

# Chapter 2

## What Is Biotremology?



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**Abstract** When a new discipline emerges in science with many unique characteristics, but others that are shared with sister disciplines, defining the boundaries is critical. What is and is not part of the core precepts of this discipline is probably easier to establish within the community than what exists along the edges. Due to our perceptual bias in favor of airborne mechanical signals, a distinction between bioacoustics and biotremology, the former studying communication by sound and the latter by surface-borne mechanical waves, may appear unnecessary. In this chapter, the authors make the first concerted effort to define *biotremology* with comprehensive arguments, in order to address the specifics of this modality, while still leaving space for exploration and growth of this still-emerging field. Biotremology studies are not limited to intraspecific vibrational communication, but also include other behaviors guided by substrate vibrations.

### 2.1 Introduction

In the most basic sense, biotremology is the study of *vibratory* communication behavior through use of substrate-borne boundary, or surface, mechanical waves (Hill and Wessel 2016). Biotremology is thus one of the newest science disciplines,

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having only been identified, as such, by a name since 2014. Consequently, for some researchers, biotremology is the word with which we identify from the very start of our careers; however, for many, vibrational or seismic communication, or even communication via substrate-borne sound, still feels more familiar. The first recommendation for a name was *tremology*, suggested by J. Endler (2014) to emphasize the study of vibrations or tremors. This name also serves to acknowledge the early use of *tremulation* to describe one mechanism for producing signals in this communication modality (Busnel et al. 1955, for a translation see Chap. 4) by that scientist to whom this book is dedicated, and the increase in awareness of the mechanism after its consistent use in the literature (Morris 1980; Morris et al. 1994). From that beginning, the term *biotremology* was introduced to further clarify the scope of work included in the new field for the broader scientific community, distinguishing it from studies of naturally produced mechanical waves in the environment from an abiotic source. This introduction of a name was made as part of an argument that this new science can be unambiguously distinguished from our better known sister-discipline, which focuses on auditory communication through sound (Hill and Wessel 2016). Use of the biotremology modality, itself, is considered to be ancient, perhaps evolving along with chemical communication in the early Metazoa (Endler 2014), and research continues to reveal more evidence of just how ancient it is. Further, the communication modality is widespread, especially in arthropods and vertebrates, yet the field is still considered to be emerging and gaining recognition at a rapid pace (Cocroft et al. 2014).

Animal behavior linked to this vibratory communication modality has been described for at least 3000 years (see Tributsch 1982; Snarr 2005), yet even descriptions in the early twentieth century did not suggest that signals were being exchanged via an unknown silent pathway. Rather the descriptions were reports of interesting examples of communication associated with production of barely audible sounds (Pearman 1928; Emerson and Simpson 1929). Even the seminal work of F. Ossiannilsson (1949), which was based on systematic observation of morphology, behavior and description of signals produced by almost 100 species of small cicada relatives, was unable to confirm his suspicion that the essential mating stimulus traveled through the substrate. In fact, he left us with the suggestion that whether we wanted to call the signaling mechanism sound or vibration was simply a matter of taste. The confirmation of the vibratory signal was left to H. Strübing (1958, see full translation, 2014), who was aware of Ossiannilsson's inconclusive results (2006), and during her long career published at least 25 biotremology papers on both descriptive and experimental work (Wessel 2014).

It is a rare and humbling gift to be able to experience and document the emergence of a new scientific discipline as it is emerging. The greater gift is to do so while pioneers are yet able to sit together and describe to peers and students their own wonder and excitement as they worked toward a greater understanding of the compelling questions they pursued. Many of these pioneers worked and survived almost in isolation, while asking questions that may have seemed important only to themselves. It must be even more inspiring for students, whose careers will build on the collective knowledge gathered prior to the emergence, to actually be

able to probe and question the living human sources, rather than to form their own interpretations based on readings, alone. Because of the generosity and essentially unprecedented level of collaboration of these pioneers and their students, the science of biotremology has been able to accelerate in numbers of taxa studied, and to incorporate knowledge from related disciplines, as it continues to emerge.

Another huge boon for the discipline is in the willingness of the pioneers to fully and generously collaborate with newcomers and multiple generations of students, instead of withdrawing to rest on their laurels. A fairly common experience is for founders to hold onto the form and focus of the earlier schools of thought, yet in biotremology, there truly seems to be a practical sense of the common good of the science. When those who contributed to terminology to describe a new behavior of their study animal were asked to consider that behavior as part of a larger mechanism, they did not resist what others might have considered a demotion of the status of a now widely used term, which had been coined by themselves. When many of us who talked of *seismic* communication by our study animals were educated to understand that we were effectively eliminating participation in our new school of study by all those who worked with animals that signaled through plants, or the water surface, or honeybee combs, or spider webs, there was almost an overnight shift in the vocabulary. There was some collaborative discussion, but essentially no arguments, as we worked to rapidly establish ourselves as more than a fringe element. Because of this multigenerational cooperation, our shared vocabulary has gone from an interesting but non-cohesive set of terms, borrowed from physics and engineering and newly coined words for newly discovered behaviors, into a sustainable, evolving terminology that is supported and used by the vast majority of the researchers in biotremology.

## 2.2 Why Can Biotremology Not Be Accommodated Within Bioacoustics?

During the emergence of biotremology as a discipline, the term *bioacoustics* has been almost exclusively restricted to a cross-disciplinary area that merges biological and physical theory in the study of *sound*. Even within biology, and even within animal communication, bioacoustics describes some aspect of the study of sound, with sound being carried through the atmosphere, or more rarely through water, as mechanical waves that are detected by some sort of *ear*. From the ear, which acts as a receiver mechanism and a transducer, information carried in mechanical waves through the medium is carried through nervous tissue to some processing area, such as a brain or ganglion. In the earliest stages, and still today for some practitioners, the concepts that define biotremology were most logically and simply assigned space within the bioacoustics subdivision of animal communication theory . . . both could still be referred to as sound from this perspective. Yet, patching up a shared paradigm was not without problems.

The commonalities shared by sound and what has been called *vibration* are obvious and numerous. Both sound and vibration are propagated through a medium via mechanical waves, which based on the vocabulary of physics makes both these waves *acoustic* and both *vibration*. No one would argue against an assertion that studies of these two phenomena are more closely related than either of them is to any other animal communication modality. Yet, there are differences.

By the commonly accepted definition, sound is carried via compressional waves, also known as P-waves, or pressure waves, and detected by pressure receivers or pressure-difference receivers, known as ears. Whether the medium through which sound propagates is the atmosphere (a gas) or the hydrosphere (a liquid), the same waveform is the physical stimulus detected by the animal ear. In fact, if compressional waves travelling through the lithosphere (a solid) actually stimulate some sort of ear in a totally subterranean animal, rather than one in an air-filled burrow, then substrate-borne sound also exists. At this time, knowing that energy contained in vibrations travelling through a medium will transfer to another medium at a boundary between the two, the case for pure substrate-borne sound has not been made, convincingly (but see Brownell and van Hemmen 2001).

While physicists or engineers accept that a vibrating source emitting mechanical waves simultaneously creates both airborne and substrate-borne components, for biologists the transmission medium has many fundamental implications, even beyond recognized physical effects of substrate on the propagation of mechanical waves. Airborne and substrate-borne components of a mechanical signal originating from the same source follow different pathways, not only through the environment. On the one hand, airborne sound travels through a relatively homogenous medium, while due to unpredictability and heterogeneity, natural substrates with their differing physical properties can limit the effective range of the vibrational component by damping and degradation of vibrational signals. On the other hand, for example, the majority of insects relying on far-field airborne sound in their communication detect sound via paired ears on their body (reviewed in Yack 2004), while they receive substrate vibrations via various types of vibroreceptors located in all six legs (reviewed in Lakes-Harlan and Strauß 2014).

Moreover, conventional wisdom is that information detected as airborne sound or substrate-borne vibration is processed in functionally different networks within the central nervous system (see Virant-Doberlet et al. 2006; Stritih and Stumpner 2009; Strauß and Stumpner 2015). Taking into account that the vibrational sense and communication are also evolutionarily older than audition and airborne sound communication, our current body of knowledge suggests it is more than likely that they also follow different evolutionary paths. Yet, very little research has focused on the *perception* and processing in the nervous system of information carried from vibroreceptors in all animals, or via bone conduction in vertebrate animals. We are still at the stage of studying these vibroreceptors and *detection* of signals and cues, while how the information is processed is still a black box. The studies that have considered both structure and function in an evolutionary context are few. The argument has been advanced that the insect auditory organ has evolved from the vibration-sensitive subgenual organ (see Shaw 1994). Likewise, earlier

studies in primates have revealed that information detected by both auditory and somatosensory (vibration) receptors in macaque monkeys (Schroeder et al. 2001) and humans (Fuxe et al. 2002) project to a multisensory region of the auditory cortex in the cerebrum. Thus, for one environmental event that is both “felt” and “heard,” information is processed in the same region of the brain, regardless. Furthermore, the environment with its unpredictability and heterogeneity of the natural substrates imposes different, as well as much stronger, constraints and effects on the evolution of signals and behavior in the vibrational than in the auditory channel. Clumping acoustic and vibrational communication together as one modality, therefore, hides some crucial aspects and hampers our understanding of mechanical communication, in general. In this context, we also wish to emphasize that due to our perceptual bias in favor of airborne sound, researchers often by default describe every stimulus and signal formed by mechanical waves as sound, even when the modality is clearly vibrational (see Matsushashi et al. 1998; Ghosh et al. 2016).

After collectively struggling for at least 5 years with the issue of where our work and its developing vocabulary fit into the larger study of animal communication, we proposed a working vocabulary that left the term bioacoustics as the division of animal communication that studies sound. Biotremology became the new term for the study of communication and behavior associated with all non-compressional mechanical waves (Hill and Wessel 2016).

Until perhaps the last 5 years, most researchers working within the school of thought now called *biotremology* were focused on substrate-borne vibrational communication in a limited number of taxa (i.e., mammals, frogs, spiders, and insects in the Hemiptera and Orthoptera). Sorting out the evolutionary relationships and common mechanisms used to send and receive signals, the neural processing paths, the variations based on ecological context, the variations based on functional context, and the unique behaviors of each group have dominated time and effort for many years. Most of the work has fit within the paradigm of communication signal theory (i.e., Endler 1993), especially in defining what constitutes a *signal*. Yet, other behaviors that employ the same sending and receiving mechanisms and neural pathways fall outside our current understanding of the relationship between signaler and receiver organisms. Within the communication signal theory paradigm, the term *cue* has been used to describe a non-evolving use of information by non-intended receivers that do not, in turn, change behavior in such a way that the fitness of the sender is increased (see review in Bradbury and Vehrencamp 1998).

For example, predators and prey do not employ strategies that define a classic communication system, yet we include the study of predators and prey in biotremology because of the intrinsic use of *vibrational behavior*. Within the realm of biotremology, predators perceive prey by detecting what we think of as *incidental* vibrations in the medium and have evolved morphology and behavior that increase the probability of efficient, successful prey capture due to detection and neural processing of these incidental stimuli. At the same time, prey species have coevolved traits that exploit morphology and behavior and allow them to elude capture as they detect and respond to the vibrations produced by the predators. This perspective does not easily integrate with the current definition of *cue*, which

has been considered to be passively acquired information without any influence that might be interpreted as selective on the prey's morphology or behavior. Yet, if a predator encounter is frequent, rather than a rare event, some prey responses predictably lead to survival, while the absence of the response (or employment of some different response) leads to death. Should a mechanism in either class of response be heritable, the response traits will be under positive or negative selection and behavior will evolve. Using this same reasoning, the predator's behavior could also evolve without either predator or prey actually communicating in the traditional sense. Thus, in biotremology to date we have been referring to the stimulus in these exchanges as cues.

### 2.3 Behavior That Defines Biotremology

From the pioneering works of Ossiannilsson (1949), Strübing (1958), Gogala et al. (1974) and Ichikawa and Ishii (1974), insects from the order Hemiptera have been one of the groups at the center of biotremology studies. In agreement with the August Krogh principle that “for many problems there is an animal on which it can be most conveniently studied” (Krebs 1975), these small and inconspicuous insects probably provide the most comprehensive insight into life in the vibratory world (Wessel et al. 2014). Relying on substrate vibrations in intra- and interspecific interactions is particularly common in hemipteran insects and, in some groups, animals rely exclusively on vibrational signaling (see, e.g., Wessel et al. 2013).

To provide one example, in illustration, the leafhopper *Aphrodes makarovi* (Hemiptera, Cicadellidae) provided an insight to selection on duetting vibrational communication systems. In this species, mate recognition and location is mediated exclusively by species- and sex-specific vibrational signals. Partners form a precisely coordinated duet characterized by a species-specific structure (Derlink et al. 2014; Kuhelj et al. 2015a, 2016). Each vibrational exchange is initiated by a male advertisement call to which a sexually receptive female replies, thus triggering male search for the female on the plant. While in this species a higher calling rate increases the probability of the male locating the female (Kuhelj et al. 2015b), it also has a detrimental effect on the male's survival, due to eavesdropping predators (Virant-Doberlet et al. 2011) and indirect costs arising from high energy expenditure (Kuhelj et al. 2015b). Although calling effort is negatively correlated with longevity, some males invest more in calling in early life and die younger, while the others invest more in calling in late life and survive longer. The duration of a female reply, which is highly variable, is negatively correlated with male calling effort (Kuhelj et al. 2016). By increasing her reply duration, a female can significantly reduce the male's direct and indirect costs associated with signaling and searching, thus ultimately affecting male reproductive success. In turn, the male–female duet in this species entails more complex interactions than just temporal coordination, and males show high plasticity in adapting their signaling behavior to the duration of the female reply. However, in a competitive setting the

most important factor in obtaining the female for mating appears not to be the calling effort invested in finding the female, but the ability to locate the female before the rival (Kuhelj and Virant-Doberlet 2017). In the presence of a rival, the males obtaining the female invest more in competitive behavior (interference by masking signals and exploitation by eavesdropping on a duet maintained by the rival, then silently approaching the female). Importantly, studies done on *A. makarovi* showed that a comprehensive understanding of male mating success, as well as female preferences, in duetting systems requires investigations in a setting that is complex and more realistically represents situations in nature.

## 2.4 Behavior Near the Limits of Biotremology

Biotremology encompasses the study of behaviors, and use of the knowledge based on these behaviors, in ways that are not traditionally included in communication research based on sound waves. For example, the entire body of research based on induced rapid hatching is outside the animal communication paradigm for the same reasons described for predator-prey systems (see Sect. 2.2). Yet, research on induced rapid hatching via substrate-borne incidental cues has been invaluable in expanding our knowledge of detection of these cues by otherwise understudied taxa, and revealing the ability to discriminate these waveforms from those induced by rain, wind or other environmental events (Warkentin 2005; Warkentin et al. 2006). We also have learned about new structures and mechanisms that one day may be found to be rather common. Likewise, this new knowledge from outside the communication paradigm can be used *within* the paradigm after it has been discovered.

Another area of focus within biotremology is the exciting use of lessons learned from more traditional studies in an applied way to address very real problems of the human existence. As a result of a growing realization of the ubiquitous nature of vibrations in the environment, and about the importance of vibrational signals and cues in insect behavioral decisions, the interest in exploiting substrate vibrations in pest management also increased in recent years (Čokl and Millar 2009; Mankin 2012; Polajnar et al. 2015). Every movement of the insect body or its parts induces vibrations in the substrate and such incidental vibrations induced by walking and feeding can be used for monitoring. Detailed knowledge of the biology, ecology and behavior of the target species is essential in order to exploit or manipulate insect behavior. Many insect pests rely on vibrational signaling in pair formation. Current applications of biotremology include the use of species-specific vibrational signals emitted in sexual communication for automatic detection (Korinšek et al. 2016) or for playback to attract insects to traps (Mazzoni et al. 2017) and interruption of mating behavior by playback of natural or synthesized disruptive vibrational signals (Mazzoni et al. 2009). Although vibrational mating disruption is a novel approach (Eriksson et al. 2012), it already has been transferred to the field in vineyards (Polajnar et al. 2016; Krugner and Gordon 2018). In the future,

human agricultural and natural resource sciences, which continually search for better and safer Integrated Pest Management practices, will greatly benefit from use of knowledge gained in studying mating behavior to interrupt or prevent continued mating of a crop or forest pest. Again, the improvements in technology possible, and new knowledge of mechanisms and behaviors shared, by studies relegated to either pure or applied science in the past have benefited from strong collaborations among biotremologists.

Lastly, the biotremology community has recognized and embraced the important role of education and art in complementing and advancing more traditional scientific investigations (see Chaps. 22–25). Since our field is still emerging, a simple agreement among the community has been possible to consider contributions from education and art to raise awareness of this entire world of natural behaviors that have mostly gone unrecognized by humanity, including many who work in animal communication.

## 2.5 Conclusions

The depth and breadth of the science of biotremology is, thus, still being refined, even as we seek to fill in the framework built to study the classic communication systems that first captured the attention of our founding scientists. Our school of thought continues to bridge discipline boundaries as we recruit fresh eyes and new toolkits to gain access to seemingly intractable questions. Our research questions push investigations into new taxa, new contexts for taxa where this sort of vibrational communication is already known, and even into understudied ecological habitats and niches. We have recently proposed a clear separation of space between what we all know as *sound* and *vibration* (Hill and Wessel 2016) after years of discussing whether they were best studied together because of their commonalities, and belonged together in the same corner of the *animal communication* tent.

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