequency vibrations, the sandy substrate on which sand scorpions foraged conducted both Rayleigh waves and P-waves and conducted them slowly enough so that his scorpions could use information produced by prey in motion to locate and capture a meal (Brownell 1977, Brownell and Farley 1979a, b, c). Once the evidence was published, no dissenting camp actually emerged. These findings were then used by Briceno and Bonilla (2009) to explore vibrational communication by scorpions in other contexts and to identify a sort of tremulation ('judder') used in mate attraction and/or courtship.

The tick-tick-tick of the death-watch beetle was described in the 1600s, but Birch and Keenlyside (1991) were the first to test whether communication was through airborne or substrate-borne vibrations. Their very simple, but effective, experiment tested mating response by a female to a calling male. If they were on the same substrate, the female responded. If they were on adjacent pieces of wood, she did not. If the adjacent pieces were brought into contact, she then responded. No transducers or laser vibrometers were employed in this study, but the results strongly support the conclusion that the substrate-borne component provides the sufficient and essential stimulus to elicit a mating response. Both males and females drum in a reciprocal duet. She is stationary, and he searches for her, but he requires repeated responses from her in order to reach her location, perhaps because their body dimensions are small in comparison with the wavelengths in the drummed signals (Goulson et al. 1994). However, determining that the audible tick-tick-tick was only an artifact of the mechanism that produced substrate-borne vibrations that encoded the mating signals does not challenge the dominant paradigm. It simply requires a revised interpretation based on emerging evidence.

If we then continue to standardize our terminology, increase accessibility of our work, and broaden the scope of study, there are at least two areas that require additional efforts if we are to successfully challenge the common ground held with

those who study airborne vibrations and hearing. As of yet, we do not have a consistently used metric to quantify substrate-borne vibration amplitude, and this impedes communication among researchers across disciplines. Airborne vibration amplitude is described in decibels, and even if others use different metrics at times, everyone knows what is meant by dB. We do not have a common amplitude metric for substrate-borne vibration studies, but perhaps a candidate is available in the wings, waiting for an advocate to step forward. Secondly, as a community, we must address the issue of waveforms and work beyond their mystery. Those who study airborne vibrations do not have to condition playback signals when designing manipulative experiments, because the medium of our atmosphere does not filter multi-frequency signals the way that substrates do. When researchers try to switch from sound to vibration studies, they sometimes try to play a signal recorded from a natural source through the substrate without any modifications, and the observations they make are compromised by this. Indeed, we might say the observations are without merit of any consideration because the experimental design is flawed. Even some editors do not understand why the signal conditioning is vital to substrate-borne vibrational studies and trivial to airborne vibrational studies. Both of these issues may be easily addressed, but they could represent serious barriers to integration of vibrational studies within the culture of animal communication.

2.2 Conclusion

The body of evidence documenting the importance of substrate-borne vibrational communication across arthropod and vertebrate taxa, across millions of years of the Earth's history, and throughout the Earth's habitats is growing in volume and richness. Using emerging technology, as well as basic empirical hypothesis testing, vibrational communication systems are being confirmed wherever questions are being asked. When we look for use of substrate-borne vibrational signaling, we find it. In making this wealth of information more accessible to the broader community, and in establishing vibrational communication as a component of the animal communication paradigm with the same standing as communication via sound, visual, or chemical signals, we must police our own use of descriptive terminology. Before we can speak authoritatively to the broader scientific and lay communities and command their attention, we must first define the limits of terminology we use to speak to each other. Our shared core concepts can be accommodated under the umbrella of the existing animal communication paradigm. We simply need to make sure we speak with a collective voice in our own very civil, and short-lived, revolution.

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