Animal Signals and Communication 6

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Biotremology: Studying Vibrational Behavior

Springer

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Volume 6

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To
René-Guy Busnel
(30 November 1914–14 August 2017)

Allocution of René-Guy Busnel[1]

Dear Colleagues,

I am sorry that because of my age (102 years old) I am not adapted anymore to the pleasure of traveling to come in person to meet you all. I am very thankful that you have given attention to such ancient observations[2] which occurred during my active youth in science.

Tremulations were, at the time, a mere side observation in our study on the role of acoustic signals in the communicative capabilities of different animal species. We would never have imagined that these observations could lead to such an important and growing new field. Even though, we should have, since Karl von Frisch at the time was describing in detail the different forms of bee's tremulations in the hive. He did recognize in these a real vocabulary.

I wish to express my admiration for the dynamism of all your researches which allowed this new field of behavior and bioacoustics to bloom and become a science on its own. Please accept my sincerest wishes for a forceful development of biotremology in the world of experimental science.

All my thanks to Prof. Hannelore Hoch and Dr. Andreas Wessel who had the ability to discover these descriptions in the enormous amount of new facts and observations in our publications and were able to achieve such an efficient contact with us.

I am sure this first International Congress will help to give biotremology a new impact.

Good luck to you all.

Paris, France R.-G. Busnel

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[1] To the participants of the 1st International Symposium on Biotremology, 5–7 July 2016, San Michele all'Adige, Italy, on the occasion of the awarding of the Insect Drummer Award.

[2] See Chap. 4, this volume.

Acknowledgments

We gratefully acknowledge and thank the Fondazione Edmund Mach, Valerio Mazzoni, and his local organizing committees (Floriana Marin, Anna Eriksson, Gianfranco Anfora, Cristina Castellani, Gonzalo Cervantes, Michela Angeli, Alessandro Gretter) for hosting Biotremology 2016 and 2018, our first two international conferences for the newly emerging science of biotremology. These provided an excellent opportunity to meet as a community, to talk in person, and to form alliances that have allowed our new scientific discipline to grow rapidly and to flourish in a very short period of time. We appreciate the patience, support, and enthusiasm of Andrea Schlitzberger, our Springer Project Coordinator, and Lars Koerner, our Editor at Springer Nature. We further thank Vincent Janik and Peter McGregor, editors of the Animal Signals and Communication series in which this volume is included, for their support and encouragement. AW particularly thanks Hannelore Hoch and the Museum für Naturkunde Berlin for a workplace. Last but not least, we would like to thank all biotremologists for their dedicated work and exciting research.

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Part I

Studying Vibrational Behavior: Ideas, Concepts and History

Chapter 1
Quo Vadis, Biotremology?

Peggy S. M. Hill, Valerio Mazzoni, Peter Narins, Meta Virant-Doberlet, and Andreas Wessel

Abstract In the past 5 years since the publication of the forerunner of the present volume, we have witnessed a dramatic increase in research, published and ongoing, in the field of vibrational communication—the range of taxa studied and of methods used is expanding rapidly, the questions asked are multiplying and are more sharply delineated. This international collaboration of editors, representing Germany, Italy, Slovenia, and the USA, attempt as authors to provide an update on the status of the new, and still-emerging, scientific discipline of biotremology, comprising recent research, reviews, and first attempts to synthesize. Introducing and examining the highlights of the content of this 25-chapter book give the reader a preview in the form of a snapshot of the chapters that follow. In addition, these authors have the freedom to explain fine points and aspects of the bigger picture of the field. Perhaps most importantly, they can suggest what is left to learn at this moment—in effect, "Quo vadis?" Where are we going?

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1.1 Introduction

“Quo vadis, biotremology?” Where is this still-emerging discipline headed in the near, and in the more distant, future? If a field that is growing at the current pace of biotremology (Cocroft et al. 2014a) can be managed, or directed, what impact do those currently working in the field have on managing the growth? What is their responsibility, and who is empowered to decide whether individual entities are doing their part? This is the challenge for this potentially youngest of biology disciplines, which has only carried a name of its own for fewer years than can be counted on one hand (Endler 2014). Where is this movement going?

In this first, and introductory, chapter to Part I and the volume, we editors use the structure of the part topics to consider the directions in which the field is already moving. This allows us to harness the latest research and enthusiasm of our authors to describe where we are now, where we are moving in the short term, and what defines our dreams for the future with respect to the shared vision that unites us as biotremologists. We attempt not only to define *biotremology* for those who are unfamiliar with the new term but also to answer the question asked by even senior researchers in the field, “What is biotremology?” (see Chap. 2). Chapter 3 provides a general model for thinking about biotremology within the context of other sensory modalities. This can aid us in more easily recognizing gaps to address in our future research, as well as posing a series of topics and questions that might be fertile ground for future study. In addition, we present a classic paper (in translation) from the pioneer researcher who coined the term “tremulation” (see Chap. 4).

In 2014, we published our first edited volume as a community (Cocroft et al. 2014b). In the introductory chapter for that book was a figure representing average number of peer-reviewed papers published in our field per year at 5-year intervals between 1990 and 2010 and based on five specific search terms in Google Scholar: vibrational communication, vibratory communication, substrate-borne communication, substrate-borne signals, and seismic communication. The results were as follows: 1990–1995 (11), 1995–1997 (15), 2000–2005 (19), and 2005–2010 (26). This represented accelerating positive growth over a relative short time period.

Since then the numbers have dramatically increased. A reliable and easy to follow indicator for the growth of the field is the use of the term *biotremology*, which had been proposed as a name for this scientific movement within our network in mid-2014 but introduced to the broader community in a publication in early 2016 (Hill and Wessel 2016). Searches in Google Scholar only for the term *biotremology* show an increase from one publication in 2014 (included in the database not before mid-2015) to 62 in January 2019. Even on a year-to-year basis, and using this error-prone unscientific method of comparison, numbers of publications have increased more than double per year between 2014 and 2018. While the growth is sustainable, with an overall exponential increase, a significant rise since spring 2018 is evident (Fig. 1.1).

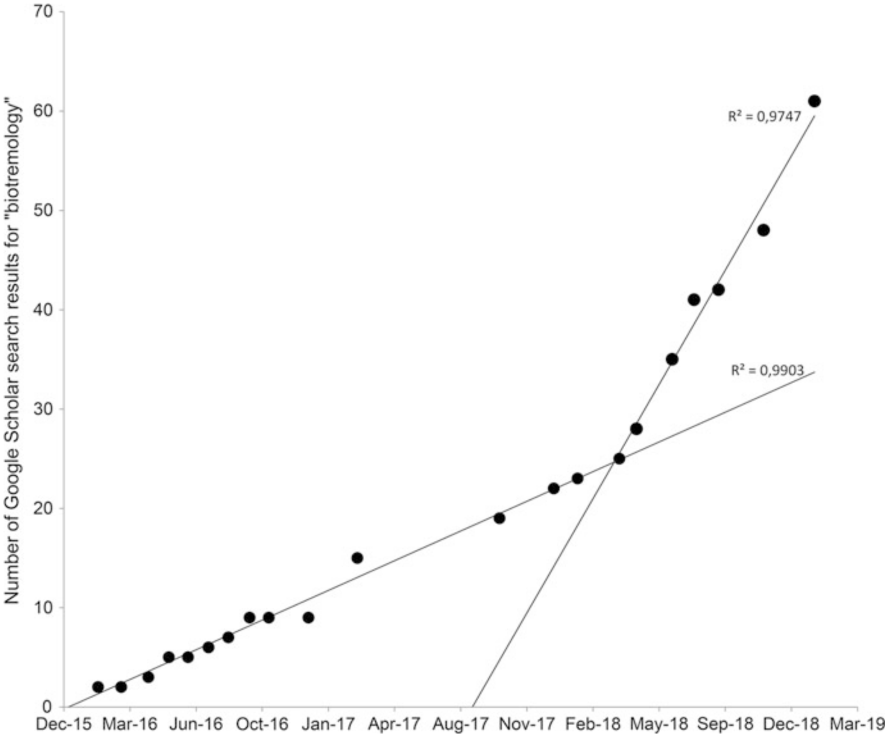

Fig. 1.1 Results of Google Scholar searches for the term *biotremology*, over the period from December 2015 to January 2019. The search results reflect the actual numbers for a full search on a certain day, and did not use the "custom range"-function for a retroactive limitation of search time periods. This method allows for a finer temporal resolution, but includes a "time lag" as the publications do not appear immediately in the database. The regression lines comprise the periods from December 2015 to March 2018, and April 2018 to January 2019, respectively. For each of these two time periods the increase in search results is highly significant, linearly. Figure credit: AW

Further, a look at the topics reveals a broadening of scope for biotremology spreading away from the core study of animal communication to include studies of questions from technology and environmental noise to neuroscience and art. Many more publications now simply use biotremology as a key word term as part of a theoretical base, as they would in a paper that focused on bioacoustics or chemical ecology. Many more taxa are included under the umbrella of biotremology from across the range of life-forms, and many more research groups are emerging from around the world to join and enrich the conversation.

1.2 The State of the Field: Concepts and Frontiers in Vibrational Behavior

A representative sample of the current state of the field of biotremology could yield active research lines in a dozen or more different areas. All would be part of this new field that is held together by the common thread of studying behavior in some way related to non-sound mechanical vibrations. For example, even though we have borrowed technical terms from engineering and physics to help us describe and discuss findings in biotremology, there are very few publications with an engineering focus. An overview of biotremology on natural substrates addresses this issue, and the problems encountered with both heterogeneous substrates and noise (see Chap. 5). Yet, some areas, such as evolution, are not at all adequately represented.

In the recent past (Cocroft et al. 2014a), concerns included the lack of study of environmental noise, and the strict separation of studies of the airborne and substrate-borne communication channels in many taxa. Currently, these two concerns are much less urgent due to an increase in research in these areas, but research framed in an evolutionary context is still rare. Noting that most of our research on sexual behavior (mate location and pair formation) stops with copulation, Chap. 6 reports on a literature review of vibrational communication within a mated pair during and after copulation. A number of questions are posed, whose answers could contribute to the study of sexual selection of sending and receiving organs, as well as signals and behavior. To date, very few publications in biotremology address questions in evolution, possibly because very few taxa have been adequately studied to the extent that the questions can be asked. Yet, even in well-studied taxa, such as the stinkbugs in the Pentatomidae, major new strides are made in understanding complex reproductive behavior if an integrative approach is used to study multimodal signals, such as airborne sound, pheromones, substrate-borne vibrations, touch, etc. (see Chap. 7).

1.3 Practical Issues in Studying Vibrational Behavior

In the past decade, our perception and understanding of the vibrational communication modality has changed significantly; however, our own perceptual bias in favor of airborne sound communication still hampers our understanding of challenges that animals relying on substrate vibrations in their intra- and interspecific interactions are facing in their environment. Above all, we lack more personal experience of the complexity of the natural vibratory world (i.e., vibroscape) around us, something that we intuitively recognize when dealing with airborne sounds in our environment. However, in order to understand the nature of selection imposed by the environment on the vibratory channel, it is necessary to determine the sources and their relevance in the evolution of signals and behavioral strategies of the signalers and receivers under realistic ecological conditions. Due to technical and logistic challenges, biotremology studies were traditionally carried out primarily in the laboratory, and although we are already aware of the richness of the natural vibratory world around us, it is also patently clear that we know very little about it. In order to get an insight into a more ecological context of vibrational communication and obtain information about the strategies animals use to communicate and behave in the presence of other conspecific and heterospecific signalers and receivers, as well as abiotic noise under natural conditions, taking our equipment to the field is crucial (see Chap. 8).

In recent years, progress in computer technology, affordability of electronic equipment, and development of algorithms for signal recognition have led to many applications of automated detection and recognition of animal species that rely on identifiable sounds. Although automated vibrational signal recognition is a useful tool—either to speed up the analyses of vibroscape recordings or to monitor insect pests—the application of such an approach still lags far behind the use of automated airborne sound recognition. However, designing such an autonomous automated recognition and playback system, capable of working in real time, also provides a powerful tool to study coordinated reciprocal interactions characteristic of many vibrational duets (see Chap. 9).

1.4 Vibration Detection and Orientation

Much of our research, as biotremologists, has been devoted to describing signal or cue production mechanisms, characterizing the variation in species-specific signals used in different contexts, and describing the variety of receivers of these signals across animal taxa. Very few taxa have a representative whose ability to detect signals and cues has been studied extensively. Less is known about the perception processes (see Sects. 1.8 and 2.2), even in taxa with well-known detection abilities. This section is devoted to reviewing evidence that mammals and insects are capable of detection and possibly orientation toward the source of a signal or cue. Each chapter employs case study analyses along with a review of the literature.

Mammal communication is perhaps fascinating to humans because we, too, are mammals. For all the interest, surprisingly little research has been conducted to confirm the ability to produce and detect non-sound vibrational signals in most mammals (see Chap. 10). The story is further complicated by the potential for mammals to detect substrate-borne vibrations with end organs of the somatosensory system (most have Pacinian corpuscles that function in this role) and also for these vibrations to travel through various bone-conducted pathways to converge with hearing pathways in the ear. In Chap. 10, the potential for mammals to detect substrate-borne vibrations through the somatosensory and auditory systems is reviewed through the extant literature and evaluated based on these findings. Through the use of case studies, the literature on two mammals that are perhaps the best studied with respect to vibrational behavior (the elephant and the blind mole rat) is specifically reviewed to document and evaluate what is known of their ability to detect, and perhaps orient toward, a substrate-borne vibrational stimulus.

A great deal more is known about the organs capable of detecting substrate-borne vibrations across insect taxa, even if some groups are better-studied than others, and substantial variation is known across the Insecta (see Chap. 11). For example, while most insects have a subgenual organ in the interior tibia of their walking legs as their most vibration-sensitive receiver, beetles and true flies do not. The full range of all leg vibration receivers rarely has been explored fully for most insect taxa, but in Orthoptera, these organs have been used as factors that provide evidence of phylogenetic relationships and other evolutionary implications (see Chap. 11, and review in Lakes-Harlan and Strauß 2014). Most compelling in Chap. 11, however, is the authors' next step to include case study analyses to reveal the very real challenges in comparative studies imposed by differences in experimental design while making neurophysiological measurements. By not employing a standard protocol across insect taxa, or in some cases not clearly identifying parameters that most influence measurements of vibratory thresholds, comparative studies are often an exercise in comparing apples and oranges. The authors discuss the importance of things like leg position and stimulus calibration in measuring vibratory sensitivity.

Insect orientation to vibrational cues and signals has often in the past been confirmed through behavioral studies that do not carefully exclude other signal modalities, such as the use of chemical, visual or sound stimuli (see Chap. 12). For this reason, the ability of insects to orient to a vibration source has been questioned and remains controversial, for example to some peer reviewers, even when the greatest care is taken with precision in the experimental design. In Chap. 12, case studies are used to review vibrotaxis in a few well-studied taxa within the contexts of behavior and substrate properties, following a discussion of the potential for orientation based on vibrational cues and signals propagating through common substrates.

1.5 Biology and Evolution of Vibrational Behavior in Some Well-Studied Taxa

This part contains chapters that are reviews of some aspects of vibrational behavior in a range of animal taxa: Of the largest living land mammals (elephant), anuran amphibians (frogs), and two taxa of insects, the very small insect order of heel-walkers and a large diverse order of social insects, the termites. The commonalities in these chapters may be found more in the authors, than the taxa studied. In each case, vibrational behavior in these "well-studied taxa" are being presented by those scientists who arguably know the most about them, at least one author of each chapter having studied vibrational behavior in the group for 15–34 years. Therefore, while not all are widely-known animal taxa, they are intimately well studied by the authors who present them to us.

Mammals are known to have two specific systems associated with detection of vibrational signals and cues: Somatosensory and auditory pathways (see Chap. 10 and Sect. 1.4). In Chap. 13, published evidence for the use of both pathways is presented and discussed, along with details of potential sending mechanisms. While much is known from experimental data obtained using geophone transducers with wild elephant herds in the field over a period of 20 years, questions remain unanswered in this complicated story. The primary focus is narrowed here to bone-conducted vibration detection, and new research is presented from anatomical and 3D laser vibrometry data that enable comparisons of elephant and human sensitivity to low-frequency vibrations in the bones (ossicles) of the middle ear. Clearly, elephants have the capacity to send and receive vibrational signals and cues over great distances, but teasing out the importance of each is still a fascinating work in progress.

All amphibians tested are known to be sensitive to substrate-borne vibrational signals and cues, and some of them are extremely sensitive. Likewise, they have two pathways similar to those of mammals for conduction of information from the substrate to the ear, as well as two interesting common mechanisms for production of substrate-borne vibrations. In Chap. 14, four frog and two toad species are highlighted for their sensitivity and known characteristic vibrational behavior. Although salamanders can be highly sensitive to substrate-borne vibrations, resulting behaviors in contexts where information detected from the vibrations is actually used has still not been confirmed. As to date only relatively few species in the Anurans have been studied for this largely cryptic communication modality, a wide range of associated phenomena are to be expected in future research.

The order Mantophasmatodea, or heelwalkers, is the most recently discovered high-ranking insect taxon and was described first in 2002. It is known from only 21, yet described, species in sub-Saharan Africa. Males and females both produce drumming vibrational signals, apparently used primarily for mate location. The male signals can be used to distinguish species, and all species have highly sensitive receiving organs, consisting of five different scolopidial organs in each of their six legs. The current state of what is known about these recently discovered insects is reviewed in Chap. 15, and a phylogenetic framework for further evolutionary studies is introduced.

In contrast, termites are known from 2600 species in seven families around the world, but not everyone knows that they are a fully eusocial group of cockroaches (see Chap. 16). The extensive literature on vibrational communication and behavior in termites is reviewed in Chap. 16, including sending and receiving mechanisms and a wealth of fascinating descriptions of contexts in which substrate-borne vibrations are used. A very special feature in termite communication is the construction of a self-build vibrational environment, the nest, and the evolutionary selective forces acting on this. The organization of the topics in the chapter facilitates access to this very large set of detailed information.

1.6 Applied Biotremology

Applied Biotremology has grown considerably in the past few years. In less than a decade, from a mere curiosity, it became the center of interest of multinational companies in the field of pest control, especially for those that consider alternative solutions to chemicals as their core business (see Chap. 17). With the movement around the globe of people and commercial products, invasive species have, in many cases, increased dramatically in numbers to become major pests of crops, as has the glassy-winged sharpshooter in California vineyards in the USA. Efforts to control damage by this species have led to research on introducing vibrational waves into the grape vine stems to prevent communication required for mating (see Chap. 18). From 2017, vibrational mating disruption has been applied in a commercial vineyard in Northern Italy, while more research is being conducted on many other crop pests, such as stinkbugs (see Chap. 19), psyllids (see Chap. 20), and whiteflies. These same procedures are also being studied to protect forests from invasive bark beetles (see Chap. 21). Vibrational signals have many common points with the now "classic" semiochemicals, and for this reason they should be addressed as "semiophysicals" or "semiomechanicals". We think that the constant and rapid development of technologies (i.e., electronics, informatics, and energetics) is quickly filling the gap to become applicable to this purpose, and for this reason it is time to include substrate-borne vibrations in the farmers' and foresters' toolbox, because the methods that emerge from lessons learned have a valuable potential for use as a tool for pest control in the future.

1.7 Outreach and Resources

One issue that has slowly become clear to those of us trying to define the boundaries of biotremology is that of common mechanisms … for producing/sending, receiving/detecting, and perhaps even processing for perception, of signals and cues … across taxa. Evolution has provided an intriguing array of possibilities in, for example, the use of *tremulation*, the production of vibrations by body motion that does not involve percussive contact of a body part with the substrate on which the animal is living. Vibrations are transferred to the substrate from the body of an individual by whatever structure couples the body to the substrate. We know from the research that has given us the name, biotremology, that a broad range of animal taxa communicate through tremulation, and this mechanism is known across all taxa studied that have the ability to move in such a way as to tremulate. It requires no evolution of a specialized structure necessary to the production of vibrations, other than those involved in the ability to move, which is characteristic of all animals. This one example supports the wider ranging challenges and opportunities for biotremology that have led us to the contributions of this final part of our book.

We have known, since the earliest conferences where the authors of chapters in this volume first met, that much is required of us in increasing awareness of our emerging field. Publications of scholarly articles and presentations at international meetings are vital but so is education of the coming generations of citizens of the world, not merely of students whose interests already are focused on a career in biotremology. Thus, we are proud of a teaching methods contribution (see Chap. 22), which makes the task of organizing laboratory exercises seem so easy that we are much less intimidated by the first step. Further, the techniques are linked to pedagogy in such a way as to help all those who are required to consider assessment of learning outcomes in their course syllabi, or even funding requests for laboratory equipment.

The commonality of mechanisms across taxa has also stimulated the development of a VibroLibrary at the Animal Sound Archive of the Museum für Naturkunde Berlin (see Chap. 23). Researchers can not only compare digital files of species-specific signals to pursue questions of relatedness and evolution but also increasingly dig deeper into commonalities of signal parameters associated with mechanisms across taxa. A chapter in this volume will help increase awareness of the availability of this valuable resource, as well.

The final two chapters in Part VII, and thus of the book, are very special inclusions. They explore the interface of science and art. Specifically, the spider web and its construction are examined as a communication device for the spiders who build the web, as well as a platform for potential communication between spiders and humans, even if simply the sort of communication that evolves with awareness of the world of the other living form (see Chap. 24). Likewise, the commonalities among human-produced sounds and vibrations and those of other animals have long been recognized. Why else would we refer to the ones we most appreciate and enjoy as *songs*? The term *bioacoustic music* will be introduced to most of us for the first time through a dialog between a scientist, who is also a musician, and a musician who is also a scientist! They write, "This chapter is not about science," (see Chap. 25). Yet, for both of our final two chapters, the commonalities among science and art, and especially with the technology that humans create in an attempt to access the artistic world created by the non-humans, is provocative and inspiring. It helps us to penetrate the surface and look deeper into animal communication and thus allow ourselves to engage the beauty of the world inhabited by our study species. This, too, has a home in biotremology.

1.8 What Is Left to Be Learned?

We look forward to exploring new and under-studied areas and to unlocking secrets beyond our imagination, as we have done already in just a few years of coordinated study and use of new technology in biotremology. Yet, in our field we also should benefit greatly from studies of the past. Endler (2014) stated, "Vibration and chemicals are the oldest modes of communication and both probably evolved from the original cell-cell mechanical and chemical interactions within early metazoans" (p. vii). This position is almost completely unexplored. There is a sense in our community that we need to focus more efforts on the evolution of communication and behaviors tied to substrate-borne waveforms. There certainly is a broad-ranging diversity of sending and receiving organs across animal taxa that yet function as common mechanisms. Anonymous reviewers often voice a criticism that our collective arguments are not based on an evolutionary framework. How many times has the ability to use information contained in these non-sound producing waveforms evolved? Based on what we know, it might be very few. We will never know if we do not look, and few studies have looked. However, we have learned that structures required for tymbal vibration, drumming, and stridulation had all evolved in insects by 230 million years ago (Hoch et al. 2006). This gives us a starting point for investigation that goes both backward and forward in time from that era. To twist the warning of Santayana (1905) into a more hopeful iteration, if we do know the ancient history that led to our discipline, we can use that base to shape our future acquisition of knowledge.

One very important area, rich in the potential for new knowledge that could stimulate further research in dozens of directions, is that of *perception* of a signal or cue. Much of our work with communication in biotremology has been focused on how information is sent or received, and increasingly how it is filtered as it propagates through the substrate … how the substrate facilitates or impedes information transfer. We have learned a great deal about how signals and cues are detected from a working group in our own community (Lakes-Harlan and Strauß 2014; see also Chap. 11), but how the information is processed in the animal's nervous system is still something of a cipher for many study systems (see discussion in Chap. 2).

Of particular interest to this discussion of perception and neurological processing is the information detected from non-sound mechanical vibrations. Every movement, including genuine signaling behavior and incidental cue production, produces a combination of surface-borne waves (Rayleigh, or R-waves; Love, or L-waves; Pressure, or P-waves and perhaps others not yet associated with mechanical waveforms used in communication: see Markl 1983; Gogala 1985; Aicher and Tautz 1990; Hill and Wessel 2016; reviewed in Hill 2008). Each of these waves possesses different propagation characteristics, but all are initiated by the same individual or group movement. When considered as a unit, such a combination of different waves can be used for spatial orientation. For example, Brownell and Farley (1979) showed that scorpions use the differences in the propagation velocity of P-waves and R-waves (150 m/s:50 m/s), which they perceive with different sensory organs (tarsal hair receptors v. basitarsal compound slit sensilla). Such a combination has a greater potential (information) transmission capacity than pure P-waves (sound), if animals could perceive the complex 3-dimensional particle oscillations. Thus, we need 3-dimensional measurements as a standard to estimate the real information content of a vibrational signal, and knowledge about the 3-dimensional perception by animals, to know whether they can make use of them and to better understand the perceptual world of animals.

Another promising future direction for biotremology is to overcome the difficulties in studying pure vibrational propagation in the laboratory. To use an analogy, it has long been known that studying an animal's response to underwater sound in relatively small aquaria can be an exercise in frustration. The sound emitted from the underwater source (e.g., a speaker) may strike the intended receiver, but will inevitably be accompanied by multiple reflections from the walls and floor of the tank. Eliminating these reflections is non-trivial and has motivated workers to study underwater sound detection by animals either in enormous tanks (Grimm 2011), in enclosed bays (Houser et al. 2005) or in the open sea (Au et al. 1974).

Similar constraints exist for researchers studying the biological response of animals to seismic propagation in soil or sand in a laboratory enclosure. Preliminary progress in this area has been made recently in reducing P-wave reflections from the walls of a sand tank by lining the entire tank with open-cell foam, and by burying the transducer 2–3 cm beneath the sand surface and orienting it so that it faces the surface at an angle of 45°. Moreover, the back of the transducer was embedded in a layer of open-cell foam. These procedures resulted in nearly complete elimination of interference patterns and reflections in the sand tank with dimensions 90 × 90 × 20 cm (Narins et al. 2016).

We have much to learn about the role of plants in biotremology, and this area was not covered (Endler 2014) in the earlier book in this series that came from our biotremology community (Cocroft et al. 2014b). Since then, studies have shown that plants should not be viewed as just another inert substrate that supports a communication channel. In fact, we have learned that plants can set up chemical defenses when stimulated by plant-borne vibrations that are induced by a feeding herbivore and that the plant can discriminate vibrations induced by wind or signaling insects from those of feeding insects (Appel and Cocroft 2014). Further, a new study of the behavior of frogs signaling from a plant surface reveals that the substrate not only will filter and change some parameters of the call-induced vibrations, but the behavior of the frog can be directly influenced by the characteristics of the resulting vibrations that travel through the plant (Narins et al. 2018). This study is doubly valued because it also addresses the interaction of airborne and substrate-borne communication channels that were a major concern 4 years earlier (see Sect. 1.2) and encourages further research with vertebrate animals in this area.

In fact, much is to be learned from integrating studies of substrate-borne vibration with airborne vibration, chemical communication, and visual communication in studies of multi-modal communication systems. The opportunity to join these conversations has been built on mostly recent research in signal production and detection that revealed at least some of the complexity yet to be explored in biotremology.

While it is now recognized that vibrational signaling is one of the most widespread forms of animal communication (Cocroft et al. 2014a), the complexity of the natural vibroscape remains unknown and how species relying on substrate-borne vibrations interact at the level of community is virtually unexplored. The first ongoing studies revealed complex and dynamic vibroscapes (see Chap. 8), and we can start not only asking questions about interactions shaping the evolution of vibrational communication, but also how the vibroscape can help us to understand ecological processes and ecosystem dynamics, thus extending biotremology to ecotremology (Šturm et al. 2018).

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Chapter 2
What Is Biotremology?

Peggy S. M. Hill, Meta Virant-Doberlet, and Andreas Wessel

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 perceptional 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 (Foxe 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 perceptional 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 Matsuhashi 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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Chapter 3
Biotremology and Sensory Ecology

John A. Endler

Abstract Biotremology has developed enormously since the previous book in this series was published in 2014. As is common in a rapidly growing subject, the growth is uneven with some aspects of biotremology, as well as some species groups, covered more deeply than others. This chapter attempts to encourage work in all aspects of the subject by presenting a scheme that summarizes most of the component processes, puts biotremology in the context of other sensory modes, and briefly discusses some of the gaps in the field.

3.1 Introduction

In the 5 years since the previous book in this series (Cocroft et al. 2014a) was published, the new field of biotremology has grown and expanded enormously in breadth. Biotremology has become a vibrant field. We now have more information on more organisms (both invertebrate and vertebrate), more mechanisms, more and improved techniques to detect, record, and even discriminate vibrations from different species, and we have a good idea of how vibratory signals are generated, transmitted, and received in a few species. Initially, there was almost no information on the vibroscape of any species, the environment as sensed by species with vibration receptors, but now its importance is being realized and data are being collected. A major difference between vibratory landscapes and the visual, sound, and perhaps chemical and electrical sensory landscapes is that vibroscapes are very heterogeneous over small distances and times. This makes characterizing them, and estimating signal/noise ratios in order to understand vibratory communication, much more difficult than in other sensory modes. In addition to summarizing the latest results and new techniques, three new research directions are also presented in this book: the use of vibrations to disrupt and control insect pests, field recordings to

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census vibratory species communities for use in both conservation and agriculture, and the first consideration of vibratory communication immediately before, during, and after copulation. In addition, four final chapters show how biotremology is an excellent way to teach science, a proposal for a vibration archive, and how vibratory organisms can be used in interactive performing arts. Chapters 1 and 2 (this volume) do an admirable job of summarizing all the chapters; so I will not summarize them here. Instead, I will present a general scheme for thinking about biotremulation processes, derived from my thoughts whilst reading the chapters, and also use it to put biotremulation in perspective with other sensory modes. This may help organize research as well as make research gaps more obvious. I will then discuss, in the context of the scheme, some of the questions generated by the chapters and the scheme.

3.2 Mating Sequence

I will present the scheme for mating as a way to organize our thoughts, concepts, and research. Mating is one form of communication in which conspecifics come together for reproduction. Signaling and communication also include conspecific social signals, both cooperative and agonistic (Maynard Smith and Harper 2003), but also signaling between predators and prey (Bradbury and Vehrencamp 2011; O'Hanlon et al. 2018). Vibration signals can be sent and received in any of these contexts. For example, *stotting* (Bradbury and Vehrencamp 2011) includes a visual signal but may also produce both sounds and vibrations due to jumping and ground thumping, and any of these modes can be received by both conspecifics and potential predators, and used to minimize predation risk. Another example of vibration used to minimize predation is the use of vibrations in plants caused by a mammalian browser, discriminated from vibrations due to wind, used by *Crematogaster mimosae* ants to trigger defensive behavior (Hager and Krausa 2019). I am concentrating on mating because it includes longer behavioral sequences and processes than many other forms of communication, except possibly social communication in complex animal societies, and therefore allows a general discussion of how vibrations and other signals can be used.

I will use *mating* as shorthand for all processes leading to gamete union and zygote formation. Other social interactions, such as male–male interactions, and information flow in complex societies (e.g., ants and termites) fit into the scheme up to, but not including, copulation (except in some primates). There are two parts to the scheme: (1) processes facilitating communication and mating during the mating sequence (Fig. 3.1) and (2) changing processes with changing distance between communicating individuals (Fig. 3.2). I have intentionally made the scheme general enough to apply to all sensory modes and allow multiple modes in the same sequence.

A successful mating (in the sense of all processes leading to zygote formation) consists of both a sequence and network of interacting processes from detection

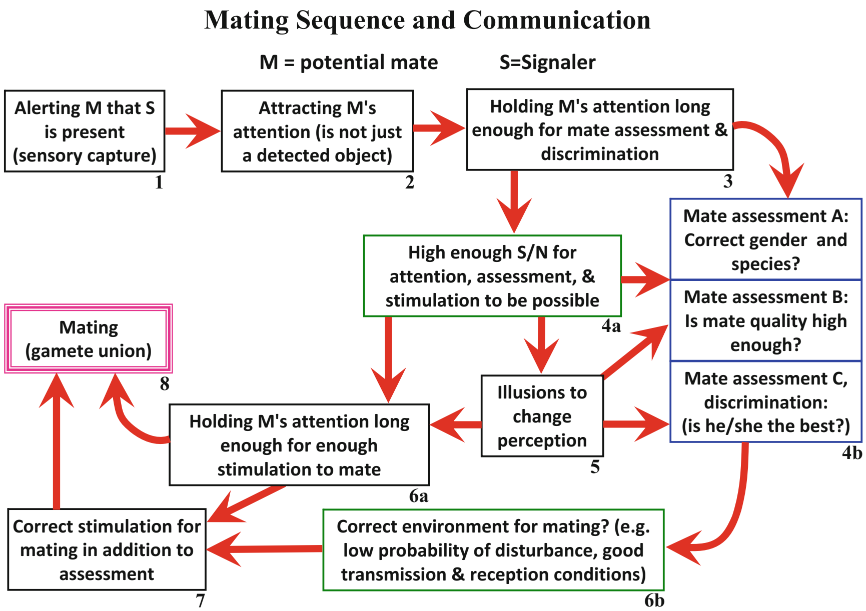

Fig. 3.1 The sequence of processes leading to mating (gamete union). Arrows indicate functional and evolutionary links. Box colors indicate whether the processes are primarily internal (black), environmental (green), or perceptual (blue). Numbers are the stage numbers for reference in the text. This diagram must be regarded as preliminary; as knowledge expands, this diagram will have to be revised. It is just a starting point

through discrimination, choice, stimulation, and physical activity; this is shown in Fig. 3.1. These processes occur regardless of the sensory mode or modes used, and jointly depend upon characteristics of the sender, receiver, and the environment.

Note that Figs. 3.1 and 3.2 include processes that occur before, during, and after copulation processes; the latter two can be called post-pairing. Post-pairing tends to be a separate literature from the former, but for more complete understanding we really do need to consider both components. Chapter 6 (this volume) goes into this in more detail but does not distinguish pairing from copulation, which may involve different signals and sensory modes. The process of sperm transfer and fertilization is another process involving mechanical and chemical communication but is the subject of yet another isolated and not yet fully integrated body of literature. The term mating also has various meanings, and I will use it here to include all processes between contact, copulation, and zygote formation. *Mating* is often used as a synonym for copulation, but copulation does not necessarily result in zygote formation, so that misses a lot of interesting biology. For an excellent discussion of the consequences of pre- and post-pairing components in the context of sexual isolation and speciation, see the study by Coyne and Orr (2004).

The first stage (1, Fig. 3.1), which is often ignored in studies of mating, is alerting the receiver that the sender is present. Alerting signals (Ord and Stamps 2008;

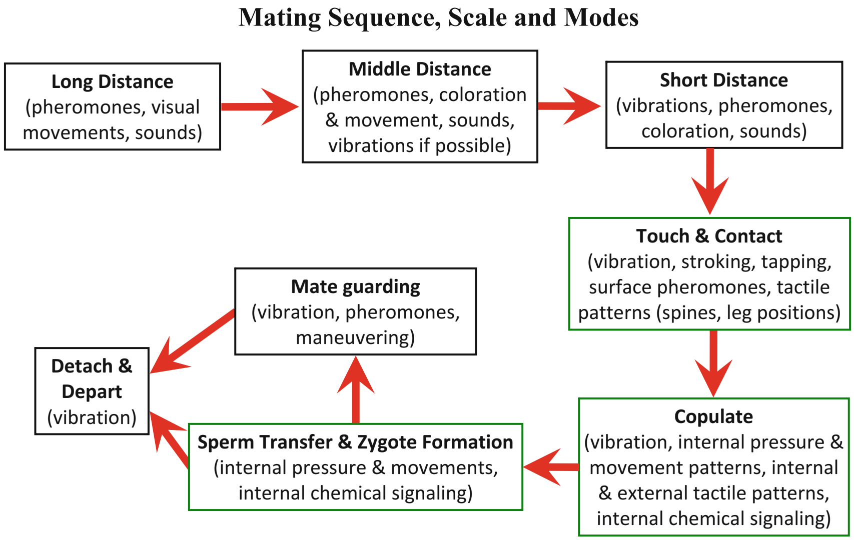

Fig. 3.2 The mating sequence as a function of distance between emitter and receiver, and sensory modes most useful at each stage. Distance is relative to the body length and also to the spatial scale of environmental heterogeneity. Long distances are more than, say, 500 body lengths, medium distances are 100–500 body lengths, and short distances are 1–100 body lengths, but this needs confirmation in large comparative studies and is likely to be affected by spatial heterogeneity in the sensory landscape. Arrows indicate functional and evolutionary effects. Box colors indicate whether the pairs are separate or in contact. Like Fig. 3.1, this diagram must be regarded as preliminary and merely serves as a starting point

Bradbury and Vehrencamp 2011) are often the first part of the temporal sequence within a signal, or they can be sent separately from the main signal. Their only purpose is to alert the potential receiver(s) that a potential signal source is present, as distinct from the sensory background. This is strictly a matter of detection, and of course can be achieved in one or more sensory modes simultaneously.

The second stage (2, Fig. 3.1) is attracting the receiver's attention in the sense that the receiver now actively attends to and receives the signal and does not treat it as just a discernible object in the sensory background. This is the start of communication. Communication depends upon the physical structure of the signal as well as the signal's information content (e.g. Endler 1993). The physical structure affects signal efficacy, and the signal content (information) is part of the reproductive strategy. The functional system includes the emitter (sends the signal) and receiver (receives the signal), but the receiver needs to minimize sources of receiver exploitation ("eavesdroppers", parasites, etc., sending false or misleading signals) and the emitter needs to minimize emitter exploitation (predators and parasites taking advantage of the salience of the signal). For further discussion, see studies by Endler (1993) and Maynard Smith and Harper (2003). The bulk of vibratory work currently concentrates on this stage, but other aspects of vibratory communication will likely be added in the near future, as strongly encouraged by this book, especially in Chaps. 1 and 2.

The third stage (3, Fig. 3.1) is holding the receiver's attention long enough for mate assessment and discrimination. This is an essential part of communication, but has not been investigated in as much depth as signal structure and information content. At stage 3, reception has started, but it has to last long enough for perceptual and cognitive processes to work. Note that many papers unfortunately do not distinguish reception, detection, attention, and/or discrimination and so may miss important and fitness-affecting processes that work differently in these stages.

The third stage leads to two parallel fourth-stage processes (4a and 4b in Fig. 3.1), corresponding to content and structure, and will affect their evolution. Holding attention must last long enough for mate assessment, which depends upon information content. Holding attention depends upon the signal/noise ratio (S/N) being high enough for attention, assessment, and stimulation to be possible (4a in Fig. 3.1). Details and efficacy (resulting in high S/N in the receptors) will be a result of evolutionary feedback between attention, mate assessment, and properties of the environment: the sensory landscape. Holding attention also depends upon the nature of the signal and how it interacts with processes in the brain.

Holding attention must work long enough for complete information to be received (4b in Fig. 3.1). Information must be sufficient for three processes within mate assessment: (a) determination that the emitter is the correct species, (b) determination that the emitter is of high enough quality to be worth mating (above a quality threshold), and (c) determination that this particular emitter is better than other available emitters or potential mates. Thus, there are three levels of discrimination, which all depend upon both signal reception and signal perception. Signal reception might take place very quickly since it is basically a peripheral sensory process, but signal perception depends upon multiple processes in the brain, not only processing of incoming information, but also comparing it to memory and prior experience. Thus, perception may need comparatively more time than reception. This may occur not only as a result of more synapses than reception, but also because chemical changes (in the synapses and generally via hormones) may also be required to initiate and retain perceptual processes.

Stage 4 requires enough information for signal perception leading to decisions about the sender. However, perception can be modified compared to reality because all stages leading to perception are potentially subject to natural selection and divergence. *Illusions* are mechanisms that affect perception of signals and the formation of perception of the correct mate (stage 5). Evolutionary feedback can result in the evolution of illusions because anything that works to aid or change assessment will be passed on to future generations, regardless of whether or not it is strictly "accurate" or "honest". Illusions (sometimes also known as dishonest signaling) are known in visual, chemical, and auditory modes, and could also evolve in vibrational signals. They can also affect the other processes in the mating sequence (Fig. 3.1).

Once perception of the correct potential mate is achieved, there are two components at the sixth stage, which are additional attention holding and lack of disturbance (6a and 6b in Fig. 3.1). Unambiguous perception and high S/N are needed in order to hold the potential mate's attention long enough for sufficient stimulation to mate (6a). This is in addition to holding the receiver's attention long enough for perception leading to mate assessment. Note that this includes attention long enough to start and complete copulation. Some arthropods, fish, and reptiles use spines as additional ways to hold the mates together to give enough time for zygote formation, possibly reducing the need for sensory/endocrine attention holders after mate assessment or augmenting them.

Making decisions based upon perception also requires the correct environment for pairing, copulation, and zygote formation (6b in Fig. 3.1). This requires not only the cognitive processes of mate assessment and choice, but also the cognition required for choice of location and time to avoid interruptions (interlopers, predators, parasites, etc.).

Sensory stimulation must be correct and last sufficiently long enough to encourage copulation and gamete union (7 in Fig. 3.1), and this also depends upon holding the receiver's attention (6a in Fig. 3.1). Successful gamete union (8, Fig. 3.1) and subsequent development are the fundamental basis for natural selection and so will affect the evolution of every stage in the mating sequence, including both the efficacy (design) and strategy (content) of communication. Whichever sensory modes are used will depend upon the evolutionary history and genetics of the species as well as the sensory landscape. Vibrations can be used at almost every stage in the sequence, and will be favored when other sensory modes are more poorly received or are relatively inferior transmitters of information at any particular stage. Each stage has different requirements and so different processes are likely at each stage.

There are several conclusions we can make from a consideration of the phenomena outlined in Fig. 3.1. The mating sequence includes many stages, but not all stages have been studied thoroughly, nor have they all been studied in different sensory modes and different taxa. The mating sequence is affected by physical properties of the environment, physical properties of the signal generating anatomy and the signal receiving anatomy, the neurobiology of reception, perception, and also prior experience encoded in memory. Microhabitat and timing choices also affect the success of mating. During most of the sequence, two parallel processes occur, those affecting the quality of the received and perceived signal (a function of the signal design) and those affecting information content, decoding, perception, and choice (signal content). These two processes interact with various and changing relative importance during the mating sequence. There are many parts of this sequence, which are poorly known and differentially known in different taxa. An additional impediment to our understanding is the relative lack of communication between those studying pre-copulation and post-copulation phenomena (roughly, stages 1–6 and 6–8) as well as insufficient consideration of other sensory modes acting in series and in parallel with the study's target mode.

Figure 3.2 presents the mating sequence as a function of distance between emitter and receiver and suggests which sensory modes may work best at each stage. Some of this was discussed, or implied, in several chapters of this book.

Alerting and attention-getting signals (1, Fig. 3.1) usually occur at longer distances (relative to the body size of the sender); consequently, sensory modes that travel reliably over longer distances are better for use as alerting signals. This restricts vibratory signals for many species, but pheromones, visual movements, and sounds can easily work at longer distances. Alerting signals are often much simpler than the main signals. This results because longer distances, with resulting noise and distortion-induced restrictions on signal quality, and hence information content, favor simpler repetitive signals (Dusenbery 1992; Endler 1993; Ord and Stamps 2008) and there need be no useful information in alerting signals, except possibly species-specific components in areas where congeners are present. But, depending upon the environment, distance and media properties limit what sensory modes work best for both alerting and main signals.

Signal efficacy in any mode improves as the distance between emitter and receiver is reduced. This suggests that almost any sensory mode can be used at intermediate distances. Of course, this depends upon the degree of spatial and temporal homogeneity of the media over the intermediate distance, as well as the media's physical properties. For effective plant vibratory communication the emitter and receiver both should be on the same plant, or plants that contact or are physically close enough to allow vibrations to travel between the plants, either as vibrations or vibration-sound-vibration transfers (Eriksson et al. 2011). Vibratory conditions may have different kinds of constraints on sand, soil, or stone. Effects of reflection off boundaries (where there are impedance mismatches, Dusenbery 1992) cause additional problems, not only in signal quality through reverberation and destructive interference, but, even if the signal quality is high, resonance can cause a cyclic increase and decrease of amplitude with distance. Places where the amplitude goes to zero or a local minimum, and increases again further away, are called *nodes*. It is most unfortunate that the word node also applies to parts of plants, specifically to the locations where leaves, flowers, fruits, and other stems branch off a given stem. Moreover, there is rarely any spatial correspondence between vibratory nodes and plant nodes; so we need to be very careful when talking about nodes. Chapter 19 (this volume) describes this well: "The vibration active space is a network of one- or two-dimensional spaces including the trunk, primary limbs, secondary branches, and twigs, which modulate vibration amplitude at each bifurcation point." Similar patterns could occur in other substrates because most substrates are spatially and temporally heterogeneous. Geometry affects transmission, distortion, and frequency-specific distribution of nodes. Dynamic changes in media properties and noise entering the media could change all these patterns. Vibratory node positions depend upon the locations of senders and receivers, the spatial variation in cross-sectional geometry and density of the substrate, the geometric relationships between the media and its boundaries, and the frequency of the vibrations, leading to spatially and temporally complex and frequency-dependent geometric patterns of signal structure in the vibroscape. The pattern can be even more complex if other conspecific and/or heterospecific signals are input into the substrate at the same time.

Short distances (a few body lengths) are excellent for substrate-borne vibrations, pheromones, visual signals, and sounds, although at even shorter distances vibrations and pheromones are probably most efficient for communication. For example, if an eye is too close to a color pattern, it will not be able to receive the entire pattern geometry or track pattern motion. These constraints become much stronger when distances are short enough for physical contact, and will favor different sensory modes and signal structures in different parts of the mating or other signaling sequence.

Mating requires physical contact, and this shifts the kinds of sensory modes that are most efficient. Here, substrate vibration, touch (tapping and stroking), and contact pheromones or compounds (e.g., cuticular hydrocarbons) will be the most efficient. In addition, geometric patterns of spines and touching patterns may also transmit information, as could leg positions. Touching patterns are very little studied except in ants and termites where temporal patterns of antennae touching are very important in social communication. The effect of spatial rather than temporal touching patterns is essentially unknown.

Touch-based communication is almost treated as an aside by people studying communication generally (aside from social insects), and it is also treated as an aside by those studying vibratory communication (but see Chap. 6, this volume). It can also be used as a late part of anti-predation defenses (e.g. O'Hanlon et al. 2018), which is a form of predator–prey communication (Bradbury and Vehrencamp 2011). This brings up a semi-philosophical issue of just what biotremology should include. Specifically, should it include touch? Touch and vibration potentially use many (but not all) of the same receptors; so this suggests keeping them together. However, many, if not most, temporal patterns in touch signals are not cyclic or rhythmic, unlike classical vibratory signals. It is worth asking the question, should we have a separate field called tangology, or tactilology, for the study of communication by touch, or should it be included in biotremology? We could include it in biotremology because the major difference is acyclic versus cyclic signals, if that is in fact true. If it is part of an identifiable field, touch-based communication will get more explicit attention. On the other hand, as in the argument against including substrate-borne vibrations in the study of sounds (see Chap. 2, this volume), this approach risks losing a lot of the richness in the diversity of communication processes, and actually missing important phenomena. No matter what named field it ends up in, the use of touch in animal communication systems is badly neglected except in social insects.

Copulation requires more than simply physical contact, and allows communication by vibrations, external and internal touch, sensors of internal pressure, internal movement patterns, internal (and external) tactile patterns caused by spines and other anatomical structures, and internal chemical signaling. Aside from internal chemical signaling during copulation, including conflict of interest, the function of information transfer in copulation is poorly known, and the function of mechanoreceptors in receiving information during copulation could easily yield a lot of new information about mate choice during and after copulation (see Chap. 6, this volume). Proprioceptors could also yield useful information to both parties during copulation. Note that by information transfer in copulation I am not referring to transfer by DNA but information transfer needed to achieve union of gametes. Obviously, copulation includes both kinds of information transfer.

Copulation should result in sperm transfer and zygote formation. The mechanics of this could be a source of further information used in mate choice by the female (or male pipefish); information could come from internal pressure changes, movement patterns, and chemical signaling. In addition, there are biochemical and molecular interactions between egg and sperm in which chemical information is transferred. Choice is still possible at egg–sperm union, as suggested by the fact that many zygotes fail to form after fertilization. Egg–sperm interactions are the subject of a fairly large literature, but this is also not integrated with other aspects of mating. In any case, the mechanical aspects of fertilization in information transfer and use relative to mate choice are not well known. Within-animal vibration is probably not a part of this stage, unless the sperm transfer is produced in repeated pulses that could be modulated to transfer information in addition to the DNA itself.

In many species of invertebrates and vertebrates, copulation is followed by (or includes) mate guarding, in which the male tries to prevent interference or even displacement by other males or prevents a subsequent mating that might displace his sperm or sperm packet. Here, the same sensory modes could be used as are used before copulation because they can be used to communicate to rival males or other individuals. Substrate- or surface-borne vibration, pheromones, and physical maneuvering can communicate efficiently in mate guarding. Finally, whether or not there is mate guarding, a copulating pair will detach, and this can be followed by further communication, including surface-borne vibration.

There are two main conclusions one can make from Fig. 3.2. First, vibration can be used in most but not all stages in the mating sequence, and its use during contact, copulation, and mate guarding could be much more widespread than in earlier stages. Second, different combinations of sensory modes are needed for each stage in the mating sequence. This is particularly obvious when comparing events before, during, and after copulation. The combinations at each stage will evolve based upon environmental (external and internal), physical, and chemical properties that change among stages. The factors favoring particular combinations of sensory modes, and properties of each mode, should be investigated because they are likely to yield general new insights into animal communication. For any sensory mode, historically there has been too much concentration on single processes and not enough consideration of the use of multiple sensory modes or how they change between the mating stages.

3.3 Specific Comments and Questions

In the following section, I present some questions arising from one or more chapters (this volume), although they are not necessarily explicitly stated in the chapters. I do not mean to criticize any of the previous work, but just point out the gaps in our current approaches. Gaps and new questions are inevitable in a new scientific field and this chapter is merely meant to be a "mudmap" to unexplored and poorly explored areas.

Evolution is still poorly covered in biotremology, as noted in several chapters. Of course, part of the problem is that so few species in any group have been studied, and many species are needed for a phylogenetic, comparative, or other evolutionary analysis. For most groups, there is simply not enough data, but this is changing. The Pentatomidae (stinkbugs) are described in fascinating detail in Chap. 7 (this volume). The authors hypothesized that vibratory communication evolved independently of chemical communication in some species, but did not present a phylogeny and did not do a phylogenetic analysis that could have tested this interesting hypothesis directly. Chapter 15 (this volume) showed a phylogeny with male and female signal traits in heelwalkers (Mantophasmatodea), but did not discuss the character changes nor did they do a phylogenetic analysis. Chapter 21 (this volume) showed a phylogeny of bark beetles (Scolytinae in the Curculionidae) with traits. There does appear to be a phylogenetic pattern in the traits and possible multiple instances of evolution of the same trait, but again no phylogenetic analysis was performed. Hoch et al. (2006) examined vibratory signaling in a relict living Peloridiid to reinforce phylogenetic inferences about the origin of signaling in Heteroptera, and this is a good example of testing hypotheses resulting from ancestral state reconstruction. An excellent example of the kind of analysis that should be done more often and will likely yield major new insights into the evolution of vibratory communication is Strauß's (2017) study of the phylogeny of orthopteran mechanosensory organs. His work combines microanatomy and neuroanatomy and allowed conclusions about both function and evolution, which would not have been possible otherwise. Joint phylogenetic work on sense organs, vibration production mechanisms, and vibratory patterns is likely to yield major new insights into both function and evolution, and possibly also solving some taxonomic headaches. The current sparseness of phylogenetic analysis in biotremology may result simply from lack of familiarity because most of the phylogenetic literature simply works on morphology or molecular traits, and we are less likely to read the (often highly technical) phylogenetic literature. It may also result from simply not having enough data from multiple taxa in a clade to produce a tree with sufficient resolution to answer questions, at this time. Moreover, we are still hard at work improving and inventing new methods to record vibrations and the vibroscape, two very challenging subjects that produce essential data for evolutionary studies. There is massive potential for understanding evolution of vibratory signaling, if phylogenetics could be integrated with biotremology. We need more data and more application of evolutionary methods, and this could lead to exploration of entirely new questions about the evolution of vibrations and vibratory communication. Explorations of the origin of vibratory communication, and the joint evolution of vibration and other sensory modes, are also full of possibilities.

Given the massive spatial and temporal variation in the local properties of the vibroscape, is it possible to define and identify vibratory habitats in a similar way that biomes are identified? We would expect a much finer mosaic of microhabitats in the vibroscape than the general landscape, and so much data need to be collected before this will be possible. The rapid development of clustering and other modern geo-statistical methods could be a great help here.

Within vibratory communication, what substrate and signal generation properties favor particular kinds, forms, and modulation patterns of vibration waves over others for particular purposes? Is there a general pattern that is distinctly different for alerting, orientation, detection, attraction, and information transmission? Do animals that communicate by vibrations use signals with characteristically different parameters depending upon purpose, substrate, background noise, and number of other vibratory-communicating species (part of "noise")? Do animals using substrates rich in reflections (and hence vibratory nodes) use different suites of parameters and wave types than those using substrates with rare and/or predictable reflections? To what extent does wave type depend upon the type of substrate rather than the function of the wave in communication? For further discussion, see Hill and Wessel (2016).

Can we predict the direction of evolution, or just the species-specific pattern of what form vibratory communication takes (signal design and timing), from the environment, biophysics, and evolutionary history? How often has evolution taken the same direction? Is it a matter of an ancient form of communication gradually diverging from the ancestral form in different ways in different lineages (for example, Hoch et al. 2006)? Does it appear independently several times in different lineages, and if so what favors new appearances? If the latter is true, is this a result of repeated gain and loss of vibratory communication? Did vibratory communication originate from vibrations resulting from cutting or chewing (ants: Roces and Hölldobler 1996; termites: see Chap. 16, this volume), walking, sensing struggling prey (Dusenbery 1992), and/or an elaboration of proprioceptors? Does each kind of origin favor particular patterns and forms of vibratory communication, as well as other sensory modes?

Can we predict which sensory modes are used, and the sequence of sensory mode evolution? For example, did vibratory sensing evolve from existing sensors or entirely new sensors? Could it even evolve from cell–cell interactions during morphogenesis, which are at least partially based upon biomechanics and movement (e.g. Odell et al. 1981; Oster and Perelson 1987; Peskin et al. 1993)? Does the appearance of one sensory mode make it possible for others to be developed and possibly even supersede the earlier-appearing sensory mode? For example, did hearing evolve from vibratory sensing (Shaw 1994) or from entirely new sensors? Or does selection for specific modes derive primarily from environmental restrictions? Probably all these factors affect sensory mode evolution. Does triggering of behavior at each stage of mating (or other behaviors) occur additively or non-additively among different sensory modes? Are some modes and signal designs more useful than others at a particular stage, but the one actually used changes in later stages owing to significant changes in efficiency of each mode? How often does this occur? As mentioned in Chap. 12 (this volume), many studies of vibration do not examine the possible use of other sensory modes. Figure 3.2 suggests that being too focused on any sensory mode could lead to poor understanding of any species. This is a risk from requiring a very different "toolbox" for each sensory mode and we need to work around it.

Multimodal signaling involves using more than one kind of signal within a given sensory mode, as well as using different sensory modes. It has two different advantages over unimodal signaling: (1) sending the same information via different channels (within or among sensory modes) is a very good way of minimizing noise and also allows more complex information to be sent and (2) sending different information by different channels allows sending more and more complex information more quickly than if it had to be sent by a single channel, even when noise is not limiting. As a countervailing factor, using more channels makes it more likely that more predators and parasites will be able to receive the signals. See Chap. 7 (this volume) and especially Hebets et al. (2016) for a discussion. Although many people working in each sensory mode probably know this, there is a significant tendency to ignore other modes and not to consider their relative importance. What conditions favor each kind of multimodal signaling and how often has this occurred during the phylogeny of various taxa? Are some taxa, or some environments, more prone to one form over another? Are some taxa more prone to particular sensory modes as well? A related question is what factors favor duetting rather than one sex sending and the other receiving during pre-pairing stages of mating, and is this related to noise levels, predation, or both (Dusenbery 1992)?

In spite of extensive discussions of signal reception and the environment, including one chapter on vibration modeling (see Chap. 5, this volume), the concept of impedance matching was not discussed. For a vibratory signal to pass between media with different properties, which have different impedances, devices to reduce the impedance mismatching are needed (Dusenbery 1992). To make matters more complex, impedance matching depends upon wave frequency as well as physical differences in the disparate media. This is especially important in signal generation, transmission (signaler to media), and reception (media to receiver), as well as signal recording and playback by equipment (Hill and Shadley 2001; Hill 2009; Cocroft et al. 2014b). It is also the source of reflections, distortions, and nodes. For an excellent discussion of impedance matching in the context of signal transmission, reception, and fidelity, see Dusenbery (1992). Considering impedance problems as not simply "damping" could yield significant new insights into the form and evolution of vibratory signals, and may allow new predictions about signal form and behavior. Signaling conditions and media are spatially and temporally dynamic, sometimes even in the same media (Hill and Shadley 2001; Cocroft et al. 2014b), and this means that dynamic filtering and dynamic impedance matching may allow more accurate and less distorted signal reception than if the properties of impedance-matching devices were static (see Chap. 5, this volume).

Why do beetles and diptera not have vibration sensors in legs? Perhaps this is less surprising in flies, given that walking is only a minor part of their life, except possibly for the Dolichopodidae, which so far as I know have not been studied for vibratory communication. Further, as suggested in Chap. 7 (this volume), has vibratory communication evolved with an elaboration of proprioceptors, walking, and incidental vibrations from walking and other activities? A phylogenetic analysis of this question would be very interesting, as well as possibly answering the question of why beetles and (at least some) diptera are different.

How often is there two-way communication among species, including between insects and plants, and prey and predators, as well as different animal species? Is this opportunistic evolution or active coevolution, or both?

Signal reception is far better understood than signal perception. Perception includes both extracting information from a signal and comparing it to prior experience encoded in memory or other neural and endocrine functions. These functions can be addressed either by neurobiological methods such as recording from various neurons and nervous system imaging (e.g. Chap. 2), but it can also be investigated by cleverly designed behavioral experiments, such as those which are most elegantly developed in the large literature on bee and human vision. What are we missing by not exploring perception as much as reception?

What is the contribution of local, and local average, media properties to population divergence and speciation? Do vibroscapes with more spatial diversity favor more species or vibratory "dialects" within species? Do some plant families promote vibratory insect speciation more than others owing to higher media diversity than other plant families? Similarly for soil types and ground signaling species?

How often has microhabitat (time and space) choice evolved in place of, or to enhance, methods of minimizing effects of the high spatial and temporal variation in both media and noise properties? For example, how often is signaling restricted to lulls in wind, or either wetter or drier conditions that may affect transmission fidelity and speed in soil and plant stems? How often do species choose particular substrates that have the best transmission properties, even within a given plant species and location within a given plant (as in Magal et al. 2000)? Does this specialization favor speciation? If so, this suggests larger clades in microhabitats with more diverse vibratory substrates.

What is the role of proprioceptors during pairing and copulation? To quote from Chap. 7 (this volume) on stinkbugs: "abdominal chordotonal organs may play a proprioceptive role because of their position in the abdomen. One group, specifically, is connected with ligaments to fat body cells close to the chitinous plate that connects the abdomen and thorax, but also in the vicinity of muscles whose synchronized contraction produces vibratory communication signals." Internal sensors like these in any species could play a role in communication, control of behavior during pairing, copulation, and sperm transfer, and therefore affect fitness via reproduction.

Although amphibians and mammals are discussed, there is a largely unexplored richness in vibratory communication by fish, reptiles, and snakes. The lateral line in fish responds to pressure waves in water rather than on the surface, and this is used for a variety of purposes just as vibratory sensation is used on land (Coombs et al. 1989, Montgomery et al. 1995; Bleckmann and Zelick 2009). Without ears but with long bodies, snakes could use vibrations for a variety of purposes (for example, Young and Morain 2002; Young 2010), and many lizards move or even strike the substrate with their feet or tail, and the "push-up" display of many lizards could also generate substrate vibrations as in tremulating insects. Birds could use vibrations to detect approaching predatory snakes in vegetation, and male Lyrebirds (two species in the genus *Menura*) actively shake vines and dance on a constructed mound during their sexual display (Higgins et al. 2001; Dalziel et al. 2013), which could potentially send vibrations to females resting on the same vines or nearby ground. There are almost certainly other taxa that may be using vibratory communication.

In summary, there is tremendous potential for major new discoveries within the field of biotremology, as well as from integrating it with similar research on other sensory modes and the literature on sensation and perception.

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Chapter 4
Body Tremulations and Their Transmission as Vibrations for Short Distance Information Transfer Between *Ephippiger* Male and Female

René-Guy Busnel, Francois Pasquinelly, and Bernard Dumortier

Abstract In the genus *Ephippiger* (Insecta: Ensifera: Tettigoniidae: Orthoptera) males signalize their reproductive state to females by emission of acoustic signals which comprise ultrasound components; these signals carry over long distances (several tens of meters) and apparently trigger tactic behavior/positive phonotaxis in the female. The orientation of females to locate males is nearly exclusively achieved by sound. However, in the natural environment, males which usually stay on branches or shrubby plants in ca. 50 cm to 1 m above the soil, upon perceiving vibrations of any kind (either by individuals of the same or other species) will perform a particular behavior which is reported here—to our knowledge—for the first time: the male will start alternating emissions of sound and bouts of tremulations of the entire body. In case an approaching female is in close vicinity of a male displaying such behavior, she will confirm her presence by performing similar tremulations. By simultaneous but separate recordings of sound emissions and tremulations, we could show that in *Ephippiger bitterensis* Chopard and *E. ephippiger* Fiebig these are indeed independent phenomena and constitute two separate communication channels.

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4.1 Introduction

Males of *Ephippiger* species use the emission of an acoustic signal which is rich in ultrasound components, as a means of information for the females about their genital state (of reproduction); moreover, this signal which carries over long distances (around several tens of meters) also serves to guide females towards the males; this orientation to locate males being practically exclusively achieved by sound.

In its natural environment, the male always stays on a branch or on shrubby plants in 50 cm to 1 m above the ground (thistles, Carline thistles), and, as soon as an insect, male or female, of the same or of another species, touches the plant, or is put on the plant by hand, the male, receiving the vibration of the substrate provoked by the visitor, starts alternating its emission of sound with a tremulation of the entire body, a phenomenon, which to our knowledge, has not previously been recorded for these insects. In some cases, the female in close vicinity to the male which she has successfully located by sound, confirms her presence with a tremulation of the same kind (Fig. 4.1). These are the tremulations which we have studied in *Ephippiger bitterensis* Chopard and *Ephippiger ephippiger* Fiebig (Figs. 4.2, 4.3 and 4.4).

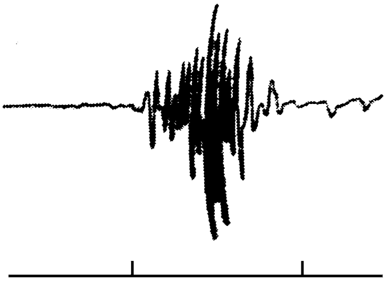

Fig. 4.1 Tremulation of a *Ephippiger ephippiger* female. Time interval: 1 s

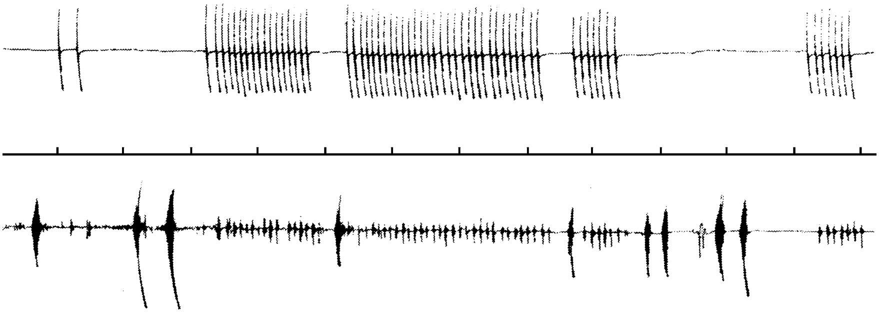

Fig. 4.2 Alternation of song-tremulations in *Ephippiger bitterensis* male. The song signal is represented by the upper trace, the tremulations by the lower. The figure shows nine tremulations. The small vibrations registered between tremulations correspond to movements caused by stridulation. Time interval: 10 s

Fig. 4.3 Alternation of song-tremulations in *Ephippiger bitterensis* male (traces as in Fig. 4.2). Time interval: 1 s

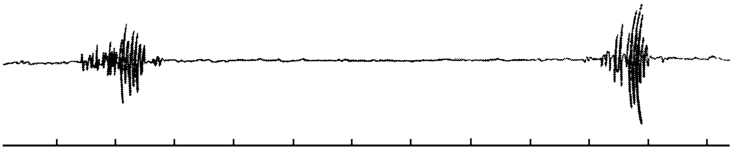

Fig. 4.4 Two tremulations of a *Ephippiger ephippiger* male: Time interval: 1 s

4.2 Method

To effectively conduct this study, we used an experimental set-up consisting of an aerial microphone to pick up the acoustic signal, which was positioned in ca. 20 cm distance of the plant on which the male was sitting. This microphone was connected to a recording electromagnetic oscilloscope (through a groove connection) to an amplifier and to a rectifier. The plant was also connected, with a fine wire, to a sensitive pen of the microphonic motion detector by Busnel and Pasquinelly (Busnel et al. 1953). This device carried the vibratory signals, transformed into electric signals, to a second electromagnetic oscilloscope (with a similar branch like the first), also hooked to the same kind of writing device on paper (Rekordine). The sensitivity of the second pick-up allowed to register the "deplacements", which are of the order of microns (a drawing of the experimental set-up is given in Fig. 4.5). This set-up allowed us to synchronously record the acoustic and vibratory behavior of the insects on the plant.

On the basis of these oscillograph recordings a detailed study of the different tremulations of the females and the males was made possible. Recording no. 1 gives an example of this type of oscillograms, and we would like to stress, that the lower trace which illustrates the recording of vibrations on the plant, clearly shows that the body movements of the male during emission of acoustic signals also causes a slight vibration of the substrate which can be very well distinguished on the recording (see Figs. 4.2 and 4.3).

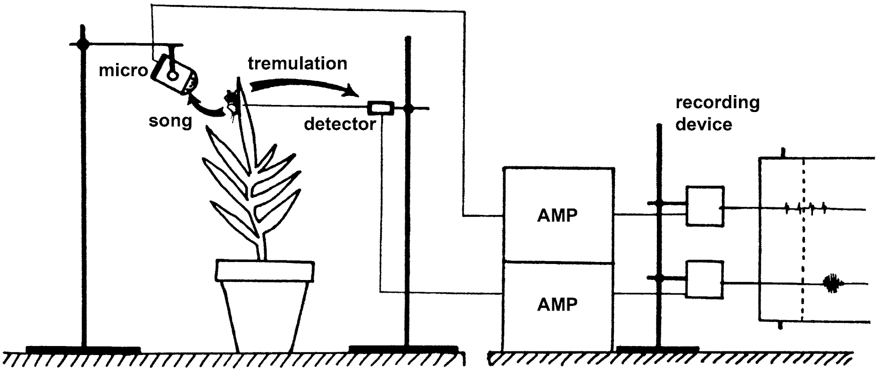

Fig. 4.5 Experimental set-up to synchronously record songs and tremulations of *Ephippiger* males (see Sect. 4.2)

Study of tremulation characteristics: The length of the tremulations is measured on the oscillogram taking into account a median reading error estimated at 1 mm, as it is difficult to precisely determine the beginning or the exact end of the vibration. This error is in the order of ca. 5/100 s.

4.3 Results

4.3.1 Duration of Tremulation

The tremulation is very short, and this is why it has been overlooked by entomologists. It ranges from 0.5 to 1.25 s in *Ephippiger bitterensis* (76 tremulations from 2 males were analyzed) and from 0.55 to 0.90 s in *Ephippiger ephippiger* (of 108 tremulations analyzed), and from 0.40 to 1.25 s in the female (of 18 tremulations analyzed). These values are shown in detail in the frequency histograms in Figs. 4.6 and 4.7.

4.3.2 Number of Oscillations per Second

A detailed analysis of the number of vibratory cycles occurring in a series of tremulations allowed us to obtain a mean value of their frequency (cycle/s). For *Ephippiger bitterensis* this is 25 c/s; for *Ephippiger ephippiger* males it is 21 c/s, and for *Ephippiger ephippiger* females it is 15 c/s.

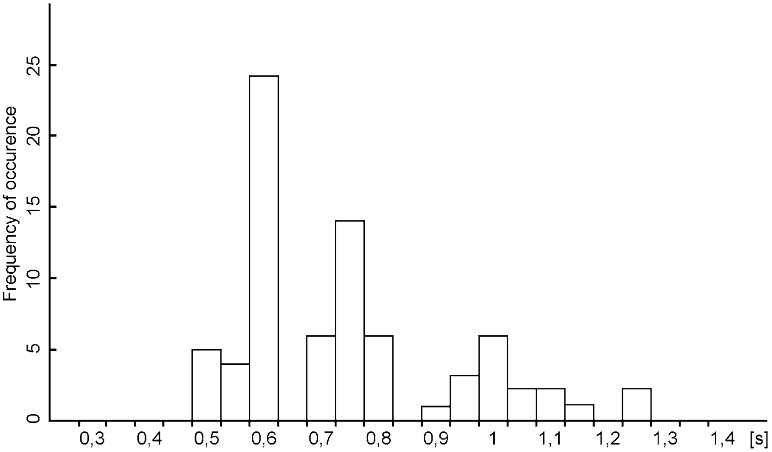

Fig. 4.6 Distribution of duration of tremulations in males of *Ephippiger bitterensis* (76 recordings analyzed, class interval 50 ms)

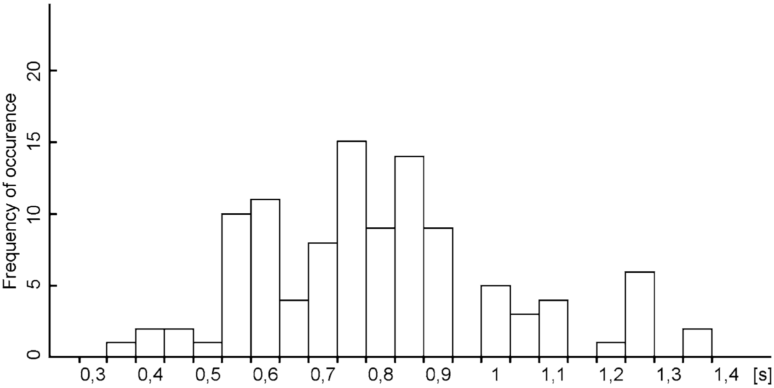

Fig. 4.7 Distribution of duration of tremulations in males of *Ephippiger ephippiger* (108 recordings analyzed, class interval 50 ms)

4.3.3 Amplitude of Oscillations

The recording of movements of the substrate with this technique, depends in part on the position of the animal and the specific value of amplitude (which is a function of the amplification chain) is thus of no interest. The relative values of the amplitudes within the same signal is however significant since it demonstrates well the development of the phenomenon over time. The maximum amplitude is observed in the 2nd third of the tremulation, perhaps due to the stronger movement of the insect itself or by utilizing the amplification of the movements proper to the substrate. It is remarkable that the insect very abruptly stops its own oscillations and

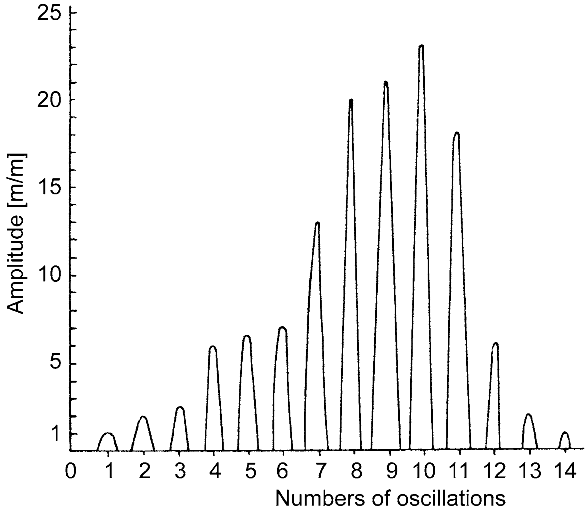

Fig. 4.8 Pattern of amplitude (above baseline) of the graphic recording of a tremulation in an *E. bitterensis* male

those of the plant, much like "pulling a brake" (see Figs. 4.3 and 4.8). These results seem to apply to the two species, as well as to *Ephippiger ephippiger* females.

4.3.4 Interval Between Two Tremulations

There is no obvious rule in the interval separating two tremulations. It is dependent on the presence or absence of a male, or female visitor, and of the visitor's immobility or movements. We are therefore dealing with external factors which are not analyzable with certainty.

4.3.5 Separation of Two Modes of Information: Song and Tremulation

We never observed simultaneous emissions of song and tremulations. In fact, the male uses song when alone on the plant (this is the long distance signal), and tremulation only starts once a female touches the plant. In case the female walks up the plant rapidly, the male is inclined to tremulate; when she stops during her walk, the male sings again and does not tremulate unless the female resumes moving. Nevertheless, the different behaviors do not always strictly correspond to this pattern. It should be mentioned that the male does not tremulate if the human experimenter touches the plant, whereas he will tremulate if it is an insect, even a male of the same or another species. It will also not tremulate if the wind moves the plant. One can therefore assume that it distinguishes with great accuracy the substrate vibrations caused by an insect visitor or those which concern other vibrations.

4.3.6 Reaction of the Female to Tremulations

The female reacts to the tremulation and to a sound signal. Its movements seem uniquely conditioned to these two types of messages: at short distance (2 cm), she only reacts in a taxic manner, moving in direction of the male, following one of the two signals. She stays entirely immobile between two signals, regardless their nature (acoustic or mechanic).

4.4 Conclusion

The males of *Ephippiger bitterensis* and *Ephippiger ephippiger* (we have observed the same phenomena in several other species of *Ephippiger*) utilize two modes of information to convey their position on the plants, to females, as well as for locating them. We have described one of them, tremulation, transmitted through the substrate, which has not been observed before. The females may equally signal their presence through tremulations of the same type. It seems that one can think of comparing this use of numerous signaling modes in Orthoptera, to the behavior of other species, that it may be a mode of taxic information [tapping the soil with the hind tarsi in certain Acrididae (Jacobs 1953), abdominal movements of the female of *Lamarckiana* (Burtt 1946)].

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Part II

The State of the Field: Concepts and Frontiers in Vibrational Behavior

Chapter 5
Physical Basis of Vibrational Behaviour: Channel Properties, Noise and Excitation Signal Extraction

Sebastian Oberst, Joseph C. S. Lai, and Theodore A. Evans

Abstract Socially living insects rely on efficient and accurate communication and source localisation for survival. Insects communicate multimodally using visual, chemical or mechanical cues. Vibrations are often considered to be a primitive mode of exchanging information, but vibrations are independent of sight or airflow, and can reach the destination cryptically and reliably. However, other than in air or water, the vibration communication channel in nature is usually a heterogeneous substrate with nonlinear material properties. Communication is hindered by increased signal complexity under the influence of noise and distortion. This chapter gives an overview of biotremology on natural substrates and the difficulties associated with noise and heterogeneous materials. The noise control engineering principle is used to extract the excitation signal from substrate response vibrations and the communication channel properties. It is argued that in order to obtain insight into the role of vibrations in insect behaviour, the ability of insects to adapt to changed situations and environmental conditions by making use of the substrate as a filter needs to be studied by means of the excitation signal rather than the response signal alone.

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5.1 Introduction

Animals, in particular arthropods, use vibrational communication signals for their courtship, to defend their territory or cues to detect prey, predators and competitors (Cocroft et al. 2014a). Sound and vibrations and their interactions with the properties of the communication channel play an important role here. However, vibrational communication (biotremology) is arguably the least studied communication mode in animals, even though its transmission is little hampered compared to visual or olfactory communications: information can be transmitted reliably in the dark over longer distances even in the presence of strong air currents (Bell 1980). This is because of the late recognition that many animals use vibrations and the inherent difficulty in studying the properties of natural substrates and their interactions with both the source signal and the environment (Mortimer 2017). Also, plants have been reported to respond to vibrations: *Arabidopsis thaliana* responds to chewing vibrations of the noctuid caterpillar *Spodoptera exigua* by increasing the production of growth inhibiting chemicals (Appel and Cocroft 2014).

While responses on rather homogeneous or engineered substrates can be readily analysed in the frequency domain (amplitudes, frequencies, damping, mode shapes), natural substrate materials are generally heterogeneous and behave nonlinearly with intriguing wave propagation properties, compared to linear structures (Fletcher and Rossing 1998; Pamel et al. 2017).

As schematised in Fig. 5.1, a communication signal's active space consists of (1) a signal $X(f; T)$ generated at the source (S) using a transmitter (T); (2) its transmission through a medium (the channel, generally fluid, solid or both, here $H_{xy}(f; T)$ the *transfer function*); (3) the background noise level (N) and (4) the response $Y(f; T)$ perceived at the receiver (R) with a certain threshold sensitivity before it reaches its destination (D) (Shannon 1949; Brenowitz 1982). The channel, its properties and its complex interactions with the environment are crucial, but often underestimated elements in biotremology, to study the evolution of vibro-acoustic biological signals, mate selection and male-male competition (Forrest 1994; Mortimer 2017). One prominent example is that of termites, where

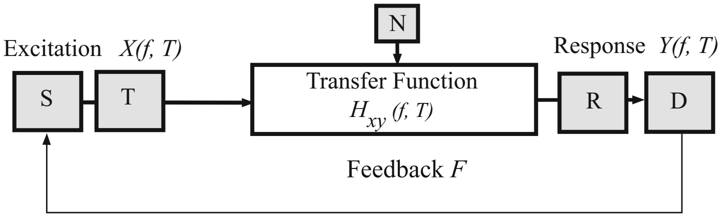


Fig. 5.1 Schematic of noise control engineering principle; $X(f, T)$ and $Y(f, T)$ with frequency f and period length $T = \frac{1}{t}[\mathrm{s}^{-1}]$, represent the Fourier transforms of the source $x(t)$ and the receiver signal $y(t)$; further depicted are the information source (S), the transmitter (T), the receiver (R), and the destination (D), and noise (N) acting on the communication channel (Shannon 1949)

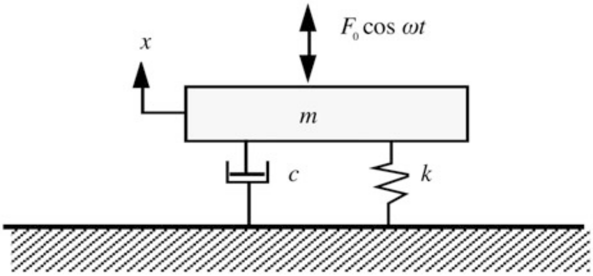


Fig. 5.2 A simple 1DOF oscillator with viscous damping

the substrate and its vibration transmission properties have at least three major functions: (1) food source (Evans et al. 2005); (2) building material (for different purposes) (Inta et al. 2007; Oberst et al. 2016) and (3) main communication channel (Hager and Kirchner 2013; Oberst et al. 2017).

In engineering noise control, the response R in Fig. 5.2 only indicates whether the noise exposure is excessive or not. To implement effective noise control strategies, the characteristics of the noise source S have to be quantified since R is affected by the properties of different transmission paths, i.e. the transfer function H_{xy}. While the characteristics of a machine or device such as a noise source do not change irrespective of the transmission path, it is entirely possible that a biological source could change its excitation to either reduce its signature as a passive defence mechanism (Matthews and Matthews 2010; Klowden 2013) or to increase its signature for communications with other biological sources of the same or different species. Hence, just like engineering noise control, it is important to study the properties of the transmission paths and to extract the excitation signal to study the behaviour of biological sources, rather than relying simply on the response R.

In this chapter, the fundamentals of vibration are first introduced with discussions on how both the source (living organisms) and solid channel (substrate) may be modelled in terms of mechanical oscillators. This is then followed by discussions on signal transmissions, how to extract useful information (including source signals) from response signals (with examples), the limitations of current signal processing methods and the potential of source signal extraction for better understanding of the behaviour of insects that use vibrations for communications.

5.2 Fundamentals of Vibration

5.2.1 Forced Vibration of a Simple Oscillator with Viscous Damping

The most basic type of mechanical vibration is produced by a so-called simple oscillator with viscous damping, alternatively also known as a one degree-of-freedom (1DOF) mass-spring-damper system (Fletcher and Rossing 1998). As shown in Fig. 5.2, a 1DOF oscillator may consist of a mass m (in kg) attached through a spring with spring constant k (in N/m, stiffness) and a viscous damper with coefficient c (in Ns/m, damping) to a rigid support. The mass m is constrained to translations in the x-direction parallel to the spring and damper. This system has only 1DOF because its state at any instant is completely specified by the x-coordinate of some selected point on the mass relative to its static equilibrium position. When an external force $F(t)$ is applied to the mass, the restoring force components, due to the spring and the viscous damper opposing the applied force, are $-kx$ and $-c\dot{x}$, respectively, where t is time and $\dot{x}$ is the first derivative of displacement x with respect to time t. By applying Newton's second law, the equation governing the motion of m can be written as:

$$m\ddot{x} + c\dot{x} + kx = F(t) \tag{5.1}$$

When F takes the form of a sine or cosine function of t, it is considered a harmonic excitation:

$$F(t) = F_0 \cos \omega t \tag{5.2}$$

where ω is the circular frequency in rad/s, and F_0 is the amplitude of the force in N. The general solution to Eq. (5.1) with harmonic excitation can be written as:

$$x(t) = A\mathrm{e}^{-\zeta\omega_n t} \sin(\omega_d t + \Phi) + X \cos(\omega t - \Theta) \tag{5.3}$$

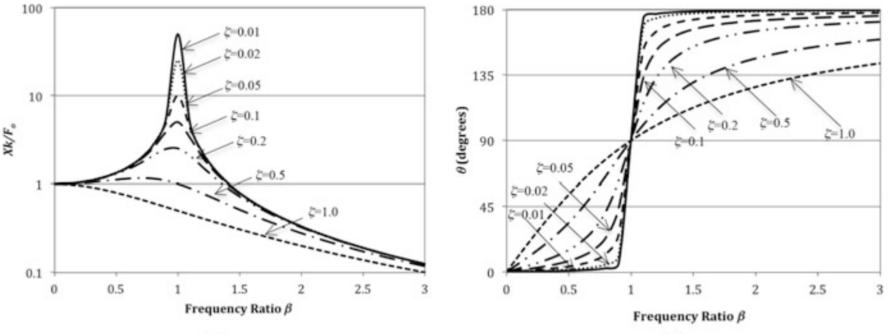
where the first term is the transient response and the second term is the steady-state response; A (the amplitude) and Φ (the phase) for the transient response are determined by the initial conditions; $\omega_d = \omega_n\sqrt{1-\zeta^2}$ is the damped natural frequency, $\omega_n = \sqrt{\frac{k}{m}}$ is the natural frequency and $\zeta = \frac{c}{2\sqrt{km}}$ is the damping ratio; X (the amplitude) and Θ (the phase) of the steady-state response are given, respectively, by

$$X = \frac{F_0}{k\sqrt{(1-\beta^2)^2 + (2\zeta\beta)^2}} \tag{5.4}$$

$$\Theta = \tan^{-1} \frac{2\zeta\beta}{1-\beta^2} \tag{5.5}$$

where $\beta = \frac{\omega}{\omega_n}$ is the frequency ratio. The phase Θ indicates the time difference between the response and the excitation and is important for understanding the interplay between different vibrating parts.

The normalised magnitude of vibration $\frac{Xk}{F_0}$ and phase Θ of the steady-state response for a range of damping ratios ζ in Fig. 5.3a, b, respectively, show that a



(a) (b)

Fig. 5.3 Steady-state response of a simple oscillator for various damping ratios ζ; (**a**) variation of normalised magnitude $\frac{Xk}{F_0}$ with frequency ratio β; and (**b**) variation of phase Θ with frequency ratio β

1DOF oscillator has one natural frequency at which $\frac{Xk}{F_0}$ is maximum and at which the phase Θ changes from 0° to 180°. In addition, $\frac{Xk}{F_0}$ decreases with increasing ζ.

5.2.2 Multi-Degree of Freedom and Continuous Systems

Just as a 1DOF oscillator has one natural frequency, a system of oscillators with n degrees of freedom has n natural frequencies, each of which corresponds to a different natural or normal mode of the system. Each individual mass, when subjected to harmonic excitation, performs simple harmonic motion about its equilibrium position with different amplitudes and damping.

Unlike the discrete mass-spring-damper system, a continuous system is one with distributed mass, stiffness and damping and has an infinite number of modes. For each mode, a node is where the motion is zero and an antinode is where the motion is maximum. There will be a phase change of 180° as a node is crossed. A node/antinode can be a point, a line or a curve. An example of the $(1, 2)$-mode shape of a circular disc in Fig. 5.4 shows one nodal circle and two nodal diameters.

5.2.3 Modelling and Analysis of Source and Substrate

Irrespective of whether a structure is discrete or continuous, the modal properties of each of its modes may be modelled by a mass-spring-damper system. Very often only the first few modes are important and hence a source, be it mechanical or biological, may be modelled using a limited number of mass-spring-damper oscillators arranged in series or in parallel in three directions (if necessary). Similarly, a substrate may be modelled as such. The advantage of modelling a

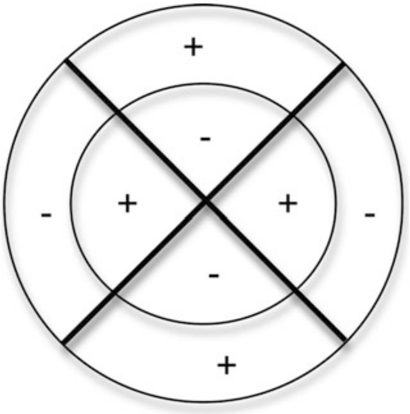


Fig. 5.4 Schematic of the (1, 2)-mode shape of a circular disc showing one nodal circle and two nodal diameters: + and − indicates motion that is 180° out-of-phase

biological source and substrate is to be able to answer a number of questions about the behaviour of the source for different substrates by comparing the predicted response with the measured response, hence providing more insight into the role of vibro-communications in biological sources.

5.3 Transmission Paths—Channel Properties

Here, two transmission paths are considered: that of plant fibres and that of soil, either being excited by structure-borne vibrations or airborne sound.

5.3.1 Signal Transmission in Plant Fibres

Stem motion in plants is more complex than a simple bending motion of a beam due to simultaneously acting types of waves and a non-constant major axis of the stem (McNett et al. 2006). This additional complexity might be important in vibrational sensing in insects and is preferably measured using more than a single vibration sensor (McNett et al. 2006). Plant fibres themselves act as waveguides and allow, apart from airborne sound, a very quick dissemination of information with wave speeds ranging from 10 to 100 m/s in stems (Appel and Cocroft 2014). Fleshy stemmed plants are less narrowband in their filter characteristics than woody fibres (Bell 1980; Cocroft et al. 2014b). The efficiency to convey information depends on its source strength, its distortion during propagation, environmental perturbations/noise and the ability of the receiver to extract information (Forrest 1994). Many insects are most receptive to low frequencies (<100 Hz, due to low-frequency receptor neurons, campaniform sensilla, joint chordotonal organs and Johnston's organ) and mid frequencies (<500 Hz, tuned interneurons at different levels of the ventral cord) (Howse 1964) and therefore communicate through plants by dispersive bending waves with little energy loss below a few kHz (Michelsen et al. 1982).

Vibrational waves reflect between the roots and the top of the plant and standing waves may result (Michelsen et al. 1982). Waves can be initiated directly in the plant or can be emitted from neighbouring plants and travel as longitudinal pressure waves in air to the destination plant; depending on the wave characteristics either the transmitting or the destination plant can have ideal filter characteristics to transmit only certain information or act as a beacon triggering behaviour, which could be required, for example, for subsequent mating behaviour sequences (Keuper and Kühne 1983; Symes et al. 2016). If transmitted as bending waves, vibrations have a frequency pattern that rapidly changes with the substrate's structure (knotholes), and the intensity of the vibratory signals does not decrease monotonically with distance due to reflections (Michelsen et al. 1982). Casas et al. (2007) showed by non-dimensionalised wave propagation analysis that arthropods, living on rush stems (*Juncus effuses*), would produce non-dispersive waves at frequencies higher than 5 kHz. For high frequencies Timoshenko beam theory is required to model the wave propagation; for frequencies lower than 5 kHz, Euler–Bernoulli beam theory, which neglects shear and rotary inertia effects, has been shown to be sufficient. Since most environmental noise is about 1–3 kHz, high frequency oscillations have higher signal integrity than low frequencies, as dispersive waves interfere stronger with low frequency environmental noise up to 2 kHz (Michelsen et al. 1982).

Feeding signals of termites or caterpillars are related to acoustic emissions and wave propagation properties of the substrate in the μm range. They are non-broadband signals and more complex and cryptic in nature than termite alarm signals (which consist of rather loud, periodic head banging) because the information must be transmitted to nestmates and is not intended for predators or competitors. Baensch et al. (2015) experimentally studied the principal behaviour of acoustic emissions for fast and slow cracking wood; the latter produced a significantly higher proportion of high frequency content (>400 kHz compared to about 200 kHz). These properties are particularly beneficial for wood dwelling social insects, such as termites, and it seems possible that the mandibular action and chopping speed influence the characteristics of vibrational emissions. In contrast to bees and wasps (Hymenoptera), which use mainly visual and chemical cues (pheromones), termites communicate mainly via vibrations, and only indirectly use airborne sound or electromagnetic radiation and light (Evans et al. 2005; Oberst et al. 2017).

As indicated by Inta et al. (2007), the mechanism by which termites perceive mass differences could be based on the elastic substrate response to feeding (Matsuoka et al. 1996) via detection of the magnitude (displacement, acceleration) through vibro-receptors on the body or in the legs of the insect (Howse 1964). If the spectral content is unimportant, then the temporal structure of the signals is required for information transmission (Inta et al. 2007; Oberst et al. 2016). Termite alarm signals (impacts) are broadband and relatively loud: the excitation of a number of resonance frequencies enables the transmission of information (repetition rate, amplitudes) over long distances even for strongly damped structures (Hager and Kirchner 2013). High signal integrity (clear, complete and unimpaired) is essential for termites to stay cryptic and still be able to communicate with nestmates while feeding on moist wood or clays by using micro-vibrations in the presence of environmental noise. While termites eavesdrop on walking signals of predators (e.g. ants) and further avoid them by walking much quieter (and cryptic, possibly using near field cues), their headbanging alarm signals, as long-distance communication, likely emerged from ant walking cues (Oberst et al. 2017).

It is likely that a specialisation in communication over the feeding signal and its complexity are correlated with parameters such as a tree's age, the foraging location (in the tree) or other host plant specifics (development stage, etc.), cf. Bell (1980). However, there is limited understanding of how vibrational communication changes with environmental signals, i.e. the presence of danger due to predators, competitors or agitated/alarming nestmates. The role of different substrates (clay, wood) and their roles as a filter are important since termites control their response and may adapt their behaviour to changes in substrate properties and environmental conditions (Brenowitz 1982).

5.3.2 Signal Transmission in Soils and Clays

The signal transmission energy spread through soils and inorganic material such as stones can be cylindrical (i.e. attenuating with a loss of 3 dB per doubling of distance from the source) or spherical (−6 dB per doubling of distance from the source) on the sound source characteristics. That of plant fibres is often restricted to one- and two-dimensions, either stems or fibres and leaves (Michelsen et al. 1982). Further, while smooth stones transmit vibrations quite well and almost perfectly reflect sound, soil- or sand-borne vibrations attenuate quicker with distance (Brownell 1977; Auersch 1994) with attenuation coefficients between $\alpha = 0.37 \times 10^{-3}$ s/m (weathered rock) and 2.15×10^{-3} s/m (loose sand) for Rayleigh wave excitation in pile driving (<500 Hz).[1] Bio-seismic cues have attenuation rates of about 3 dB per doubling of distance from the source and are used as long-range communication tools by elephants with an ideal frequency range of below 40 Hz (O'Connell-Rodwell et al. 2001).

Waves propagate in fluidic media with low and high viscosity such as air or water, propagating as longitudinal pressure waves; in solids, shear motion (transverse waves) is possible (Fletcher and Rossing 1998) and, in heterogeneous material, is accompanied by changing wave propagation characteristics (Nesterenko 2001). Different materials or composites behave differently under dynamic loading; shear

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[1] Attenuation coefficient α in Bornitz' formula $A_r = A_i \frac{r_1}{r} e^{-\alpha(|r-r_i|)}$, with A_i being the vertical amplitude component of a Rayleigh wave at distance i, $|r - r_1|$ being the distance between the source and the recording point (Auersch 1994).

waves (S-waves) are slower, but travel longer distances than bending waves (P-waves) and surface waves (Rayleigh, Love) (Fletcher and Rossing 1998; Royer and Dieulesaint 2000). Most studied animals use Rayleigh or bending waves; however, other wave forms are possible: scorpions (Brownell 1977) or fiddler crabs (Christy 1982; Aicher and Tautz 1990) also sense or produce compression and transverse boundary waves (Fletcher and Rossing 1998; Royer and Dieulesaint 2000).

Communication through sands and clays, as relevant in the fiddler crab (Christy 1982; Aicher and Tautz 1984), sand scorpions (Brownell 1977) or ant lions (Devetak et al. 2007; Devetak 2014), requires superior sensing capabilities. Yet little is known about the transmission of the vibrational communication signals through termite-built clays and its dependence on microscopic structures (particle size, granularity, water saturation), cf. Kandasami et al. (2016) and Oberst et al. (2016). While the particle size does not influence the stability of termite constructions, small cavities in the mound walls may play a crucial unknown role (Kandasami et al. 2016) as their function could be similar to that of honeycomb structures in advanced manufacturing for increased energy absorption (Santosa and Wierzbicki 1998). However, open cell structures also influence vibrations, acoustics and damping in structures. Dancing honeybee workers build small open cells in varying sizes in certain areas of the honeycomb; dancing at these locations produces stronger substrate-borne vibrations for recruitment of up to three times more nestmates (Sandemann et al. 1996). Similarly, termites, which use vibrations much more extensively than other eusocial insects, could design parts of their foraging sites as communication hubs by including differently constituted clays with varying density and macroscopic structure. In this context, studying active space networks (ASN) that include the underground parts such as roots and parts of the ground/soil, as well as various potential receivers and senders, could be of interest (Mazzoni et al. 2014).

5.4 The Noise-Control Engineering Principle

5.4.1 Classification of Noise

Noise is defined as *unwanted* sound or signal (Randall 1987; Forrest 1994; Kantz and Schreiber 2004). There are biotic (conspecific or heterospecific cues or signals) and abiotic noise sources, such as wind or rain, which is generally below 2 kHz (Forrest 1994), or anthropogenic noise caused by traffic and heavy machinery. Noise reduces the ability of a receiver to detect or discriminate information contained in the signal (Brumm and Slabberkoorn 2005). Noise can be classified as either static or dynamic, depending on its influence on the underlying deterministic dynamics (Kantz and Schreiber 2004). Other classifications are concerned with the origin of the noise: whether it originates within the receiver or from the communication channel itself (channel noise, within the sensory pathway of a receiver; Ronacher et al. 2004) or whether it is a high-dimensional process parameter as opposed to the low-dimensional deterministic signal that carries most of the important information for the dynamics (Kantz and Schreiber 2004). Noise can be separated mathematically into different types: linear and additive (independent of signal, no memory), multiplicative (amplitude dependent) or nonlinear with amplitude, frequency and phase dependency (Walls and Ferre-Pikal 1999).

Noise represents a general perturbation of the main carrier signal that influences interactions of animals with communication signals and can have a significant influence on animal behaviour, fitness and physiological, cellular or genetic processes (Kight and Swaddle 2011). Increasing the signal-to-noise ratio overcomes masking effects such as traffic noise, which leads to calls of increased intensity and/or also frequency (Nemeth et al. 2013). Another source of perturbations different from that of noise in the communication channel is signal distortion caused by material properties such as heterogeneous materials of a cluttered transfer path (airborne sound wave travels through canopies) or different impedances (Fletcher and Rossing 1998; Nesterenko 2001).

5.4.2 Filtering

For extraction of the excitation signal (source), it is necessary to have high signal quality. Noise, however, often is contained in the signal and cannot be easily removed. Accompanying high-dimensional processes run simultaneously to the dominant low-dimensional process so that filtering methods need to be applied.

5.4.2.1 Wiener Filtering

Wiener filtering is commonly used in signal processing and implemented in electronic hardware; based on the Fourier domain, certain spectral components identified as noise are weighted or even removed. Wiener filters are applied in the form of low-pass, band-pass (and notch) or high-pass filters (Randall 1987) that let low frequencies, a band of frequencies or high frequencies pass, thereby indirectly modifying the time domain waveform (Randall 1987). Wiener filtering requires a linear time-invariant system and a stationary signal that is perturbed only by additive noise; for nonlinear signals, Kalman filtering can be employed (Randall 1987).

5.4.2.2 Wavelet Filtering

For non-stationary, nonlinear signals or signals with multiple scales, a single-windowed Fourier transform is problematic and inefficient. Wavelet-based approaches (e.g. the continuous wavelet transform, CWT) allow for high temporal and spatial resolution by introducing a finite combination of scaling functions as an adaptive window, to spread the information over time-scales and various length-scales (Percival and Walden 2000). The use of wavelet filtering is very efficient due to available filter banks, and the applicability of the method to mixed signals, which includes the detection of non-stationarities. The CWT is defined as

$$\mathrm{CWT}(u,s) = \int_{-\infty}^{+\infty} y(t) \frac{\Psi^*\left(\frac{t-u}{s}\right)}{|\sqrt{s}|} dt \tag{5.6}$$

with $|\sqrt{s}|$ being the strictly positive square root of a scaling function, u time displacement, Ψ^* the complex conjugate mother wavelet and $y(t)$ is the response signal to be analysed. A mother wavelet (Haar, Morlet, Daubechies) similar to the function of a band-pass filter has to be chosen such that it approximates the behaviour of the time series (Torrence and Compo 1998). The discrete wavelet transform (DWT), used for decomposing the signal, filtering it and subsequent signal synthesis, is defined by

$$\begin{aligned} \mathcal{Y}[n,a^k] &= \sum_{i=0}^{N-1} y[i]\Phi_k[i-n], \text{ with } \Phi_k[i-n] = \frac{1}{\sqrt{a^k}}\phi\left(\frac{i-n}{a^k}\right), \\ n &= 0,1,\ldots,N-1 \end{aligned} \tag{5.7}$$

with $y[i] = y_i$ with $i \in I = \{1,2,\ldots,N-1\}$ being the discretised signal (y_k being the kth element of the time series vector, with $k \in I$), ϕ being the discrete wavelet and k being the discrete decomposition level, so that $s = a^k = 2^k$ represents a dyadic decomposition to scale the mother wavelet Φ.

A biological signal can be filtered by combining a CWT as provided with Eq. (5.6) and DWT as shown in Eq. (5.7). The CWT would determine which scale contributes most to the signal energy and which belongs to noise or distortion. The DWT is then used to isolate and discard those scales that belong to noise or distortion by minimising the loss of the signal energy; the removal of lower scales removes signal distortion, and that of higher scales increases the signal-to-noise ratio (Oberst et al. 2014).

5.4.2.3 Phase Space Filtering

To use nonlinear filtering based on attractor reconstruction in phase space, embedding techniques need to be applied to an observational time series (Kantz and Schreiber 2004). A rather simple nonlinear noise reduction replaces the central coordinate of each embedding vector (never the first and the last—initial errors would be magnified) by the local average of this coordinate, which amounts to a locally constant approximation of the dynamics, assuming continuous dynamics (physical flow data) (Pikovsky 1986; Schreiber 1993; Hegger et al. 1999). For each component y_i of an observational vector (here: response), a set of elements of the trajectory is determined for which

$$\mathcal{U}_i^{\epsilon} = ||y_j - y_i||_{sup} < \epsilon, \; \forall \; j. \tag{5.8}$$

Here, $\mathcal{U}_i^{\epsilon} = ||y_j - y_i||_{sup} = \sup || \cdot ||_2$ represents the supremum (smallest upper bound) of a spherical neighbourhood ($|| \cdot ||_2$ Euclidean norm) of radius ϵ. The neighbourhood has to be chosen large enough to cover locally the noisy data set along the trajectory, but smaller than the average global curvature of the dynamics. Each component y_i can then be corrected to the average of its values over the neighbourhood (Kantz and Schreiber 2004),

$$\hat{y}_i = \frac{1}{|\mathcal{U}_i^{\epsilon}|} \sum_{|\mathcal{U}_i^{\epsilon}|} y_j, \; \forall \; j. \tag{5.9}$$

Grassberger et al. (1993) proposed a noise reduction scheme that is based on segregating the measurements into low- (nonlinear, deterministic) and high-dimensional (quasi-stochastic) components by projecting it onto a low-dimensional (minimal) manifold $\mathcal{M}$ that houses the attractor. Noise spreads the dynamics away from the true trajectory and scatters the dynamics in phase space. For the filtering algorithm to work the noise amplitude has to be sufficiently small compared to the low-dimensional dynamics, with a correction vector being orthogonal to $\mathcal{M}$ that houses both the iterated time series and the true attractor ($\tilde{\mathcal{M}}$). The filtering procedure as implemented in the *ghkss* algorithm of the TISEAN package (Kantz and Schreiber 2004) can be applied to additive, multiplicative or also nonlinear noise (Kantz and Schreiber 2004; Oberst et al. 2015, 2017).

Figure 5.5 exemplifies the performance of the filtering method based on reconstructing the dynamics in phase space compared to wavelet filtering (Oberst et al. 2015) for the walking signal of an ant recorded on a thin veneer disc using a laser vibrometer. Both methods work reasonably well; however, the wavelet filtering introduces a small but spurious wave envelope shortly before the impact is recorded. The wavelet function is similar to a window in Wiener filtering processes. While this small spurious oscillation might not be important for the response, using even slightly erroneous signals in the inverse process might lead to large errors in the extracted source signal.

5.4.3 *Overview of Source, Transmission Path and Receiver*

Current methods using the noise control engineering principle in vibration and acoustic testing have been extensively studied in the past for linear systems and for nonlinear system identification (Worden and Tomlinson 2001; Kerschen et al. 2006; Noel and Kerschen 2017); reviews on transfer path analysis are provided in van der Seijs et al. (2006). As shown in Fig. 5.1, a transfer path analysis involves

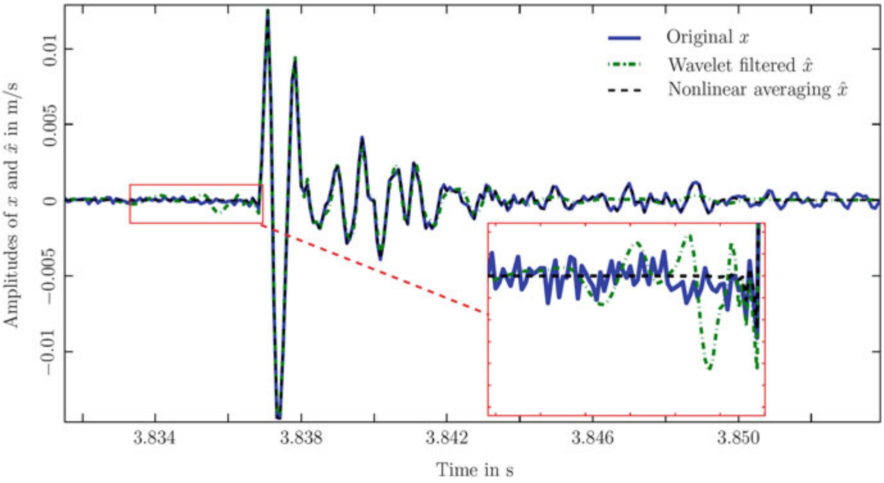

Fig. 5.5 Example of a recorded ant walking response signal on a thin veneer disc using a laser Doppler vibrometer setup in an anechoic chamber (Oberst et al. 2017); the signal is filtered using a wavelet filtering method and the nonlinear filtering based on the estimated low-dimensional manifold in phase space; reprinted from Oberst et al. (2015)

the analysis of (a) the response, (b) the energy transfer paths and (c) the excitation source (Shannon 1949).

The communication channel is mathematically described by the transfer function $H_{xy}(f)$ (the impulse response function in the time domain) using the cross- and auto-spectral densities, $G_{xy}(f)$ and $G_{xx}(f)$, of an excitation source ($x(t) = x_t$) and the system response ($y(t) = y_t$) ,

$$H_{xy}(f) = |H_{xy}|e^{i\phi_{xy}} = \frac{G_{xy}}{G_{xx}} \text{ with } G_{xy}(f) = \frac{2}{n_d T}\sum_{i=1}^{n_d} X_i{}^* Y_i, \tag{5.10}$$

where X_i and Y_i are, respectively, the FFTs of x_t y_t calculated over the ith data segment (total number n_d), T is the duration of each segment, superscript $*$ indicates the complex conjugate form, $|H_{xy}|$ is the *magnitude* of the transfer function (including the constant gain factor) and ϕ_{xy} is the *phase* (derived from poles and zeros); since magnitude and phase fully describe the dynamics, the poles and zeros, as well as gain factor, completely describe the system of differential equations. The feedback loop can play an important role since insects may adjust their behaviour due to changes in properties of the communication channel caused by abiotic noise (temperature, light, humidity) or unexpected signal distortion arising from nonlinearity or heterogeneity in the transfer path.

For periodic or near periodic signals the random error ϵ_r equals zero, with $\gamma_{x,y}$ being the coherence function between the source x and the receiver point y, and peaks in the response spectrum can be identified if the excitation frequency is not too close to the resonances as defined by

$$\epsilon_r \approx \sqrt{\frac{1-\gamma_{xy}^2}{2n_d\gamma_{xy}^2}}. \tag{5.11}$$

However, for multiple sources producing similar frequencies or a broadband spectrum, a source contribution is evaluated by turning on and off individual excitation points. Alternatively, the method of *coherent power output* could be applied (Randall 1987; Worden and Tomlinson 2001) by calculating the coherence functions γ for each *individual* source-receiver pair combination. The contribution of the ith source is then calculated using the so-called *coherent power relationship*,

$$\mathrm{COR}(f) = \gamma_{xy_i}^2 G_{xy_i}. \tag{5.12}$$

The limitations of the method described above are: (1) high signal-to-noise ratio is required for measurements; (2) the sources do not *cross-talk* between each other and (3) the relationship between the receiver and the source is linear. Obviously the switching on and off of an animal's behaviour, or controlling its excitation signal, is near impossible. In fact, source localisation based on vibrations is rarely discussed in biology, and the excitation source is usually not extracted; instead, using bioassay experiments, simply the response signal is played back, which of course includes the contribution of the communication channel (Bell 1980; Uetz and Roberts 2002; Evans et al. 2007; Fabre et al. 2012; Riva et al. 2017).

Hager and Kirchner (2013) recently showed that termites of the species *Macrotermes natalensis* and *Odontotermes* spp. transmitted their alarm signals over several metres from their mound. In order to have a strong signal, neighbouring soldiers adjusted their positions relative to the alarm signal, presumably for better reception, and joined in the drumming, chain-reaction-like, which resulted in amplification of the alarm until the signal reached the nest. The dominant spectral frequency depended on the substrate, and termite soldiers and workers responded mostly to similar temporal impulses of about 20 Hz and amplitudes above $1\,\mathrm{m/s}^{-2}$ within a frequency range of 10 Hz–5 kHz (Hager and Kirchner 2013; Oberst et al. 2017) by repeating the signal and running away, respectively. It can be assumed that the amplitude conjointly with the delay provides vibro-klinotactical cues to determine the orientation and the exact source of the signaller. Based on the vibration amplitude, some conclusions about the insect's physiology might be drawn, i.e. many insects vibrate their host plants with signal amplitudes up to thirty times above their receptor sensitivity threshold (Michelsen et al. 1982). A changed position of a termite soldier could give some clues whether the transmitted signal qualities have altered in waveform or response intensity.

5.4.4 Example: Vibration Characteristics of Communication Channels

The transmission of vibrational energy strongly depends on the character of the excitation signal and the transfer path the signal takes (Fletcher and Rossing 1998). Figure 5.6 displays two out-of-plane experimental mode shapes of a circular thin disc (60 mm diameter, 0.9 mm thickness) with *nominally* $n = 3$ nodal diameters (Fletcher and Rossing 1998) for Fig. 5.6a aluminium or Fig. 5.6b veneer (*Pinus radiata*).

The discs were centrally *excited* $X(f;T)$ by an electrodynamic shaker (Bruel & Kjaer 4809) using nonlinear periodic sweep (128 ms sweep time). Their vibration velocity *responses* $Y(f;T)$ were measured using a scanning laser vibrometer (Polytec PSV-400, 30 averages, 12.5 kHz sampling rate). While the aluminium plate shows a clear out-of-plane mode of three nodal diameters, the vibration mode of the veneer disc looks wavery and is asymmetrical owing to heterogeneous material properties and the influence of the direction of the grain.

The response signal strength depends on both the geometry (mode shape) and the material properties. Figure 5.7a depicts the measurement mesh, while Fig. 5.7b, c display, respectively, the response spectra of the aluminium and veneer discs subjected to the same excitation for two measurement points. The responses at the two measurement points are quite different; although, point 144 is closer to the excitation source, its response is weaker than that of the point 333 at the edge, especially for the aluminium plate because of its proximity to a nodal line (i.e. zero vibration amplitude). Owing to the different stiffness of the structure, the modal density of the veneer disc is much higher than that of the aluminium disc for a given frequency range, as visible in the phase spectrum.

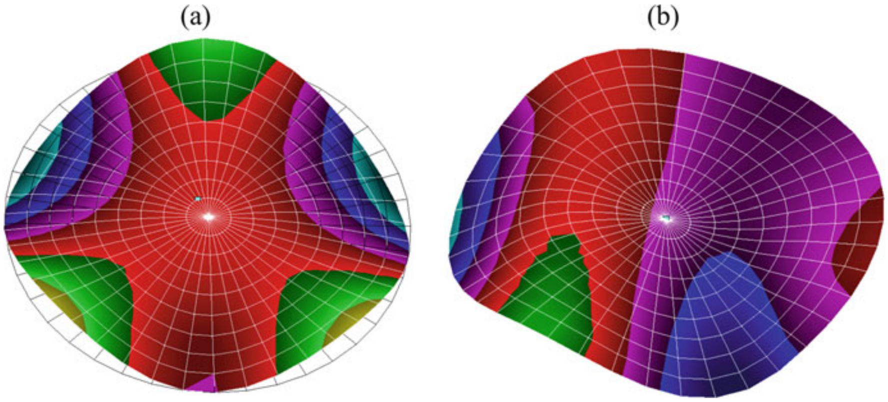

Fig. 5.6 Experimental vibration mode shapes of (**a**) an aluminium disc (isotropic material) and (**b**) of a veneer disc; 361 scan points. Both modes are out-of-plane with three nodal diameters, vibrating at 851 Hz and 1641 Hz, respectively. However the veneer disc has mixed characteristics of a circular disc and a series of parallel beams due to the grain direction

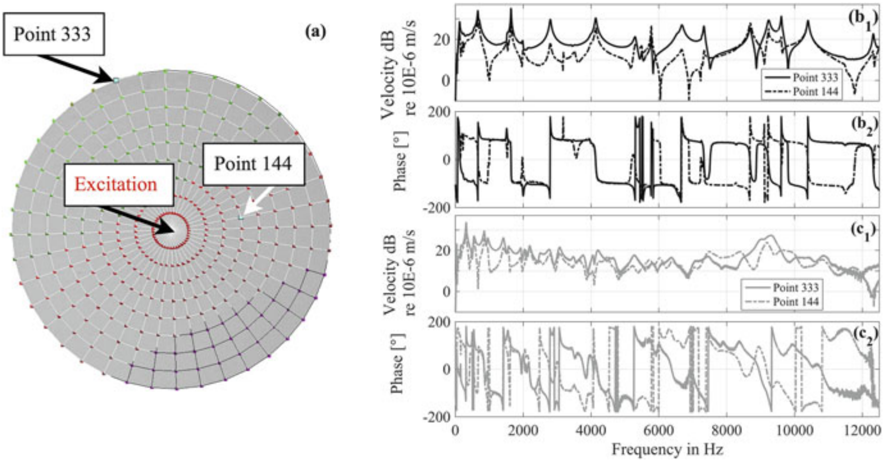

Fig. 5.7 (**a**) Overview of scan points for measuring operational deflection shape with the source and two receiver positions highlighted; output values $Y(f, T)$ and their phase angles for the (**b**) aluminium (1.64 kHz) and the (**c**) veneer disc (0.85 kHz)

5.4.5 Example: Invertebrate Substrate Response Signals

Here, the vibration response measured on thin veneer discs using the setup described by Oberst et al. (2015, 2017) highlights differences in substrate responses due to motion. Figure 5.8 provides screen shots, time traces of vibration velocities of veneer discs and estimated power spectral densities of recorded vibration velocities for a single termite (*Coptotermes acinaciformis*), an earthworm (*Aporrectodea* spp.), a house spider (*Badumna insignis*) and a meat ant (*Iridomyrmex purpureus*).

The signals were recorded using a laser vibrometer isolated with an air-cushioned vibration bench-top within an anechoic room (Oberst et al. 2015, 2017). The background noise floor indicates a dip between 0.1 kHz and 2 kHz due to the boundary conditions of the veneer disc (Garcia-Gonzalez et al. 2016).

We observed that the termite (walking), the earthworm (slithering) and ant (walking) were moving continuously; while the termite was trotting at the same pace, the ant and the earthworm gait pattern changed speed more often and the spider's walking was intermittent, changing between motionless and short running impulses (two motion-segments depicted in Fig. 5.8).

The termite walking had the lowest response level, being close to the background noise level, while the ant produced the highest vibration level, on average 10 dB higher than signals of the termite, earthworm and spider. The earthworm was only showing large amplitude vibrations when it temporarily lifted up its head (not depicted). The response spectrum of the earthworm indicates that in-plane modes of the veneer disc (at about 164 Hz) were excited, presumably produced by the muscle contractions due to the worm's pulsating motion. The termite, the ant and the spider excited out-of-plane modes due to their legs impacting the substrate vertically

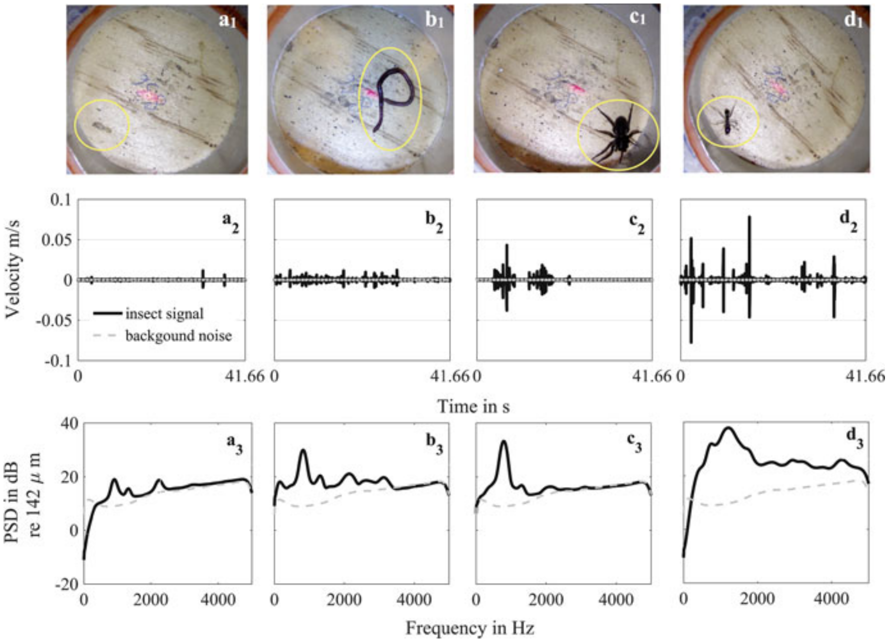

Fig. 5.8 (1) A snap shot (using a digital camera) of different invertebrates (circled) walking using a digital camera, (2) the time trace of vibration velocities of veneer discs and (3) a Power Spectral Density (PSD) estimate for (**a**) a single termite (*Coptotermes acinaciformis*), (**b**) an earth worm (*Aporrectodea* spp.), (**c**) a black house spider (*Badumna insignis*), and (**d**) a single meat ant (*Iridomyrmex purpureus*). The response of the veneer disc due to background noise is provided for comparison

(bouncing like a monopode, Blickhan and Full 1993). The termite's signal was weak and qualitatively different from the others, as the strongest excited vibration mode was not the out-of-plane mode at around 800 Hz but the in-plane mode at 2.2 kHz. The spider's response signal was narrow band in contrast to the rather broadband signal of the ant.

The chosen examples demonstrate that different motion techniques produce different vibrations. However, animals do react to their environmental conditions and to different substrate properties owing to a feedback relation shown in Fig. 5.1. The response to an excitation signal may influence the animal's behaviour. It is therefore paramount to study not only the *response* but also *substrate properties* and the change in the *excitation signal* as a response to changed substrate properties or biotic/abiotic noise (wind, rain) that could be controlled in playback experiments with bioassays in an anechoic room.

5.5 Experimental Source Identification Methods and Their Limitations

To extract the excitation source, the response needs to be located and then decoupled from the contribution of the transfer function, the communication channel.

For airborne sound (air as a homogeneous, linear fluid medium), noise source identification methods for noise emission optimisation of vehicles, wind turbines or household appliances can be applied directly: sound mapping (Quintana et al. 2009), near field acoustic holography (NAH), including statistically optimised NAH (Maynard et al. 1985; Fernandez-Grandea and Xenaki 2017), and beamforming (BF), including *refined* BF, *moving source* BF and *spherical* BF (Cox et al. 1987; Fischer and Doolan 2017).

Sound pressure (SP) mapping records, locally and point-wise, a contour sound pressure level map to characterise and localise sound sources. Owing to slow measurements, the high susceptibility to noise and its limitation to stationary signals, SP mapping is nowadays rarely used. In contrast to sound pressure, the sound intensity technique determines the acoustic energy flow vector and is less susceptible to noise or non-stationarity. In nearfield acoustic holography (NAH), a regular microphone grid measures the SP to calculate auto spectra and cross spectra and to extract a sound field's acoustical properties using a principal component analysis. *Beamforming* (BF) uses an array of microphones and beamforming calculations (signal processing) to obtain images of the sound field. A limitation of beamforming is the generation of ghost images for uniform microphone distances larger than $\frac{1}{2}$ of the wavelength of the measured sound.

Methods described above measure sound pressure originating from vibrations. Owing to spatial limitations in setting up the microphone arrays, the spatial resolution of acoustic measurement techniques is limited. An improved spatial resolution and higher sensitivities are provided using optical methods such as point, differential or scanning laser Doppler vibrometers, especially for micro-vibrations, in-plane excited motions or transient effects such as travelling structural waves (Eaton et al. 2012; Rothberg et al. 2017). If the vibrations are large enough and if the structure measured is not too filigree, accelerometers may be used but it will take significantly longer time than scanning vibrometers to complete measurements, despite being cheaper (setup, multiple point measurements). To test acoustic emissions (transient elastic stress waves), traditionally ultrasonic testing equipment is used to measure wave speeds of several hundred kHz (Baensch et al. 2015). In order to measure the whole field, either a range of point vibrometers or scanning techniques need to be employed; scanning techniques only measure at a coarse resolution or quasi-steady vibrations. Using a high-speed camera and measuring the changes in pixel intensity allow the measurement of an instantaneous full-field displacement field of a cymbal for mode shape extraction (Javh et al. 2018).

All experimental methods described above measure the response signal of a vibrating system. To extract an unknown excitation signal from a response, experimental source localisation methods are not sufficient—source identification is required. Samet et al. (2017) gave an overview of past and recent developments of vibration source identification methods, which are mainly based on inverse approaches to localise vibration sources and to quantify acting forces. The force analysis technique (FAT) uses the displacement field as calculated by a finite difference method for force quantification and localisation, as exemplified for beams, plates and cylindrical shells (Samet et al. 2017). Chen and Liu (2000) described how to use Kalman filtering with a recursive estimator to determine the input force in a mechanical 'grey box' model. By assuming homogeneous, linear-elastic materials, the transfer function can be estimated assuming an n-parametric model. Oberst et al. (2014) used wavelet filtering (signal decomposition and signal synthesis) to extract the most important scales of the response and a linear parametric model of a veneer disc to apply the matrix pencil method to extract the excitation forces caused by insects moving stones, scratching the substrate (veneer) or dropping on the veneer.

Oberst et al. (2015) used a vibration isolated laser vibrometer test rig within an anechoic room to measure the micro-vibrational responses of ants walking on thin veneer. They developed a signal processing method using nonlinear filtering (Kantz and Schreiber 2004), and an experimentally characterised veneer disc, to apply Tikhonov regularisation to extract the excitation signals of ants. However, inverse (blind) source identification methods suffer from non-uniqueness of the solutions. A strong sensitivity to perturbations or noise, and the necessity of obtaining a complete set of transfer functions, complicates matters, which requires long computation and experimental times (Naikm and Wang 2014).

5.5.1 Example: Extracting Source Characteristics Using Blind Deconvolution

Extracting source characteristics using only the transfer function and the response belongs to the class of non-unique, inverse problems (Naikm and Wang 2014). Ill-conditioned matrices, signal distortion and various kinds of noise complicate its application, and even for analytical periodic signals, the deconvolution process becomes problematic (Oberst et al. 2015). For weak responses (biological micro-vibrations) measured on natural, heterogeneous solid substrates (wood, clays), there is a large variability and measurement uncertainty that needs to be handled (Cocroft et al. 2014b). Oberst et al. used a linear spectral parametric model of a veneer disc response, composed of exponentially damped sinusoids, to estimate the transfer function (Oberst et al. 2014).

$$\tilde{Y}[n, a_i] = \sum_{i=1}^{M} a_i e^{s_i n} + w[n], \text{ with } a_i = |a_i| e^{j\Phi_i} \text{ and } s_i = \alpha_i + j2\pi f_i. \quad (5.13)$$

where $\tilde{Y}[n, a^j]$ is the modelled response; $w[n]$ is white observational noise; M is the number of complex exponentials; $|a_i|$, Φ_i, α_i, f_i are the real amplitudes, the phase, the damping coefficients and the eigenfrequencies and $j = \sqrt{-1}$ being the imaginary number. In Oberst et al. (2014), a model order of five sufficiently approximated the wavelet filtered signals. Even though most of the noise was removed through filtering, the variability of signal lengths was problematic and the matrix pencil method (MPM) was therefore used for parameter estimation (Oberst et al. 2014). Then, the transfer function (*filter* function) could be extracted by designing a linear filter. However, owing to the substrate's heterogeneity and inherent nonlinearity, a linear parametric model assuming homogeneous properties is found to be insufficient; also the MPM only works properly for non-ill-conditioned matrices, which is not the case here. Hence, only the impact of an ant dropping onto the substrate could be extracted; biting and scratching excitation remained obscure (Oberst et al. 2014). Further, the use of accelerometers mass-loaded the veneer disc and was prohibitive in detecting small structure-borne vibrations.

It is more accurate to characterise the transfer function by direct measurements; using the acoustic wave of a loudspeaker as an excitation source (*force*) and a laser vibrometer's measurement as a receiver (*response*) signal[2] (Oberst et al. 2015).

$$x(t) * h(t) = y(t) \xrightarrow{\mathcal{F}} X(\omega)H(\omega) = Y(\omega) \xrightarrow{(\cdot)} \mathbf{XH} = \mathbf{Y} \tag{5.14}$$

Equation (5.6) expresses the relation between the input (source) $x(t)$, the system $h(t)$ and output (receiver) $y(t)$ in the time domain using convolution integrals; by applying the Fourier transform ($\mathcal{F}$), one changes from the time domain to the Fourier space and the convolution operator changes to multiplication to obtain the response. Considering the spectrum as a list of frequency-related entries, matrix notation is employed using **bold** fonts. Calculating backwards (defining $X(\omega) = X$) and applying an inverse Fourier transform gives the system's impulse response function $h(t)$, of which only the real part $\Re$ is physically sensible.

$$\mathbf{XH} = \mathbf{Y} \xrightarrow{X^{-1}(\cdot)} \mathbf{H} = \mathbf{X^{-1}Y} \xrightarrow{\mathcal{F}^{-1}} \Re\left(g(t)\right). \tag{5.15}$$

Attempts of signal enhancement with deconvolution can be found in image processing with a point-spread function using wavelet filtering with soft/hard Bayesian thresholding (regularisation) or the Tikhonov regularisation, which adds uncorrelated noise to the denominator to improve the matrix condition (Tikhonov et al. 1977).

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[2] The laser vibrometer measurements were less contaminated with background noise, which was about 125 times lower compared to the accelerometer measurements reported in Oberst et al. (2014).

Let **X** be the discrete Fourier transform of the excitation (complex vector), **H** be the transfer function of the substrate and **Y** be the measured substrate response. Minimisation of the Euclidean norm of the difference (Gubbins 2004) $\epsilon^2 = \|\mathbf{X}\cdot\mathbf{H}-\mathbf{Y}\|_2^2$ estimates **H**. As **H** is overdetermined, the Tikhonov matrix (Γ) is included to give the following expression for the excitation.

$$\mathbf{X} = (\bar{\mathbf{H}}\mathbf{H} + \bar{\mathbf{\Gamma}}\Gamma)^{-1}(\bar{\mathbf{H}}\mathbf{Y}) \tag{5.16}$$

where $\bar{\mathbf{G}}$ denotes the Hermitian of matrix **G**, and $\Gamma = \sqrt{\lambda}\mathbf{1}$ is the regularisation matrix equal to the square-root of the water-level control parameter λ times a unity vector **1** (Tikhonov et al. 1977).

Figure 5.9 shows the process of convolving a sinusoidal signal (Fig. 5.9a) with its transfer function (Fig. 5.9b) so that its response (Fig. 5.9c) becomes a function of both; then deconvolving this response (Fig. 5.9d) with known transfer function using spectral division (1st row), and Tikhonov regularisation using $\lambda = 1$ and 10 (2nd and 3rd rows, respectively). Simple spectral division does not work well, even for simple periodic functions in the absence of noise; only Tikhonov regularisation is able to recover the original excitation signal again.

Tikhonov regularisation was applied to ant response signals of *Iridomyrmex purpureus* and *Lasius niger* to extract excitation signals as shown in Fig. 5.10a, b. Evidently, the excitation signal of the two ants is proportional to their response signal; the FFT of both signals gives a stepping frequency of 16.1 Hz (Fig. 5.10c) and 11.7 Hz (Fig. 5.10d), which is similar to that of 19 Hz found in wood ants (Reinhardt and Blickhan 2014). The median normalised excitation signal of the *L. niger* is about 45 % of the larger ant *I. purpureus* with Fig. 5.10e median stepping

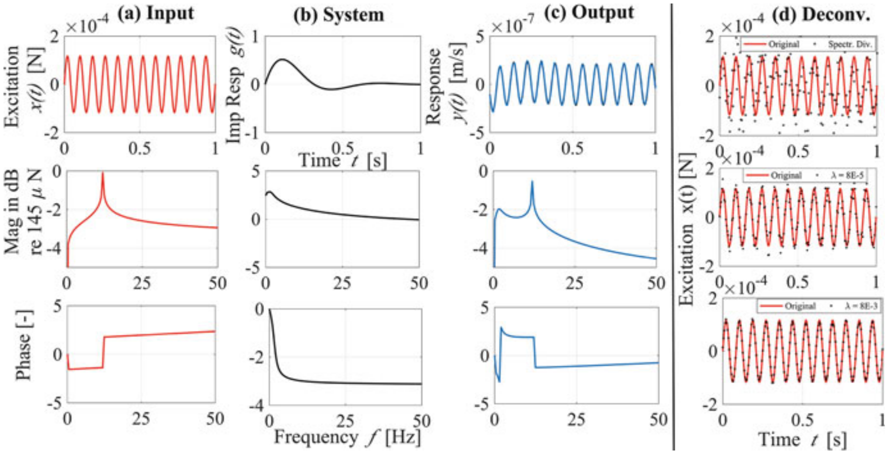

Fig. 5.9 Example of deconvolution process showing the time traces (1st row) the magnitudes (2nd row) and their corresponding phases (3rd row) of a (**a**) sinusoidal input signal $x(t) = 117.5\sin(75.39t)$ N, (**b**) an impulse response function $g(t) = t\exp{-t}$, (**c**) the response signal $\mathcal{F}^{-1}\{X(\omega)G(\omega)\} = y(t)$, and (**d**) is the deconvolved excitation signal

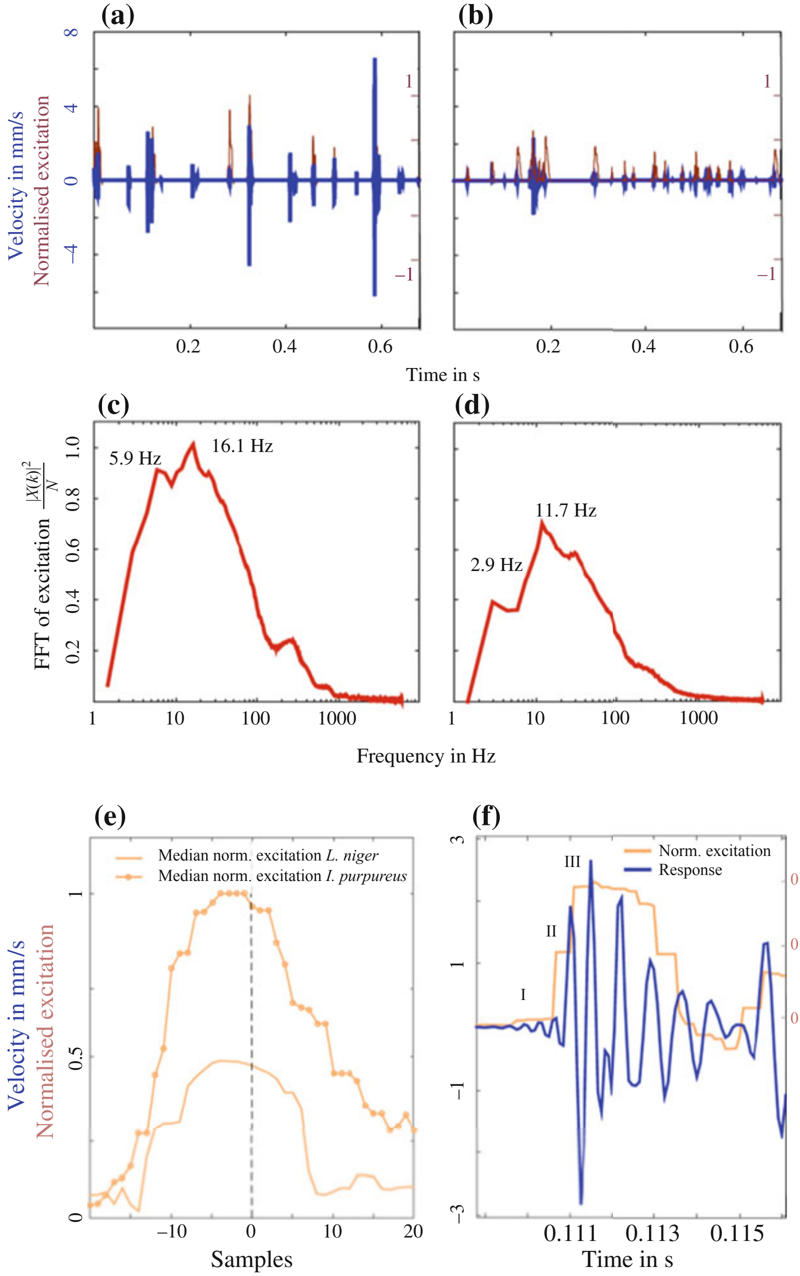

Fig. 5.10 Response and extracted excitation signals of ants (**a**) *Iridomyrmex purpureus* (*), and (**b**) *Lasius niger* (**); Fourier spectra of the extracted excitation signals with peaks at (**c**) 16.1 Hz (*) and (**d**) 11.7 Hz (**); and (**e**) median normalised excitation signals, as well as a (**f**) comparison between a typical response and excitation signal (*) highlighting a step function with various stepping patterns; figure taken from Oberst et al. (2015)

times of 1.9 ms for *L. niger* and 2.5 ms for *I. purpureus*. Interestingly, even the impulses due to different numbers of legs hitting the ground within the tripod gait pattern seem to be extracted, giving rise to two staircase functions approximating a rectangle pulse.

5.6 Discussion

Communication involves the sharing of information (message) via channels (media such as air, water, solid matter) in a meaningful way between sender(s) and recipient(s), cf. Wiener (1965). Ants (and wasps), termites and bees as eusocial insects rely significantly on efficient means of communication based on pre-filtered information; the sensing system also acts like a filter. While insects communicate naturally multimodally (Hölldobler 1999), there are few studies on combined communication modalities; the effects of the communication channel as such received even less attention.

As argued in this chapter, in order to interpret a signal, any receiver has to understand the information buried in it. For airborne sound, this is less a problem since air is homogeneous; although reflections and environmental noise could degrade the signal quality. However, in structure-borne vibrations, the communication channel's material properties are heterogeneous and the vibration propagation may occur in a nonlinear fashion. Distortion effects are commonly encountered, and plant fibres, rocky materials or clays all contribute to reflections of sound/vibrations, different absorbance and signal attenuation rates.

Insects that communicate with their nestmates using substrate and vibrations have to adapt their communication strategy (altering frequency, phase relationship and amplitude) and might even use different techniques (wave forms) to communicate. Here, different substrates, also modified by the insects, might be used as filters in a different situational context: quiet feeding requires high absorption coefficients and damping to reduce transmission to the outside world, while communication between nestmates must be maintained. Alarm signals need to travel fast and reach every member of the colony or family.

To test this experimentally via bioassays, an accurate method to extract the excitation signal from the substrate response is required. Since many small insects exert minuscule forcing, it would be desirable to correlate measurements (Oberst et al. 2017) to various features, using camera recordings to calibrate a bottom up approach similar to that proposed by Blickhan (1989), in combination with an inverse approach as suggested by Oberst et al. (2015). The extracted signal properties could then be used to establish biodynamic models using mass-spring-damper oscillators to study the fundamental biology behind the excitation signal characteristics, the role of the transfer function and the response in a controlled environment. Since this method is general, different excitation mechanisms and the influence of different kinds of noise can be studied in a systematic way, also to disentangle multi-modal vibration signatures (walking or chewing sounds).

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Chapter 6
Copulatory Courtship with Vibrational Signals

Rafael L. Rodríguez

Abstract Most research on sexual communication with substrate-borne vibrational signals has focused on the early stages of the reproductive process—mate localization and pair formation. Here, I report the results of a literature review that suggests that vibrational signals are commonly used in male–female interactions during and after copulation, either by themselves or in conjunction with tactile courtship. This observation suggests that vibrational signals may function not only in precopulatory mate choice but also in cryptic mate choice. Thus, there is reason for the surreal world of communication with substrate vibrations to join the baroque realm of postcopulatory sexual selection.

6.1 Introduction

In this chapter, I seek to bring together two exciting lines of research on the evolution of behavior that have proceeded in parallel, largely independent of each other. The first area is the study of communication with substrate-borne vibrational signals. This modality of communication is turning out to be widespread in many animal taxa, and many species use it in varied and complex social and ecological interactions, accomplishing impressive feats of localization and navigation (Cocroft and Rodríguez 2005; Drosopoulos and Claridge 2006; Hill 2008; Cocroft et al. 2014; Rodríguez and Desjonquères 2019). The second area is the study of courtship that occurs during and after copulation. Behavior designed to court mating partners is also taxonomically widespread; through signaler–receiver stimulation or back-and-forth male–female exchanges, it is an important determinant of variation in reproductive success within populations and reproductive isolation between

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populations (Eberhard 1994, 1996, 2009; Schilthuitzen 2014; Peretti and Aisenberg 2015; Rodríguez 2015).

Both of these areas saw foundational publications in the 1980s that were followed by a marked increase in attention and work, and are currently flourishing. Progress in each has brought profound insights into the factors that are important in the social and sexual lives of animals, and into the evolution of complex and extravagant behaviors and morphologies. There has been, however, what to my mind is a curious lack of integration of research between these two areas. I am not aware of research on copulatory courtship and cryptic mate choice that explicitly considers a potential role for vibrational signals. And in the realm of sexual communication, most of the research on substrate-borne signaling has focused on pair formation and mate localization, with relatively little attention to later stages of the reproductive process.

There are good reasons for there to be a meeting of these fields, however. The mechanisms designed to impart vibrational signals onto the substrate seem "ready-made" to stimulate the body of the mating partner once physical contact is achieved. Further, if, say, the female has already been responding positively to the male's precopulatory courtship signals, he may be able to sustain her favor by continuing to use the same signals following contact. Even if signals of a different type or modality were best suited for courtship during or after copulation, a transition during which both signal types overlap for a while may be more likely to succeed than an abrupt change.

Here, I look for cases of animals known to use substrate-borne vibrational signals in pair formation and ask if there is evidence that they continue to use such signals in courtship during or after copulation—i.e., during or after genital coupling. This seemed to me to be the best inroad currently possible. To ask the question, the requirement was for studies to have continued to pay careful attention to behavior once copulation was initiated, which is often not the case (see below). Consequently, the answer cannot currently be robust in terms of prevalence within or across groups. However, I think it is possible to ascertain whether increased attention is likely to be profitable.

For those cases in which substrate-borne vibrational signals continued to be used during or after copulation, I also asked whether the same or different signal types are involved. It could be, for instance, that different kinds of vibrational signals are best suited for communication at a distance versus courtship in physical contact, or that once in copula tactile signals such as rubbing are more appropriate. Finally, I asked if vibrational signals were used alone or in conjunction with tactile courtship behavior during copulation.

6.2 Methods

I conducted a literature search on Web of Knowledge, complemented by my own reference collection and consultation with experts. In Web of Knowledge, I searched for papers with the keywords "vibrational signal" + "mating behavior", or “vibrational signal” + “copulatory courtship”. I included results pertinent to evolution and behavior (excluding, e.g., topics like biochemistry and cell biology). Finally, I selected the papers that provided detailed observations of behavior during and/or after mating (many papers state that they present descriptions of mating behavior but in fact offer accounts of pair formation only). I included a paper on Japanese beetles, *Popillia japonica*, which do not seem to use vibrational signals in pair formation from a distance but do use them before, during, and after genital intromission (Rodríguez et al. 2015). I also included a paper on two species of *Ozophora* seed bugs for which there is only information about their copulatory behavior but not their pair formation behavior (Rodríguez 2000), because substrate-borne vibrational signaling is widespread in the Heteroptera in general and in Lygaeidae in particular (Cocroft and Rodríguez 2005).

I excluded from analysis cases where signaling continues while the male is mounted on the female but prior to genital intromission (e.g., Cocroft 2003; Percy and Day 2005). These cases are interesting, but I wished to focus on the potential for a role of substrate-borne vibrational signals in copulatory courtship and cryptic female choice.

These criteria yielded a sample of 23 species of insects and spiders from 22 genera, 13 families, and 6 orders (Table 6.1). I do not expect this list to be exhaustive. However, it seems to me to represent a good portion of the information that is currently available. For each of these species, I noted whether they continued to use substrate-borne vibrational signals during copulation; if so, whether they used the same or different signals types; and whether they used vibrational signals exclusively or in conjunction with tactile copulatory courtship behavior (e.g., the male rubbing or tapping the female with his legs).

6.3 Results

An example of one of the scenarios to be found in the literature is shown in Fig. 6.1. In Japanese beetles, *Popillia japonica*, males produce vibrational signals while they attempt to mount females, continuing through genital intromission and after, as they remain on the females’ back for mate guarding (Rodríguez et al. 2015). The males’ signals could be recorded from the substrate (vine trimmings) even when the males were fully on top of the females. Males also stroked the females’ elytra with their legs, most commonly prior to intromission.

In the full sample of 23 species that use substrate-borne signals in pair formation and for which there are sufficiently detailed descriptions of mating behavior (Table 6.1), 20 species are also reported to continue to use vibrational signals during/after copulation (Fig. 6.2, outer doughnut). This represents 87% of the species for which the question can currently be asked. Similarly, the answer was in the affirmative for 19 out of 22 genera (86%), 12 out of 13 families (92%), and all 6 orders.

Table 6.1 Studies included in the tally of the use of substrate-borne vibrational signals in courtship before and during copulation

	Vibrational signals during/after copulation	Different signals before vs. during copulation	Same signal before vs. during copulation but with quantitative differences	Tactile courtship during copulation	References
Araneae					
Hololena curta (Agelenidae)	y				Xiao et al. (2015)
Holocnemus pluchei (Pholcidae)	y	y?			Huber (1995)
Physocyclus globosus (Pholcidae)	y	n?		y	Huber and Eberhard (1997), Peretti et al. (2006)
Coleoptera					
Popillia japonica (Scarabaeidae)	y	n	n	y (mostly before intromission)	Rodríguez et al. (2015)
Hemiptera					
Anoeconeossa bundoorensis (Aphalaridae)	y (after copulation during egg laying)				Wood et al. (2016)
Scaphoideus titanus (Cicadellidae)	y (first few min; unclear if by male or female)	n			Mazzoni et al. (2009)
Javesella sp. (Delphacidae)	y		y		Claridge and de Vrijer (1994)
Nilaparvata sp. (Delphacidae)	y		y		Claridge and de Vrijer (1994)
Enchenopa binotata complex (Membracidae)	n[a]				Cocroft et al. (2008)
Umbonia crassicornis (Membracidae)	y (not clear whether by male or female)				Losinger (2016)
Diaphorina citri (Psyllidae)	n				Wenninger et al. (2009)
Schedotrioza spp. (Psyllidae)	n?			y	Percy et al. (2006)

Heteroptera					
Ozophora baranowskii (Lygaeidae)	y[b]			y	Rodríguez (2000)
Ozophora maculata (Lygaeidae)	y[a]			y	Rodríguez (2000)
Acrosternum hilare (Pentatomidae)	y	y			Čokl et al. (2001)
Chlorochroa uhleri, *C. ligata*, and *C. sayi* (Pentatomidae)	y	y	n		Bagwell et al. (2008)
Euschistus conspersus (Pentatomidae)	y	n (but reduced repertoire during copulation)	y?		McBrien and Millar (2003)
Euthyrhynchus floridanus (Pentatomidae)	y	n	y	y	Briceño (2014)
Holcostethus strictus (Pentatomidae)	y	y			Pavlovčic and Čokl (2001)
Murgantia histrionica (Pentatomidae)	y (rare)				Čokl et al. (2004)
Orthoptera					
Copiphora rhinoceros (Tettigoniidae)	y (after copulation)				Morris (1980)
Plecoptera					
Capnia bifrons (Capniidae)	y	n?		y	Brinck (1949, pp. 117–120)
Perla spp. (Perlidae)	y?[c]				

[a] For the tally, I counted the *Enchenopa binotata* complex as one species because a key determinant of their sexual biology may be the lack of sexual selection following pair formation due to females mating only once (Wood 1993; Sullivan-Beckers and Cocroft 2010)

[b] For *Ozophora,* there is no evidence of vibrational signaling in pair formation, but I included these species here because there is indirect evidence of vibrational signaling during copulation for both of them (observation of hind leg vibration). As the behavior differed between them, for the tally I counted them as two species

[c] For the tally, I counted these as one species

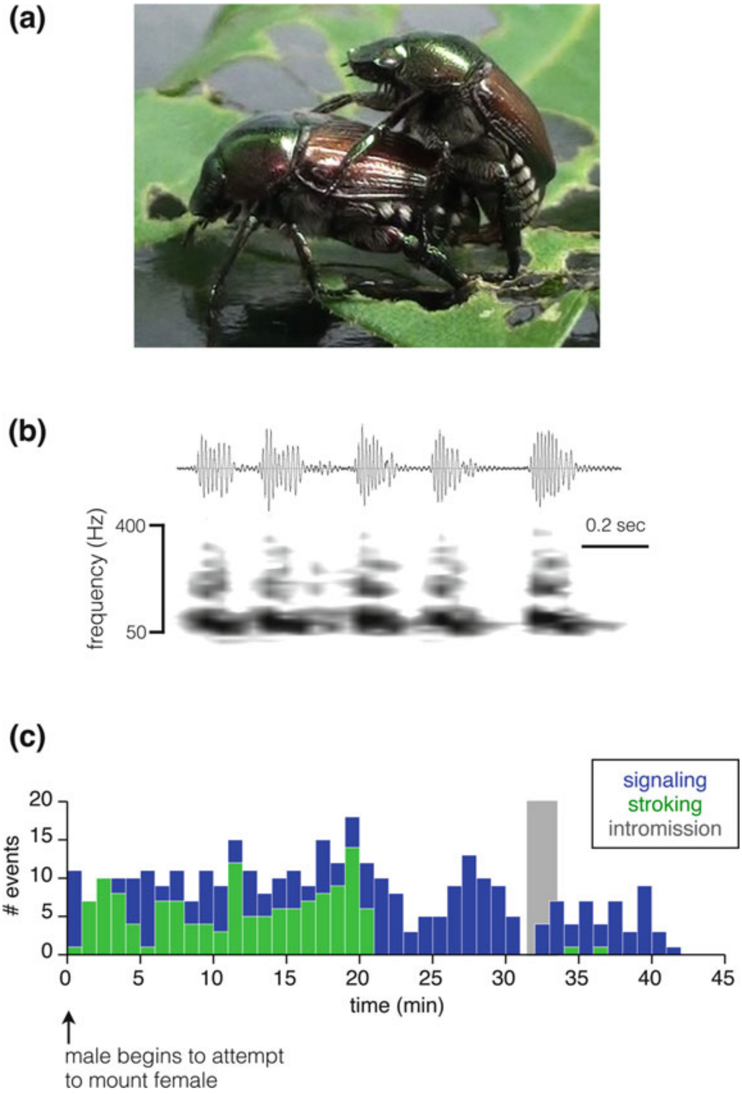

Fig. 6.1 Japanese beetles, *Popillia japonica*, are an example of a species that uses vibrational signals and tactile courtship during copulation (Rodríguez et al. 2015). (**a**) Mating position of the beetles, with the male mounted on the female's back and in genital intromission. (**b**) Vibrational signals produced by males while they attempt to mount the females and through to mate guarding. The signals consisted of short pulses having low dominant frequency delivered at varying rates. (**c**) One mating sequence showing the timing of production of vibrational signals and stroking of the female with the legs relative to genital intromission. From Rodríguez et al. (2015), with permission from the Annals of the Entomological Society of America (Oxford University Press)

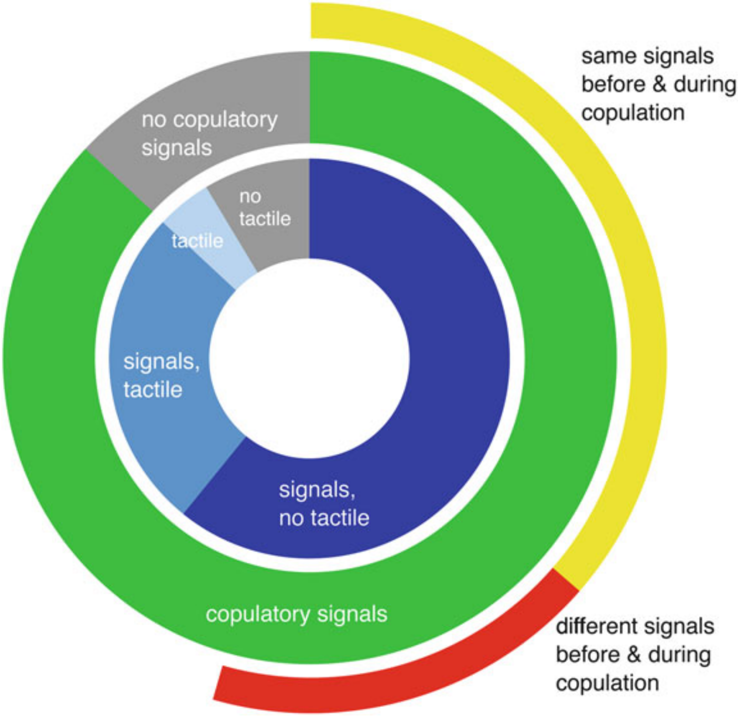

Fig. 6.2 Proportion of the species included in the literature survey that used vibrational signals as copulatory courtship (outer doughnut), used vibrational signals and/or tactile stimulation as copulatory courtship (inner doughnut), and used the same or different types of vibrational signals in pair formation and copulatory courtship (outer half doughnut)

Of the 20 species that used vibrational signals during copulation, there were 12 species for which it was possible to specify whether they used the same signal type in pair formation and during copulation, or whether they used different signal types at these different stages of the reproductive process. It was twice as likely that the same signal type would be used (eight species) than a different signal type (four species) (Fig. 6.2, outer half doughnut). And in four of the eight species that used the same signal type, there were quantitative differences between before and during copulation (Table 6.1).

Of the 20 species that used vibrational signals during copulation, there were 14 for which there was no other courtship behavior during copulation (70%), and 6 for which vibrational signals were used in conjunction with tactile courtship (30%); of the 3 species that did not use vibrational signals during copulation, only 1 used tactile courtship (Fig. 6.2, inner doughnut).

6.4 Discussion

I surveyed studies describing pair formation with substrate-borne vibrational signals and the subsequent copulation behavior. Most of the species in these studies continue to use substrate-borne signals in courtship during or after copulation. The proportion did not change very much between tallies by species, genus, or family across a variety of groups of insects and spiders, suggesting no phylogenetic artifact in the results. Of the majority of species that continue to use substrate-borne signals in courtship during or after copulation, most use the same signal types during copulation as in pair formation. About a third use tactile copulatory courtship in addition to the copulatory vibrational signals.

This review is likely to be incomplete, and it may be influenced by different kinds of publication bias. It is possible, for example, that researchers would be less likely to devote space in a publication to reporting that their study species does *not* engage in copulatory courtship (with or without vibrational signals) than to devote space to reporting that it *does*. On the other hand, it is also quite possible that copulatory courtship (again, with or without vibrational signals) would often be missed unless explicitly looked for. Consider, for instance, the following difference in the proportion of studies reporting tactile copulatory courtship in a sample of publications in which researchers were not explicitly attending to it (36%) versus in a sample of species for which researchers did explicitly look for it (81%) (Eberhard 1991, 1994). The results in this chapter may therefore represent a range of possible scenarios, from overestimation to underestimation. They do pose a series of interesting questions, however.

Why should it be common for animals, at least insects and spiders, to continue to use signals that are (presumably) adapted for communication along solid substrates once copulation has begun? As noted above, one possibility is that continuity in signaling across stages in the reproductive process may increase the likelihood of sustained favorable responses by the mating partner. However, it was not uncommon for different types of vibrational signals to be used before versus after copulation, or for tactile courtship to be used in addition to or instead of vibrational signals.

How do perception and processing of vibrational signals change between when they arrive at the receiver from the substrate to when they arrive at the receiver through its own body? Consider a male copulating with a female, standing on her back and producing vibrational signals (Fig. 6.1a). There is an input into her, as a receiver of signals, through direct contact with her body. And there may also be an input through the substrate, because her body will carry those signals to the substrate, where she can perceive them as in the stage of pair formation. Are these inputs processed separately, additively, interactively, or is one or the other not attended to? In asking these questions, it will be important to remember that the movement of the body that is caused by the arrival of substrate-borne signals may be part of how animals process those signals (Cocroft et al. 2000; Miles et al. 2001).

Are different signal types or modalities adapted for different contexts of courtship? In the literature, we see a mixture of cases, with some species using a single type of vibrational signal in pair formation and copulatory courtship, others using different signal types, and yet others using vibrational and tactile signals. These are opportunities to test whether the different signals are more likely to succeed in the different contexts. I imagine, for instance, vibrational playback experiments (through the substrate and/or the body of test individuals) that test for cryptic mate choice, as playback experiments are currently used to test for precopulatory mate choice.

Substrate-borne vibrational signals have a hugely important role in pair formation and precopulatory mate choice, with important consequences for patterns of reproductive isolation between populations and closely related species (e.g., Rodríguez et al. 2004, 2006). It seems well possible that vibrational signals are similarly important in cryptic mate choice. Further, if playbacks such as envisioned above prove feasible, they may increase the experimental tractability of cryptic mate choice (cf. Eberhard 2011). As with prior advances in this field, progress will entail innovation of experimental techniques and attentive observation of behavior—an engrossing and rewarding pursuit.

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Chapter 7
Stinkbugs: Multisensory Communication with Chemical and Vibratory Signals Transmitted Through Different Media

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Abstract Extensive field research of stinkbug (Pentatomidae: Heteroptera) biology, ecology, feeding habits and communication revealed that reproductive behaviour is a complex process that needs integrative studies in the field and laboratory at different levels. The general model of group mating behaviour includes long-range communication in the field with airborne chemical signals that gather mates on the common substrate, and then the exchange of information during calling and courtship phases by plant-borne and airborne vibratory, chemical, contact mechanical and visual signals. This basic concept of multimodal communication has been confirmed with few exceptions in more than 35 stinkbug species. Privacy in stinkbug communication with chemical and vibratory signals is achieved by the use of unimodal or multicomponent signals. Male pheromone, for example, triggers female calling and the latter signals, for some species, increase the male sex pheromone production. In the present chapter, the authors focus special attention on the stinkbug sensory system that enables detecting and processing of chemical and vibratory signals transmitted through the air and different substrates. The advances of stinkbug chemical communication and its chemoreception are presented and discussed with new examples from the literature. Recent studies of airborne and substrate-borne vibratory signals produced by body and wing tremulation increased the number of mechanoreceptors involved in communication. Integration of information takes place in common neuropiles. In summary, an update on the advances in multimodal stinkbug communication is presented and future studies

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are proposed, mainly based on mutual interaction of multimodal signals and their recognition in both field and laboratory.

7.1 Introduction

Species success depends crucially on efficient reproduction that demands communication in different environmental and social conditions. This process has been intensively studied in polyphagous plant-feeding stinkbugs of the subfamily Pentatominae (Heteroptera: Pentatomidae) (Čokl et al. 2017a) that represent a smaller group of insects with several economically and globally important pest species. Intensive investigation of their biology, ecology, behaviour, feeding habits, pest status and others (McPherson and McPherson 2000; Panizzi et al. 2000) gave us a basis to develop and optimize different biological control techniques and strategies based on the idea of interfering with communication. The general model of group reproductive behaviour includes long-range communication in the field with airborne chemical signals that gather mates on the common substrate (plant) to copulate after information exchange by signals of different modalities (Čokl and Borges 2017) (Fig. 7.1). The aim of the present chapter is to give an overview on results of investigations that have been less exposed in the past reviews; although, they bring important new knowledge and insight into the processes

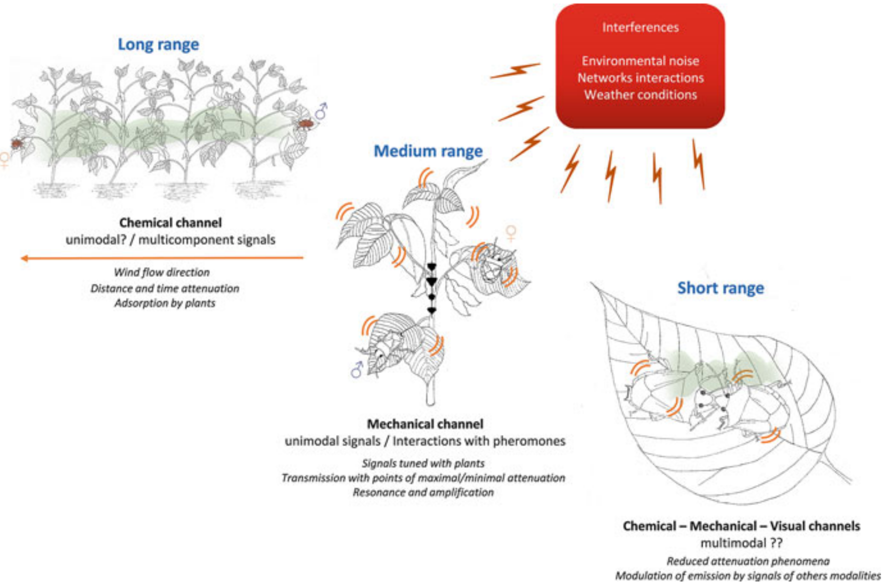

Fig. 7.1 Sequence of communication in stinkbug reproductive behaviour. Signals involved, characteristics, transmission channel and interactions. Drawings by Julia Dias Laumann

running reproduction in Pentatominae. In the following text, we separately describe different aspects of communication through the vibratory and chemical channels and afterwards we focus attention on the synergy of information exchange with signals of other modalities.

Borges et al. (1987) were the first to show that chemical and vibratory signals enable stinkbugs to communicate in different environmental conditions. The bimodal concept of information exchange is based on the fixed pattern of events, starting with the emission of male pheromone, that attracts solitary living mates in the field to gather on the same plant (Borges and Blassioli-Moraes 2017) and there triggers females to call males by the emission of vibratory signals. Female calling activates males to respond with their vibratory songs and to approach them with expressed vibrational directionality on plant crossings. Relatively, clear pattern of events running the calling phase of reproductive behaviour is followed by courtship performed by mates at close range. Short distance courtship behaviour is characterized by multimodal communication with substrate- and airborne vibratory emissions accompanied by visual, mechanical and chemical contact signals. Multimodal communication within different phases of communication with species-specific chemical and substrate-borne signals enables, among others, behaviours like mate recognition, attraction, localization and motivation for reproduction. Species specificity of male pheromone and calling song signals provide the first barrier for hybridization.

Stinkbug bimodal communication must be enhanced by visual, airborne and contact chemical and mechanical signals that are predominantly used during courting at close range. Multimodal information exchange in stinkbugs and many other insect groups is not purely understood and demands behavioural, morphological and physiological studies at both emitter and receiver sides.

7.2 Substrate-Borne Vibratory Communication

Substrate-borne information exchange during stinkbug reproductive behaviour on the plant runs predominantly by calling, courtship, copulation, repelling and copulatory songs produced by the vibration of the abdomen (Kuštor 1989; Amon 1990). Spectral characteristics of vibrational songs are characterized by the narrow dominant frequency peak around 100 Hz (with a different number of higher harmonics) and by more or less expressed frequency modulation (Fig. 7.2). Frequency tuning with mechanical properties of plants (Čokl et al. 2004, 2007) enables communication at distances well above one meter with low attenuation and limits represented by plant dimensions. Playback experiments (Žunič et al. 2011) confirmed that the high diversity of temporal and amplitude modulation pattern parameters carry information on species identity of signals with monotonous frequency characteristics (Čokl et al. 2017a). Most sensitive mechanoreceptors detecting substrate vibrations are situated in the legs (Michel et al. 1983) and threshold curves of the majority of receptor cells show tuning to frequency characteristics of abdomen vibration

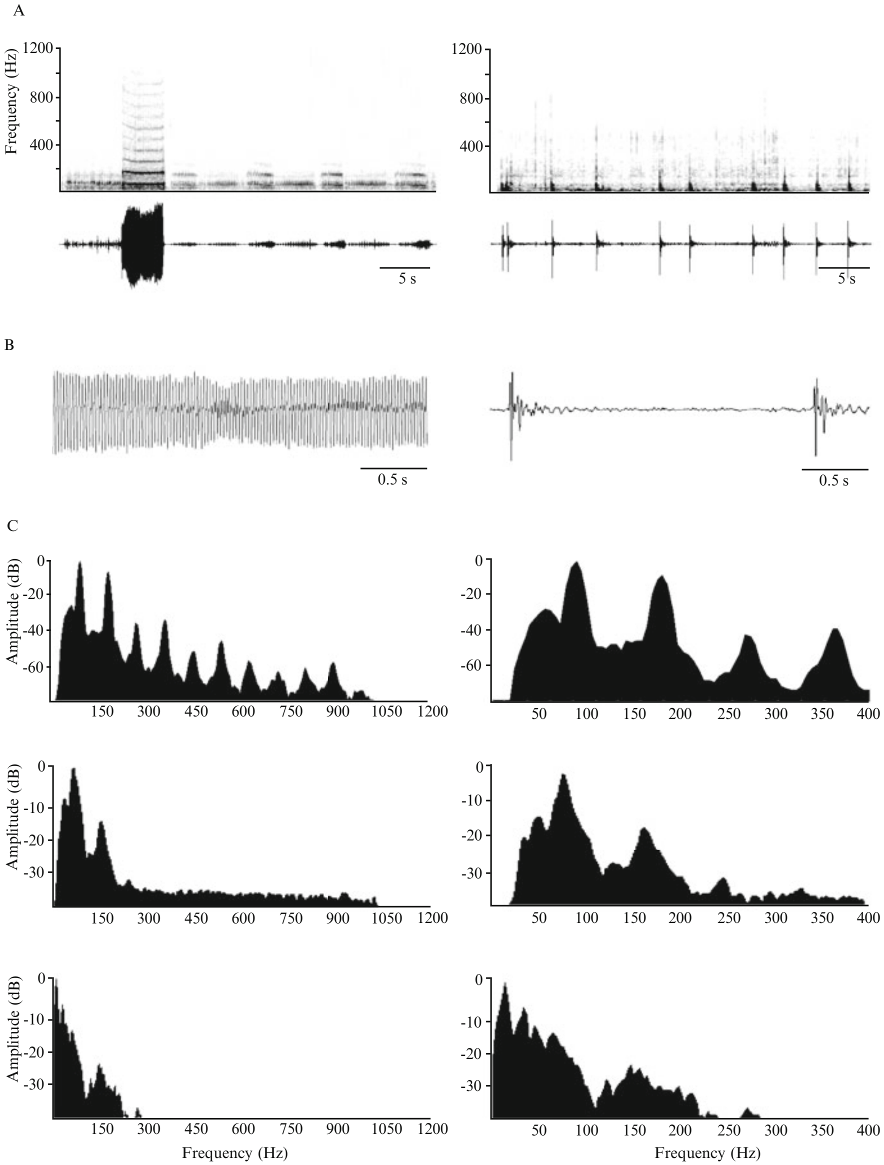

Fig. 7.2 Buzzing, abdomen vibration and tremulatory vibratory signals emitted by *Chinavia impicticornis* stinkbugs. Signal oscillograms are shown at two time scales (**a** below, **b**) and as sonograms (**a**, above). Frequency spectra of buzzing, abdomen vibration and tremulatory signals are shown within 0 to 1600 Hz (**c**, left) and 0 to 400 Hz (**c**, right) frequency range

(Čokl 1983; Zorović 2005). Narrow-band vibratory signals and a sensory system tuned to frequencies below 400 Hz (with phase-locked responses around and below 100 Hz) represent efficient peripheral band-pass filters, increasing signal-to-noise ratio that eliminates effects of low frequency noise created by wind and raindrops (Čokl et al. 2017a). Information is processed at different levels of the higher order ventral cord neurons (Zorović et al. 2008; Zorović 2011), which integrate inputs from several vibrated legs and probably synapse in the brain with sensory input from chemoreceptors that are predominantly situated on antennae (see below).

The general pattern of stinkbug substrate-borne vibratory communication is based on results obtained by research in *Nezara viridula* (L.) and a few other model species. Comparative studies in more than 35 different stinkbug species have shown various exceptions, specifics and differences reflected during calling and courtship. Many questions are opened by evaluating the impact of plants on the level of calling partner recognition by analysing vibratory signal temporal and spectral characteristics modified by the properties of the transmission medium. Finally, multimodal communication of mating behaviour demands multisensory detection and higher order neuronal integration of information provided through air and substrate by mechanical, chemical and visual signals.

7.2.1 Calling Phase of Mating Behaviour

Reviewed results of communication and behaviour analyses in 36 stinkbug species have shown significant differences in communication in the calling phase of mating behaviour (Čokl and Borges 2017). The generally accepted role of stinkbug male pheromone as the key trigger of vibrational communication does not explain several exceptions in the early phase of calling on the plant. In *N. viridula* Zgonik and Čokl (2014) recorded spontaneous calling more often in males than females. When a male and a female were placed together on a plant the authors recorded the male calling song first, as often as the female one. Both results open the question about triggers of male calling. Female-produced visual signals have been demonstrated to play an important role in triggering male calling in *N. viridula* (Zgonik and Čokl 2014). Presentation of a live, but not a dead female, often started male calling (77%, $N = 13$) in the daylight, and rarely (14%, $N = 14$) in the dark (Zgonik and Čokl 2014), indicating that females rotating their antennae induce male emission of vibratory signals.

The role of male pheromone as the trigger for the emission of the female calling song has been demonstrated in *N. viridula* and many other stinkbug species (Borges and Blassioli-Moraes 2017). On the other hand, the presence of the male pheromone is not necessary to start vibrational communication in several species. The male pheromone has not been identified yet in *Dichelops melacanthus* (Fabr.), yet males and females express similar patterns of female/male communication with different substrate-borne vibratory signals (Blassioli-Moraes et al. 2014). Vibrational communication in *Edessa meditabunda* (Fabricius) starts by the emission of male songs, and then females respond to them (Silva et al. 2012). Female vibratory signals that were recorded only as responses to male calling have been described also in species like *Chlorochroa sayi* (Stål) and *C. uhleri* (Stål) (Bagwell et al. 2008), *Holcostethus strictus* (Fabr.) (Pavlovčič and Čokl 2001) and *Murgantia histrionica* (Hahn) (Čokl et al. 2004). Our hypothesis is that vibrational communication evolved in some stinkbug species independently of chemical communication. The lack of female-identified female songs in *Piezodorus lituratus* (Fabricius) (Gogala and Razpotnik 1974) and another 16 different stinkbug species (Shestakov 2015) demands a detailed investigation.

Investigations in the last decade have shown that stinkbug males and females emit vibratory signals that are produced by mechanisms other than the vibration of the abdomen. *Euschistus heros* (F.) males and females emit buzzing signals (Fig. 7.2a, b-left) by the vibration of lifted wings, tremulatory signals (Fig. 7.2a, b-right) by vigorous shaking of the whole body, and percussion signals by tapping with front legs on the substrate (Kavčič et al. 2013). The role of percussion signals is not clear yet; however, buzzing signals in many cases precede female-male calling duets and tremulatory signals have been often recorded when mates touched each other. Shestakov (2015) described in seven stinkbug species male percussion "protest" calls produced by tapping with the abdomen on the ground when repelling silent males trying to copulate. Vibratory signals produced by alternative mechanisms open interesting fields of future research. They differ from signals produced by abdomen vibration by low species specificity of their temporal characteristics and by significantly higher amplitude and different spectral properties. Spectra of buzzing signals (Fig. 7.2c) are characterized by the narrow dominant frequency peak around 100 Hz and higher harmonics that extend the frequency range of communication up to 2 kHz. On the other hand, there are tremulatory signals dominated by frequencies below 50 Hz (Fig. 7.2c). The use of signals in such a broad frequency range demands their multisensory detection (see below) and transmission through different media.

Comparison of vibratory song parameters in different species demands standardized protocols for experiments. This includes recording of vibratory signals emitted by a single male and female placed on a non-resonant artificial substrate and observation of behaviour in isolated, unnatural conditions. Recent studies have focused on the social aspect of communication in natural conditions. The male pheromone attracts in the field several males and females to land on the same plant in different gender ratios that leads them to compete for copulation with the same mate. Rivalry has been described until now in several Pentatominae species between males (Čokl et al. 2017a) and only recent investigations have shown female rivalry accompanied by the emission of the female rival song in *Chinavia impicticornis* (Stål), *C. ubica* (Rolston) and *E. heros* (Čokl et al. 2017b). The authors also explained the role of different female calling song types used to establish different levels of rivalry with synchronized alternation of signals that had completely different temporal characteristics.

7.2.2 Insect-Plant Interactions

Plants represent the natural environment of exclusively herbivorous Pentatominae stinkbugs, giving them shelter, food, mating environment and medium for the transmission of vibratory communication signals (Panizzi and Lucini 2017). Pentatominae are highly polyphagous, they may exploit plant species of several families and genera, feed and mate on different parts of a plant, and as with other herbivorous insects, host plant switching is commonly observed in stinkbugs, too (Smaniotto and Panizzi 2015). Each plant, though, represents a complex and specific habitat of variable characteristics that may influence the morphology, physiology and behaviour of insect populations. For example, the plant chemistry affects the composition of insect pheromones, which could lead to behavioural divergence (Landolt and Philips 1997).

In addition, plants crucially influence substrate-borne signalling. Communication signals transmitted through plants are strongly influenced by the plant's size, architecture and its physical characteristics, as well as by the intensity of emitted signals, and by the sensitivity of the relevant sensory system. Transmission properties of vibrational signals may vary between plant species and even within a single plant, between different plant parts, with the distance from the source of vibrations. These environmental variables may exert relevant selection pressures on substrate-borne signals and may lead to divergence in mating traits and evolution of vibrational communication (Endler 1992; Boughman 2002; Cocroft et al. 2008).

McNett and Cocroft (2008) found a strong correlation between host plant selection and spectral composition of signals in host-specialist treehoppers, supporting the signal transmission hypothesis (e.g. signals are adapted for efficient transmission through specific substrates). Signal frequencies showed differences up to several hundred Hz, indicating that in these sympatric species, substrate transmission properties represent an important factor of signal evolution. In contrast, the magnitude of spectral variation related to the substrate was relatively small in a different membracid treehopper that is, in contrast to *Enchenopa* species, related to a wide variety of hosts (Cocroft et al. 2006). Moreover, in this study signal features were specifically associated with the individual signaller. Measurements of frequency characteristics of courtship signals showed little influence by different plant substrates in parasitoid wasps, as well (Joyce et al. 2014). Study of vibrational signalling in lacewings (Henry and Wells 2004) demonstrated that substrate preferences correlate well with song phenotype; however, the songs of two focal species propagated equally well, regardless of the plant substrate. In addition, behavioural experiments showed that individuals did not exhibit any specific response to conspecific songs played either on the host or non-host plants. These studies indicated that in addition to the environment other selective forces may influence divergence of vibrational signals, too.

Stinkbugs probably represent one of the best-known examples of species communicating by substrate-borne vibrations. Signal-substrate matching, particularly spectral tuning, is also a very well-known phenomenon in stinkbugs (Čokl et al. 2005; Čokl 2008; Polajnar et al. 2012). Stinkbug narrow-band vibratory emissions of the dominant frequency around 100 Hz are optimally tuned with the resonance properties of host plants (Čokl et al. 2005) and enable efficient communication along distances well above 1 meter with efficient filtering of noise below 50 and above 400 Hz. Such low pass characteristics of herbaceous plants significantly change signals with broadband spectra as shown in the case of stridulatory signals of burrower bug species *Scaptocoris castanea* Perty and *S. carvalhoi* Becker (Heteroptera: Cydnidae) transmitted through soybean (Čokl et al. 2006). Broad-band spectra of signals recorded at their origin (roots and soil) get changed when recorded from the stem above the soil: the broad dominant frequency peak around 500 Hz disappears and is replaced by the one around 100 Hz and its first harmonic. An additional example of the signal tuning hypothesis was provided by Polajnar and co-workers (2013). They found significant differences in spectral properties of signals in individual males of *Palomena prasina* (L.) singing on different substrates. Phenotypic plasticity (Fordyce 2006) observed in this study allowed an individual to tune signal frequency in order to match variable transmission properties of the substrate. Although phenotypic plasticity is thought to play a major role in evolution (West-Eberhard 2003, 2005), variation of phenotypes, the sources and mechanisms of phenotypic plasticity in vibrational signals have been rarely studied in stinkbugs.

Not only signal frequency, but amplitude of the signal may also vary substantially between plant substrates, with the distance from the source of signals, between individual plants of the same species, and individual signallers (Mazzoni et al. 2014). In stinkbugs, for instance, non-linear amplitude decay of vibratory signals with distance represents an obstacle for distance discrimination and vibrational directionality based on the processing of amplitude differences occurring at short distances between insect legs. Transmission of group vibratory signals through a plant's stem, side branches, stalks and big leaf veins is characterized by regularly repeated amplitude minima and maxima (Čokl et al. 2005; Čokl 2008) as a consequence of resonance phenomena (Polajnar et al. 2012). Vibrational directionality is enabled by neuronal processing of time and/or amplitude differences in correlation with direction to the source of vibratory calling signals (Virant-Doberlet et al. 2006). The amplitude difference of inputs coming from two different branches does not always favour movement in the right direction because of frequency-dependent amplitude variation with distance.

Species specificity of stinkbug signals is determined predominantly by differences in their temporal structure. Temporal parameters, however, might also be influenced by transmission properties of plants and affect signalling behaviour. *N. viridula* males, for example, differentiated the non-pulsed (FS1-np) and pulsed (FS1-p) type of the conspecific female calling song signals on non-resonant substrate but not on the plant (Miklas et al. 2001). Plant-transmitted FS1-p pulses get prolonged and fused to the extent that males recognize FS1-p signals as those of the FS1-np type of similar duration and repetition time characteristics

(Čokl et al. 2000). For instance, physical properties of the substrate significantly affected temporal characteristics of mating signals in parasitoid wasps, too, that is, courtship signals were prolonged during transmission through the host plant (Joyce et al. 2014). Studies on treehoppers and lacewings, on the other hand, indicated that temporal characteristics depend less on substrate than spectral features of vibrational signals (Henry and Wells 2004; Cocroft et al. 2006).

A noisy environment, in which there are many conspecifics and heterospecifics singing simultaneously, may also be an important source of disturbance. Several studies demonstrated that noisy neighbours reduce the recognition and discrimination of conspecific signals, due to distortion of the temporal structure of the signals, signal frequency, amplitude, and by affecting the behavioural responses of conspecifics (Miklas et al. 2003a; Polajnar and Čokl 2008; de Groot et al. 2010).

Over the past several years an increasing number of studies have examined various aspects of vibrational communication in stinkbugs, including investigations of the diversity of signals, their production mechanisms and reception, neuronal processing and related behavioural interactions among conspecifics and heterospecifics (Čokl et al. 2014; Čokl and Borges 2017). Still, we know little about the selective forces and evolutionary processes of this communication system in stinkbugs. There are only a few studies related to the magnitude of the substrate-induced changes in vibrational signals of stinkbugs. We know little about the role of environmental adaptation and phenotypic plasticity of signals in assortative mating and reproductive isolation (Endler 1992; Boughman 2002; Nosil 2012) of stinkbugs. To elucidate the role of the environment in vibrational signal divergence and in assortative mating in stinkbugs, it is necessary to conduct comparable measurements and investigations of a series of species (host specialists, and generalists) and different populations, to investigate vibrational signalling on hosts, non-host species and artificial substrates, evaluating the signalling range, etc. In addition, the selectivity of the receivers and their responses related to spectral or temporal features of the vibrations have been rarely studied in stinkbugs (Žunič et al. 2011; Čokl et al. 2015). The selection forces are not mutually exclusive; instead, they interact in their effect on signal evolution (Forrest 1994) and many aspects of evolutionary pressure (e.g. ecological selection, sexual selection and mate choice) are still relatively unexplored areas in stinkbugs.

Clear resolution of mating signals plays an important role in the recognition and localization of conspecific partners in the environment, and hence preventing hybridization. Stinkbug communication on the plant runs through the calling and courtship phase predominantly with substrate-borne vibratory signals that show statistically confirmed species-specific differences in their temporal, frequency and amplitude modulation pattern characteristics, and as such significantly contribute to reproductive isolation. Studies on the process of mate localization and species discrimination have shown different results when analysed in the field or in the laboratory, and although courtship signals are highly species-specific, individuals might still mate with heterospecifics. Laumann et al. (2016) demonstrated that *C. impicticornis* and *C. ubica* recognize conspecific mates in the early phase of communication with species-specific vibrational calling signals. On the other hand, Kiritani et al. (1963) described hybridization of sympatric *Nezara antennata* Scott and *N. viridula* species despite their significantly different vibratory song signals (Kon et al. 1988) indicating that isolation of species based on specificity of the signalling repertoire is neither absolute nor perfect in all stinkbug species. The relative importance of substrate-borne vibratory communication in species isolation has been demonstrated also in species lacking female or male songs in the calling or courtship phase of mating behaviour (see above). Finally, transmission through plants changes vibratory signal characteristics and decreases their informational value with increasing distance between mates.

Complex, multimodal signals may be beneficial, since they may provide more information than unimodal signals (Hebets and Papaj 2005). Multimodal signalling may arise under various selective pressures to facilitate transmission and successful reproduction. Research has shown that stinkbugs might communicate using transmission channels of various modalities, including chemical and vibrational, visual and tactile signals (Borges and Blassioli-Moraes 2017; Čokl et al. 2017a) (Fig. 7.1). Signals of different modalities may be very important in inter-sexual communication, agonistic and predator-prey interactions, particularly within the complex environment of stinkbugs' host plants. Communication during reproductive, as well as social, behaviours has been extensively studied in stinkbugs, but these efforts mainly investigated the characteristics, transmission and function of isolated signals. For example, whether or not, signals of different modalities are used concurrently, and how signals of different modalities interact and influence different behavioural patterns, still needs to be investigated more extensively (see Sect. 7.4). It would also be interesting to explore whether multimodal signals of stinkbugs provide redundant ("backup") or non-redundant ("multiple") information (Partan and Marler 2005). These data would be important in understanding the selection pressures that drive the evolution of communication signals and speciation in Pentatominae.

7.2.3 Multisensory Communication

Extensive investigations of stinkbug mating behaviour and communication on the plant have been predominantly focused on information exchange by the substrate-borne vibratory signals (Čokl and Borges 2017). Less attention has been paid to the role of vibratory signals produced by mechanisms other than abdomen vibration and their transmission through the plant and air. Furthermore, contact chemical and mechanical signals together with visual cues enable, among others, efficient recognition of both genders at close distance. Consequently, there are only few and scarce data on multisensory reception and processing of multimodal information provided by signalling stinkbug mates in different environmental conditions.

Abdomen vibration-produced communication signals of spectra tuned with resonant properties of herbaceous plants enable efficient substrate-borne information exchange at longer distances with increased signal-to-noise ratio within 50–400 Hz frequency range. Communication in the narrow frequency channel demanded evolution of the sensory system tuned to spectral properties of the narrow-band vibratory communication channel. Investigations in *N. viridula* have shown that the most sensitive adequate vibrational receptors are chordotonal organs situated in the legs (Michel et al. 1983) with the majority of receptor cells tuned below 400 Hz (Čokl 1983). Observation of stinkbug antennation of the plant and mate's body surface, on the other hand, indicated that antennae might contribute to reception of information from the vibratory environment outside the 50–400 Hz frequency range. This hypothesis has been confirmed by Jeram and Pabst (1996), which described chordotonal organs in antennae of the stinkbug *N. viridula*, and recently by Nishino et al. (2016), who among others demonstrated that vibratory receptor cells of the leg, antennal and abdominal chordotonal organs of the stinkbug *Plautia stali* (Scott) arborize within the same ventral cord neuropiles.

Jeram and Pabst (1996) described in the distal part of the third antennal segment (distal pedicellite) of *N. viridula* the chordotonal complex, composed of Johnston's and central organs. The 45 amphinematic scolopidia of the Johnston's organ are situated around the periphery of the distal pedicellite and fixed to the cuticle between the pedicel and flagellum. The central chordotonal organ is composed of seven mononematic scolopidia that are attached in the same joint as those of the Johnston's organ. Jeram (1996) vibrated antennae of *N. viridula* in their longitudinal direction and recorded responses of Johnston's and central chordotonal organs in the frequency range between 30 and 140 Hz, with highest sensitivity in one type of receptor cell in the frequency range between 40 and 60 Hz in one, and at 30 Hz in another, type with threshold sensitivity around 1 mm/s. Phase-locked responses of antennal mechanoreceptors described in this study enable precise frequency analysis with relevant sensitivity to detect high amplitude tremulatory and buzzing signals. Extension of sensitivity to frequencies below 30 Hz indicates that they may detect information provided by antennation of the mate's body in concert with antennal sensilla sensitive both to gustatory and tactile signals.

In the stinkbug species, *P. stali*, Nishino et al. (2016) described morphology and central projections of two groups of chordotonal organs situated in the abdomen. The pleural group is located in the fold between tergites and sternites of abdominal segments with one sensory cell in each of them, and the ventral group is found in the medio-ventral region of abdominal sternites. Furthermore, the authors described the tymbal chordotonal organ situated in the abdomen and constituted by four sensory cells fixed to the cuticular ridge between metathorax and the abdominal sternites. About 0.4 mm long and dorso-laterally oriented, the ligament of the tymbal chordotonal organ terminates anchored on the surface of a fat body, attached to the tymbal muscle.

Axons of the Johnston's and central chordotonal organs run within antennal nerves (Jeram and Pabst 1996) and their afferents terminate in antennal mechanosensory and motor centres of the brain, descending further towards abdominal neuromers with collaterals projecting in each ventral cord neuromere to the medial ventral association centre (mVAC) (Nishino et al. 2016). Furthermore, terminal arborizations of *P. stali* abdominal, tymbal and leg chordotonal organs all project to common neuropiles in the brain and ventral cord. Axons of the leg chordotonal organs finally terminate on the ipsilateral side of the central ganglion, laterally and within the medial ventral association centre (mVAC) in pro-, meso- and metathoracic neuromeres, confirming the position of vibratory neuropiles described for leg vibroreceptors in *N. viridula* (Čokl and Amon 1980; Zorović 2005). The afferents of the tymbal chordotonal organ arborize ipsilaterally in the mVAC of the meta-, meso- and prothoracic and suboesophageal neuromeres, with axons of two chordotonal organs ascending to the brain where they terminate in the antennal mechanosensory and motor centre described by Kristoffersen et al. (2008). Afferents of abdominal chordotonal organs have extensive local projections. One pleural chordotonal organ finally terminates in the central ganglion, two in the prothoracic ganglion and one in the antennal mechanosensory and motor centre of the brain. The ventral chordotonal organ receptor cells finally terminate with arborizations in the mVAC of the metathoracic neuromere. The authors labelled also antennal nerves in *P. stali* and described axon terminals in the antennal mechanosensory and motor centre of the brain that provide collaterals to mVAC of each neuromere.

High variation of *P. stali* chordotonal organ peripheral structures and conserved organization of terminal arborizations in common neuropiles (Nishino et al. 2016) fits well with the general model proposed for insects by Boyan (1993). Common projection areas of differently situated leg chordotonal organs enable peripheral co-processing of the low amplitude narrow band vibratory signals, produced by abdomen vibrations, and high amplitude low frequency vibratory input that is provided by antennal and abdominal chordotonal organs. Zorović et al. (2008) described in *N. viridula* ventral cord vibratory interneurons tuned either to low or to middle frequency sensory input, as well as interneurons with threshold curves that indicate co-processing of low and middle frequency vibratory signals. Contrary to many other insect groups where representatives communicate with sound and vibration, the stinkbug vibratory sensory system shows low sensitivity to vibrations of higher frequency: just one subgenual organ sensory cell responds best to frequencies above 500 Hz (Čokl 1983), and until now no vibratory interneuron has been found to show relevant sensitivity in this frequency range.

Observations of mating behaviour on the plant (in the field and in the laboratory) indicate that the low frequency vibratory input plays an important role in stinkbug reproductive behaviour, from early phases of calling to last sequences of courtship when females decide to accept or reject the courting male. Tremulatory signals enable airborne communication between mechanically isolated plants at distances up to 7 cm (Kavčič et al. 2013) and buzzing has often been recorded in the calling phase of reproductive behaviour prior to emission of abdomen-produced signals (Čokl, *personal observation*). Similar spectral and temporal characteristics of tremulatory and buzzing signals recorded in different stinkbug species indicate their general and species non-specific role in the advertising of presence in a larger area, with the possible attraction to the same place and a repelling function in close-range rivalry. The airborne component of both signals demands receptors sensitive to air particle movement (see below).

Nishino et al. (2016) pointed to another possible role of abdominal chordotonal organs. Communication through a narrow frequency window forces strong selective pressure to develop precise control of mechanisms that produce vibratory signals tuned with the transmission medium. The authors speculate that abdominal chordotonal organs may play a proprioceptive role because of their position in the abdomen. One group, specifically, is connected with ligaments to fat body cells close to the chitinous plate that connects the abdomen and thorax, but also in the vicinity of muscles whose synchronized contraction produces vibratory communication signals (Kuštor 1989; Amon 1990). This and other roles of abdominal chordotonal organs in plant-borne communication will be better understood after investigations of their functional properties.

The use of low frequency vibratory signals in stinkbug reproductive behaviour is limited by environmental noise produced by wind. Frequency characteristics of apple leaves vibrated by wind range between 7 and 14 Hz, with highest velocity reaching 130 mm/s at high wind speed (Casas et al. 1998). Similar frequency characteristics have been measured for wind-vibrated banana plants and bromeliads' leaves (Barth 1998). Low-pass filtering properties of the vibro-sensory system efficiently cuts off noise above 600 Hz, providing optimized signal-to-noise ratio in the frequency range characteristic for abdomen vibration-produced signals. On the other hand, low frequency signals are masked by environmental noise of similar spectral characteristics. Better understanding of their recognition demands further investigation from behaviour to neurophysiology.

The airborne component of stinkbug high-amplitude buzzing and body tremulation signals has not been evaluated. Due to the similar signal production mechanism, we can expect intensity values as measured for air currents generated by a fly during the stationary flight (Barth 2002): the airstreams around 100 Hz reach velocities up to 1 m/s when measured behind and below the fly at distances between 4 and 8 cm.

Trichobotria are adequate receptors to detect airstream movement and changes in its velocity. Their role in stabilizing and orientation of the body in space, detection of prey or predator, as well as their role in intra- and interspecific communication, has been demonstrated in different insect groups (Tautz and Markl 1978; Gnatzy and Heusslein 1986). Trichobotria belong among the most sensitive mechanoreceptors. In the firebug *Pyrrhocoris apterus* (Fallen) (Pyrrhocoridae), for example, they responded to a flying fly at distances up to 30 cm above the bug (Šolinc 2017). Investigation of their functional properties in *Cuppienius salei* Keyserlink (Barth 2002) has demonstrated different levels of directional sensitivity and a one-to-one response pattern following the frequency of medium oscillation between 10 and 950 Hz. The range of best frequencies of trichobotria in *C. salei* (40–600 Hz) decreases to lower frequencies in parallel with increasing hair length. Trichobotria are extremely sensitive, exhibiting deflection angle thresholds at or even below 0.1° in the frequency range between 50 and 100 Hz. Trichobotria show low-pass characteristics with high sensitivity up to 100 Hz when thresholds are expressed in terms of peak velocity reached during deflection.

Abdominal trichobotria have been described in nymphs and adults of the Heteroptera-Trichophora super-families Lygaeoidea, Pyrrhocoroidea, Coreoidea and Pentatomoidea (in part: Thaumastellidae, Urostylidae, Corimelaenidae, Cydnidae and Pentatomidae) (Schaefer 1975). Pentatominae stinkbugs are equipped with two pairs of trichobotria near the spiracular line of the 3rd and 4th segment of the abdomen (Rolston and McDonald 1979). Direct experimentally confirmed evidence for their role during reproductive behaviour of Pentatomidae stinkbugs is lacking. According to preliminary observation and recording of buzzing signals and results of studies in other insects, we hypothesize that they enable longer range detection of the airborne component of signals produced by buzzing stinkbugs.

Stinkbugs place antennae on plant surfaces during approaching each other and prior to copulation, they antennate the mate's body. Antennae are the site of different receptors for detecting chemical signals (see below), substrate- and airborne vibrations, temperature changes and mechanical signals connected with contact. To our knowledge there are no experimentally confirmed data on the relevance of vibratory information obtained by direct contact with the mate's body for any process of stinkbug reproductive behaviour.

7.3 Chemical Communication

Chemical communication with a diversity of signals is essential for reproduction in stinkbugs, like in other insects. Stinkbugs use semiochemicals to communicate inter- and intraspecifically for different purposes, for example to aggregate, to locate a mate, food, plant hosts, or to identify danger, such as the presence of predators and parasitoids. The semiochemicals used in communication, in general, are compounds with low molecular weight, high volatility and which are relatively stable molecules. However, the semiochemicals emitted to the environment can lose their activity by interacting with air, wind, the foliar barrier, through isomerization by reacting with oxygen, or being degraded by UV radiation. In stinkbugs there are two major classes of semiochemicals that have been considerably studied: (1) the defensive compounds and (2) the sex pheromones. The defensive compounds in nymphs and adults present very similar chemical blends, with important differences. The major compounds produced by nymphs comprise small molecules with C_6, C_8, C_{10} in a linear carbon skeleton of (*E*)-2-alkenals, 4-oxo-(*E*)-2-alkenas, alcohols and acetates. Adults also produce these compounds, but the major compounds are linear hydrocarbons, tridecane and undecane, predominately. The defensive compounds in nymphs are produced in dorsal abdominal glands, and in adults they are produced in metathoracic glands (Aldrich 1995; Borges and Blassioli-Moraes 2017). The interspecific role of these compounds still needs to be studied. Borges and Aldrich (1992) reported that defensive compounds change with the age of the insects, and that the major compound produced by first instar nymphs, the compound 4-oxo-(*E*)-2-decenal, acts as an aggregation pheromone. There are several studies that demonstrate that they function as defensive compounds against natural enemies, like parasitoids and ants (Laumann et al. 2009; Eliyahu et al. 2012; Borges and Blassioli-Moraes 2017; Weber et al. 2018). Male sex pheromones represent the other group of semiochemicals that has been well explored in stinkbugs. They show a great diversification of molecules, most of them being non-polar or with low polarity, guaranteeing their high volatility. An interesting point in Neotropical stinkbug species behaviour is that the sex pheromone always attracts only females in field experiments and laboratory bioassays, contrary to Nearctic species where the sex pheromone appears to play a role as aggregation pheromone, attracting both genders and, in some cases, also nymphs (Borges and Blassioli-Moraes 2017; Weber et al. 2018). Stinkbug sex pheromones are species-specific and the specificity is not a characteristic only between different species but also between different populations of the same species. Males of the stinkbug *N. viridula* produce sex pheromones composed of two components, *trans-Z*-bisabolene epoxide and the corresponding *cis*-isomer (Fig. 7.3). The study of the sex pheromone produced by male *N. viridula* from six different populations demonstrated that they all produce the same two components, *cis* and *trans–Z*-bisabolene epoxide, as sex pheromones but differ in their proportions (Aldrich et al. 1993; Brézot et al. 1994; Moraes et al. 2008a; Borges and Blassioli-Moraes 2017). The sex pheromone identified only in 45 stinkbug species consisted in each of them of sesquiterpenes or acetate components (Fig. 7.3). There are two recent reviews covering the semiochemistry of stinkbugs. Borges and Blassioli-Moraes (2017) reviewed the role of semiochemicals in the communication process and Weber et al. (2018) comprised the chemical structure of the semiochemicals, their synthesis, and the role of these molecules in the communication of stinkbugs.

7.3.1 Transmission of Chemical Signals Through Air

All organisms, aquatic and terrestrial, from a simple unicellular organism to the bigger ones, like insects, mammals and birds, use chemical molecules to communicate, and for this, they need to be able to capture these molecules in the air or water environment. The ability of one organism to detect a molecule depends on how these molecules are transported in the environment and on the substrate that will receive this chemical. Antennal sensilla are insect receptors that detect chemical molecules. Bigger animals probably have more facility in "catching" the airborne molecules, since they have more olfactory sensors for this task. Moths are the best and most studied example of long-range communication with airborne molecules. Male moths are able to locate the conspecific female releasing the pheromone plume at distances from ten to several hundred meters (Cardé 2016). Small lipophilic molecules disperse through the air by two processes: molecular diffusion and advection (Weissburg 2000). Molecular diffusion is the mass transport of a substance from the region of higher concentration to the one with lower concentration. Advection is characterized by bulk mass transportation. In the latter process, a blend of components flows as a unit in which the ratio of the components tends to remain constant, which is crucial in communication for odour recognition. In both processes, the transport runs in pressure gradient conditions directed by different abiotic factors, such as wind, temperature and humidity. Depending on the morphological structure of glands and cells responsible for pheromone production,

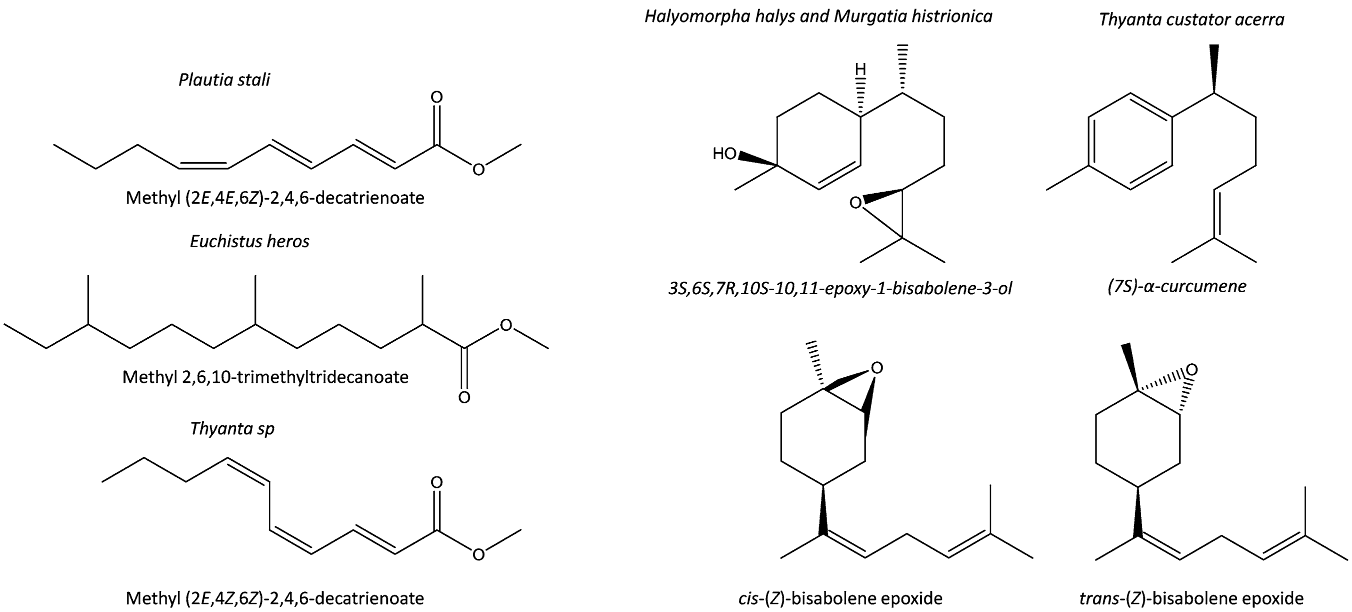

Fig. 7.3 Chemical structure of some stinkbug sex pheromone exemplifying the two main chemical classes that are produced by Pentatomidae

insects present different approaches to transfer and spread the semiochemicals with the goal of influencing the transport of molecules through the air. Several female moths adapt a calling position to improve the efficiency of pheromone transfer to the air by exposing the gland releasing the pheromone. Stinkbugs release pheromones from unicellular glands spread in the abdomen with an efficiency of transfer that still needs to be studied (Pavis and Malosse 1986; Borges 1995). Aldrich (personal communication) proposes that the defensive compounds like (*E*)-2-alkenals and its acetates are dissolved in stinkbug adults in linear hydrocarbons (tridecane or undecane). When emitted the hydrocarbons act as a solvent supporting the advection flow of components. Therefore, we could hypothesize that the components of the metathoracic glands are emitted as a blend and the ratio between the components is preserved in the pheromone plume. However, experimental studies need to test this hypothesis.

The odour plume of volatile pheromones operates as a flow in turbulence regime. Several studies use different approaches, applying the Fick and other hydrodynamic laws, to calculate the flow of odourant molecules in different media (Loundon 1999; Weissburg 2000; Celani et al. 2014). All calculations based on fluid mechanics equations use complex mathematical approaches but ignore environmental noise that changes the odour plume (Loundon 1999; Weissburg 2000). Therefore, some measured parameters may be very far from what really occurs in nature. Regardless, the Reynolds number (Re) is used to classify the type of flow of the odour molecule released into the environment. An odour plume with a low Re number flows slowly, with laminar regime characterized by slow flow and a continuous concentration gradient (Weissburg 2000). Whereas a high Re number represents a signal structure typical of an intermittent odour plume with peaks of higher concentration along with very low or no detectable concentrations of odour (Weissburg 2000). Such characteristics are typical for odour plumes of navigating insects, like moths (Cardé 2016). There are no studies describing the way stinkbug molecules transfer and transport through the air, nor how they are detected. The complexity of the system represents an interesting challenge for scientists because results of these studies will help to understand how these molecules behave in the air and will provide the basis for the development of better systems to release pheromones for practical applications. The airborne molecule is exposed to a series of noise that can change its flow and its perception by the insect.

Airborne transport of an odourant molecule depends on several conditions, including emission in an open or restricted area, in the forest or in the middle of a crop field, humidity, temperature, wind velocity and others. When an odourant molecule is released into the environment, some of the molecules will be adsorbed by plants and others will flow through the air. There are indirect signals that also can be used by insects as information to locate hosts and partners (Wilson et al. 2015). Several studies report that plants can detect other plant volatiles (Erb et al. 2014) and insect pheromones and can change their own chemical profile of plant volatiles (Helms et al. 2013). Thus, when the signalling insect releases its pheromone, and this pheromone is adsorbed by plants, it may induce emission of plant volatiles, opening the question whether the insect receiver is able to recognize that pheromone-induced plant volatiles are giving information on the vicinity of a mate. Knowledge of how molecules transport through the air, and the impact of interference on insect chemical communication, can provide the crucial information on several parameters that are important to establish an efficient field experiment. Answers are needed to the questions, as for example (1) does the ratio between the components in a blend remain constant during transmission, (2) what are concentrations of the components in the plume, (3) what is the communication distance possible when information is carried by the odour plume, and (4) does the odour plume flow within a laminar or turbulent regime. This information could be obtained from mathematical models with low cost laboratory experiments carried out in concert with those conducted in the field. All this information is nowadays obtained through extensive experimental fields with synthetic mixtures of the compounds with the aim of developing a method to control insects in the field by the use of pheromones (Borges et al. 2011; Cardé 2016). To evaluate the communication distance with the use of the *E. heros* pheromone, scientists placed pheromone traps in the field at different distances and evaluated the number of insects captured at each of them. This information optimized efficiency of traps in the field by selecting the best distance between them (Borges et al. 1998, 2011; Silva et al. 2014).

7.3.2 Reception and Information Processing of Chemical Signals

The antenna as the main olfactory organ of insects and other arthropods is a multimodal sensory organ detecting chemical, mechanical, hydro and temperature stimuli. To understand how the antenna receives the odour one needs to consider its morphology. All insect antennae have the basic structure divided into three parts. The scapus is the basal segment attached to the head and moved by four muscles. The pedicellus is the second segment attached to the scapus and moved by two muscles. In the pedicellus is positioned the Johnston's organ (see Sect. 7.2.3) that is responsible for the detection of sound and vibration (McIver 1982). The flagellum as the third antennal segment carries most sensilla sensitive to the odourant molecules. The flagellum is not attached by any muscle and is moved together with the pedicellus. Morphology of antennae is described in a few stinkbug species, like *N. viridula* (Brézot et al. 1997), *Cyclopelta siccifolia* Westwood and *Chrysocoris purpurea* Westwood (Rani and Madhavendra 2005), *Piezodorus guildinii* Westwood, *D. melacanthus* and *E. heros* (Silva et al. 2010). Stinkbugs are characterized by the filiform type of antennae with the same number of segments found in adults: scapus, two-segmented pedicellus (P1, P2) and a two-segmented flagellum (F1, F2). Antennae of nymphs consist of one scapus, one pedicellus and one flagellum. On the flagellum are located most of the olfactory sensilla involved in odour reception. Different types of sensilla can be divided into three categories:

(1) olfactory sensilla described as wall pore-sensilla; (2) sensilla with one pore at the tip that are usually sensitive to gustatory stimuli; and (3) non-porous sensilla generally described as mechano-, thermo- and hygroreceptors. However, uniporous or no porous sensilla can have exceptionally also olfactory function.

Several studies in Lepidoptera describe the function of sensilla sensitive to chemical stimuli, but there are no data describing this process in stinkbugs. Sexual dimorphism in the number of sensilla involved in pheromone detection is common in Lepidoptera. Male moths have bigger antennae with a higher number of olfactory sensilla than females (Kaissling 2014). Female Lepidoptera emit the sex pheromone and males need to locate them by following the pheromone plume. In the male's antennae of the *Antharea polyphemus* Cramer moth were identified 60,000 trichoid sensilla responsible for the detection of the sexual pheromone, and 10,000 basiconic sensilla responsible for the detection of other odours. On the other hand, the conspecific females have no trichoid sensilla, but 12,000 basiconic sensilla. Sexual dimorphism has not been identified in any stinkbug species studied so far concerning either the size or the shape of antennae. On the other hand, there are reports on differences in the number of sensilla. The females of pentatomids *E. heros*, *E. meditabunda* and *P. guildinii* have a higher number of basiconic sensilla than conspecific males. These sensilla with pores, located along sensilla from the base to the tip, are distributed on the antennal flagellum and the authors suggest that they function as receptors of odours (Silva et al. 2010).

The odour molecules reach the antenna and diffuse into sensilla through minuscule pores in the cuticle. The internal structure of the sensilla is comprised of the olfactory receptor neurons (ORN) (sensilla can have more than one ORN). The ORN is divided into three compartments: a central section called the inner dendrite or soma, the outer dendrite and the axon. The outer dendrite is the only part of the ORNs that is exposed to the sensilliar lymph, where reception of the small lipophilic molecules (pheromone) occurs. The sensilliar lymph is an aqueous proteinaceous medium containing millimolar concentrations of water-soluble odourant binding proteins (OBPs) and this medium represents a barrier for hydrophobic compounds like the pheromone. Thus, once getting into sensilliar lymph the odourant molecules bind to OBPs, which are responsible for transporting these molecules to the receptor sites in the dendritic membranes (Vogt 2003; Kaissling 2014). The odourant binding proteins can be divided into pheromone binding proteins (PBP), which are involved in pheromone transport, general odourant binding proteins (GOBP), which are involved in the transport of more general semiochemicals, such as plant volatiles and others; however, this last relationship has not yet been experimentally confirmed. A third class of odourant binding proteins was identified and named as ABPX (Krieger et al. 1996). The odourant binding proteins share certain common characteristics, such as being small acidic proteins with 120–150 amino acids, with a signal peptide in the N-terminal region, six-cysteine residues in conserved positions and an alpha-helical secondary structure. In stinkbugs 23 putative OBPs have been identified in *E. heros*, 25 OBPs in *C. ubica* and 9 OBPS in *D. melacanthus* (Farias et al. 2015). However, it is still necessary to conduct experimental studies to test the interaction of these proteins with pheromones or other odourant molecules.

The mechanism of olfactory stimulation of the neuronal system by pheromones in insects, culminating in the generation of an electrical signal, occurs in a similar way to that of ion active pumps in vertebrates. In the absence of odours, there is a higher concentration of Ca^{2+} and Na^{+} and Cl^{-} on the outer side of the membrane and a higher concentration of K^{+} and organic anions in the interior, which generate an electrochemical potential difference and polarization of the dendritic membrane. The PBP-odourant complex interaction with the dendritic neuronal receptor activates the coupled G protein, and the activation of the transmembrane phospholipase C (PLC) generates inositol-1,4,5-triphosphate (IP_3) and diacylglycerol (DAG). The IP3 increase causes Ca^{2+} influx via IP_3-dependent Ca^{2+} currents. The increase of Ca^{2+} stimulates the ion channel, opening the transmembrane protein C kinase (PKC) and increasing further cation influx. These events induce depolarization of the membrane that propagates as an electrochemical current along the axon. The membrane is repolarized in a few milliseconds due to the closure of the Ca^{2+} channels and activation of electrogenic pumps that re-establish the electrochemical potential difference over the dendrite membrane by K^{+} influx (Stengl et al. 1999).

Flying insects that follow the turbulent airborne-pheromone plume have to process the detecting odourant molecule in the sensilla (PBP) very fast not to lose the signal. This process has to run in a millisecond to release PBP and to bind it to the next odourant molecule. There are two hypotheses of how the detection system is reset to release the PBP and bind a new pheromone molecule from the plume. The first hypothesis suggests that pheromone-degrading enzymes play a role in releasing the PBP from the odourant molecules; however, the enzyme degradation is a slow process and does not explain the faster process that is observed in the antennae. The second hypothesis proposes that there are enzymes that are able to recognize the odourant-PBP complex by the exposed hydrophobic C-terminal of the complex. These enzymes could block or even remove the C-terminal, avoiding the formation of the complex of P-PBP (Kaissling 2014).

7.4 Reproductive Behaviour and Interaction of Signals of Different Modalities

In this section we discuss whether different modalities of signals act at unimodal, multicomponent or multimodal levels, review their interaction in each step of reproductive behaviour, and discuss their mutual impact on different processes at emitter and receiver sites.

7.4.1 Signal Modalities and Interactions

Higham and Hebets (2013) point out two ways to characterize signal composition. One is related to the emitter and concerns the signal's nature (physical properties) and the properties of the transmission channel. The other is related to the receiver's sensory system, which is used for signal detection. According to this, signals may be classified as *unimodal* when they transmit a unique component that is detected by a sensory system specialized to detect this specific component through a single channel. *Multicomponent signals* are thus defined as those that carry different components all together in the same sensory channel. *Multimodal signals* are characterized by components transmitted in different sensory channels (Partan and Marler 1999, 2005; Higham and Hebets 2013). Each component of a multicomponent or multimodal signal could be redundant if it codifies the same information, or non-redundant if each component has a different meaning (Partan and Marler 2005). Considering responses of receivers to single or to all components, the redundant components could elicit equivalent (no change in intensity of receiver response) or enhancement (increased intensity of receiver response) changes. The non-redundant components could elicit responses of receivers at four different levels: independence (individual response to each component), dominance (response to a unique component), modulation (higher or lower response to one individual component) or emergence (a new behavioural response when all components are presented together) (Partan and Marler 2005; Bradbury and Vehrencamp 2011).

Modelling the cost and honesty of multimodal signals demonstrated that any consequence of communication by multimodal signals could be achieved by a single one (Wilson et al. 2013). In addition, signalling through different communication channels could increase predation risk. On the other hand, switching between different sensory channels overcomes problems with noise in a single one (Wilson et al. 2013). As signals in different channels are transmitted at different rates and distances, multimodal signals could be transmitted with temporal and spatial variations that allow receivers a sequential evaluation of the information (Uy and Safran 2013). Another advantage derived from signals stimulating more than one sensory system of the receiver is the potential to increase the efficiency of their detection and processing (Rowe 1999).

Stinkbug sex, or aggregation, pheromone attracts conspecific females (sex pheromone) or adults and nymphs (aggregation pheromone) at long-range. In one group of species like *P. guildinii*, *Tibraca limbativentris* Stål and *Oebalus poecillus* Dallas these signals are clearly unimodal, and in the other they appear to be multicomponent, being composed of more than one single molecule. The previously described sex pheromone of *Chinavia* and *Nezara* species represents an interesting example. Their multicomponent pheromone is composed of the same two molecules, *trans*-*Z*-bisabolene epoxide and the corresponding cis-isomer (Fig. 7.3). Specificity is reached by different ratios of both compounds that enable communication through a private intraspecific channel. For example, the sex pheromone of two Neotropical species, *C. ubica* and *C. impicticornis*, shares one of these components (*trans*-*Z*-bisabolene) and the other is only present in *C. ubica* (*cis*-*Z*-bisabolene). Females are attracted specifically to the blends of conspecific males; although, they possess receptors for both isomers (Blassioli-Moraes et al. 2012). This evidence points at an interesting characteristic of multicomponent chemical signals of stinkbugs, suggesting that minor changes in components of the basic repertory or rates between them favour population isolation and speciation (Laumann et al. 2016). The multicomponent pheromone of the Neotropical brown stinkbug, *E. heros* is composed of three components, methyl-(2*E*, 4*Z*)-2,4-decadienoate, methyl-2,6-trimethyltridecanoate and methyl-2,6-trimethyldodecanoate in the ratio of 53:44:3, respectively (Zhang et al. 2003; Moraes et al. 2008a). Olfactometer and field bioassays showed that the synthetic mixture of the three components, as well as each individual component, attracts females (Borges et al. 1998), but similar response intensity to the complete blend has been obtained only with methyl-2,6,10-trimethyltridecanoate (Moraes et al. 2008a). The specific function of the other major component, methyl-(2*E*, 4*Z*)-2,4-decadienoate, has not been completely established. It is well possible that this compound carries other different information than the methyl-2,6-10-trimethyltridecanoate.

Pheromones of species, such as *P. stali* (Lee et al. 2002), *E. heros* (Borges et al. 2011) and *T. perditor* (Laumann et al. 2011), attract also alien species. Endo et al. (2006) suggested that *P. hybneri* stinkbugs could use the sex pheromone of *Riptorus clavatus* (Thunberg) (Alydidae) as a kairomone to search for food plants. Similar observations have been documented by Tada et al. (2001a, b). Aldrich et al. (2007) suggested the hypothesis that this behaviour could be related to a mechanism of passive defence in stinkbug aggregations. There is no experimental evidence to confirm these hypotheses. Reasons and mechanisms of eavesdropping on alien pheromones is a very interesting topic that demands greater attention. In particular, data on recognition/decoding of heterospecific pheromones and their impact on the receiver's physiological and behavioural traits are necessary for a better understanding of this phenomenon.

On the same plant, stinkbugs change the principal communication channel from air-transmitted pheromones to substrate-borne vibratory signals (Fig. 7.1). In the calling phase, signals are typically unimodal. Calling songs of females and males are composed of one type of pulse or pulse trains with very conservative temporal and spectral parameters that are readily repeated in females (Čokl et al. 2017a) (see also signals descriptions above). Male and female signals are alternated into well-synchronized duets that bring information related to species and sex identity (Čokl et al. 2017a). In addition, males could use signals of the typical steady and time-structured female calling song to orient their movement during searching for the calling female (Čokl et al. 1999; Virant-Doberlet et al. 2006).

Borges et al. (1987) first showed that *N. viridula* communicates at short-range by signals of different modalities. Multimodal communication was confirmed later in different species with detailed ethograms of the courtship behaviour, such as for *M. histrionica* (Zahn et al. 2008), *E. meditabunda* (Silva et al. 2012), *D. melacanthus* (Blassioli-Moraes et al. 2013), *C. ubica* and *C. impicticornis* (Laumann et al. 2016). During courtship, substrate-borne vibratory, short-range chemical, visual and tactile signals stimulate mating and copulation of recognized mates (Fig. 7.1).

Courtship vibratory signals have been characterized in many stinkbug species by a complex structure being exchanged between mates in different temporal patterns (Čokl et al. 2017a), indicating that they may act as unimodal or multicomponent signals. Experimental evidence to confirm or reject this hypothesis is lacking, but recent investigations in *Chinavia* spp and *E. heros* group communication (one or two conspecific males with two or three females) shows that different song components may carry different information, suggesting the multicomponent structure of these signals (Čokl et al. 2017b).

Tremulatory, buzzing and percussion signals described in Asopinae (Žunič et al. 2008; Laumann et al. 2013) and Pentatominae (Kavčič et al. 2013) enlarge the repertoire of substrate-borne vibrations. This suggests that communication on a plant is multicomponent and even multimodal when their airborne components are detected by receptors sensitive to air particle movement (see above).

Although it is widely known that short-range chemicals, such as cuticular hydrocarbons, are very common signals in insects (Blomquist and Bagnéres 2010), the knowledge of their relevance for stinkbug reproductive behaviour is scarce. Cuticular hydrocarbons have been characterized in *Bagrada hilaris* Burmeister (De Pasquale et al. 2007), *N. viridula* (Colazza et al. 2007), *C. ubica* and *C. impicticornis* (Silveira 2015), showing clear differences between species and sex. The use of cuticular hydrocarbons present in stinkbug footprints as kairomones by egg parasitoids (Platygastridae) has been reported in several works (Borges et al. 1999; Colazza et al. 1999; Conti et al. 2004; Lo Giudice et al. 2011; Peri et al. 2013; Lagõa 2016). In contrast, their function during stinkbug reproductive behaviour has gained less attention. Their possible role in insect recognition during the antennation phase of courtship behaviour was established in *B. hilaris*. Males tried to copulate with 90% of dead females that had been washed in water, but this percentage was reduced to 40% when females were washed with ethyl acetate, or to 20% when females were washed with n-hexane, two solvents that extract hydrocarbons from the cuticle (Guarino et al. 2008). Silveira (2015) identified in *Chinavia* species 14 different compounds. This very complex composition of cuticular hydrocarbons suggests that these signals are multicomponent and that different information could be carried by different compounds.

Tactile or visual signals have been poorly studied in stinkbugs, but they could have decisive participation, as information traits, in short-range courtship. The stereotyped processes of antennation, butting and leg tapping, both before and after copulation, have been described in most of the studied species.

7.4.2 Modulation of Signals of One Modality by Those of the Other

Mutual interaction of signals of different modalities at different levels of reproductive behaviour in stinkbugs is almost unknown. The dynamics of production and releasing of stinkbug pheromones has been poorly investigated. The quantity and composition of pheromones collected from males is highly variable, clearly suggesting modulation of emission (Miklas et al. 2003a). It depends on periods of the day for collection (Zahn et al. 2008; Zarbin et al. 2012), different ages of males (Zhang et al. 2003) or of their physiological state, as for example, mature or virgin, single or grouped (Miklas et al. 2001) and fed or unfed (Moraes et al. 2008b). Miklas et al. (2003b) tested the effect of vibratory signals on *N. viridula* male pheromone emissions. Female calling song significantly increased both the proportion of males emitting sex pheromone and the amount of emitted pheromone. Conspecific female calling song increased the pheromone emissions; the male rival songs or 100 Hz vibration had no effect. Higher emission of the male pheromone was obtained by stimulation with the female calling song of the male's own population, indicating high specificity of this male response. Another interesting result of this study showed that pheromone emission increased with time, with the highest value recorded after stimulation. The authors conclude that the vibration could affect a slow kinetics metabolic process, such as biosynthesis and excretion of pheromones. Similar results have been obtained in the Neotropical brown stinkbug, *E. heros* (Aline Moreira Dias, *personal communication*). Modulation of vibratory signal emission has been demonstrated in *N. viridula* (see above) also by chemical and visual signals (Zgonik and Čokl 2014).

Phytophagous insects use visual signals and cues connected with different behavioural patterns, like host plant selection displayed by *Coreus marginatus* (L.) (Heteroptera: Coreidae) (Pekar and Hruškova 2006), directional homing described in the shield bug *Parastrachia japonensis* Scott (Heteroptera: Cydnidae) (Hironaka et al. 2003) or reproductive behaviour demonstrated in *N. viridula* (Zgonik and Čokl 2014). Presentation of dead male or female bodies of different colour shades elicited emission of vibratory signals that did not differ from spontaneous calling. On the other hand, live males or females presented in daylight induced significantly more calling song signals. Higher levels of female calling can be correlated with the presence of the male pheromone (lacking in washed bodies of dead bugs). In males we can explain it by female visual signals produced by rotating their antennae when getting close to the male. In *Acrosternum hilare* (Say) (Hemiptera: Pentatomidae) Capone (1995) described another important role of vision during reproductive behaviour. The author demonstrated that males and females preferred to copulate with larger mates. Body size may be estimated by visual comparison of the length of antennae, as shown in male crickets, *Acheta domesticus* (L) (Orthoptera: Gryllidae) (Khadka et al. 2012). Time to recognize the mate and initiate courtship differed between normal and partly antennectomized males but the latter needed more time to achieve copulation.

The above-mentioned works show clear mutual modulation of chemical and vibratory signal emission. This strategy enables insects to emit signals only when the probability to detect the transmitted message is high, when it reduces predation risk and when it decreases energy waste. Intensive studies in different species are needed to understand phenomena connected with the mutual impact of signals of different modalities.

As mentioned before, the effects of tactile signals in stinkbug reproductive behaviour are practically unknown. These signals probably interact with visual, short-range chemical and vibratory signals. In some species-specific male or female songs were described together with observed touch by antennation and butting

(McBrien et al. 2002; Blassioli-Moraes et al. 2005, 2013; Laumann et al. 2016). Furthermore, many stinkbug species emit copulatory songs produced at the same time with male scrapping of the female abdomen with the hind legs (Čokl et al. 2017a).

Footprints left by insects on plants represent other chemical signals that could interact with signals of other modalities. Because epicuticle waxes of plants absorb the footprints (Colazza et al. 2009) they could act as long-lasting signals, informing receivers about the presence of conspecific in a specific area and inducing emission of signals of other modalities. Some evidence of this hypothesis was presented by Zgonik and Čokl (2014), who interpret spontaneous singing, observed when insects are on plants, as a response to footprints.

Neuronal processing of multimodal signals has not been investigated yet and integration of at least chemical and vibratory information at higher neuronal levels in the brain remains an interesting and challenging problem. Recent studies confirm that reproductive behaviour and communication of stinkbugs are very complex processes that need intensive and integrative studies in the field and laboratory at behavioural, sensorial and physiological levels.

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Part III
Practical Issues in Studying Vibrational Behavior

Chapter 8
Practical Issues in Studying Natural Vibroscape and Biotic Noise

Rok Šturm, Jernej Polajnar, and Meta Virant-Doberlet

Abstract In nature, vibrational communication takes place in an ecological context and in a complex vibrational environment that can be a major driver of evolution. Vibroscape is a collection of biological, geophysical and anthropogenic vibrations emanating from a given landscape to create unique vibrational patterns across a variety of spatial and temporal scales. Here, we discuss basic concepts and propose some basic terminology in this field of research. Vibroscape is virtually unexplored so far and we also provide some guidelines on how to approach fieldwork associated with vibroscape studies, as well as analyses of recordings obtained in the field. Vibroscape research is still facing technical challenges; however, we urge further studies in this area in order to provide much needed information on natural vibrational communities and sources of biotic, as well as anthropogenic vibratory noise.

8.1 Introduction

Our own experiences inevitably shape our understanding of the world around us. While strolling over a meadow or walking in a rain forest, we are aware of air-borne sounds emitted by animals living in these habitats and consequently, we also intuitively recognize the challenges that animals relying on air-borne sound communication are facing in these two environments (Jain et al. 2014; Greenfield 2015; Schmidt and Balakrishnan 2015). Moreover, in the last decade, soundscape ecology (Pijanowski et al. 2011a, b; Farina 2014) and ecoacoustics (Sueur and Farina 2015; Farina and Gage 2017) were brought into a research and application focus. Soundscape has been described as 'the collection of all sounds emanating from the landscape' (Pijanowski et al. 2011b) and has been used to characterize

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acoustic communities in different environments (Farina et al. 2011; Joo et al. 2011; Gage and Axel 2014; Rodriguez et al. 2014; Desjonquères et al. 2015; Ruppé et al. 2015; Erbe et al. 2015; Haver et al. 2017), as well as to get an insight into human impact on the environment (Dumyahn and Pijanowski 2011; Pieretti and Farina 2013; Merchan et al. 2014; Mullet et al. 2016; Rossi et al. 2016). Ecoacoustics emerged as a discipline using environmental sounds as an indicator of ecological processes (Sueur and Farina 2015) and has been applied among others to studies associated with biodiversity and habitat assessment (Harris et al. 2016; Rankin and Axel 2017), community ecology (Gasc et al. 2013a) and conservation biology (Krause and Farina 2016).

In recent years, our perception and understanding of substrate-borne communication has changed significantly (Cocroft et al. 2014; Hill and Wessel 2016). Although in the past vibrational signalling has been considered as a private communication channel, it is now recognized that animals live in a complex vibrational environment, in which abiotic and biotic noise and interactions with competitors and exploiters can be major drivers of evolution (reviewed in Virant-Doberlet et al. 2014). Studies carried out in the laboratory provided the first insight into interactions occurring in more realistic settings resembling the natural situation (e.g. Ichikawa 1982; Gordon and Uetz 2012; Halfwerk et al. 2016; Roberts et al. 2016; Fowler-Finn et al. 2017; Kuhelj and Virant-Doberlet 2017; Oberst et al. 2017). However, in contrast to airborne sounds, strolling over the meadow, we cannot hear vibrational signals emitted by species around us, and therefore we lack more personal understanding of the complexity of the natural vibratory world. Biotremology studies carried out in the field are, in general, rare (e.g. Barth et al. 1988; Hill and Shadley 2001; Cocroft 2003; Cocroft and Rodríguez 2005; Lewis et al. 2006; O'Connell-Rodwell et al. 2006; Tishechkin 2007, 2011; McNett et al. 2010; Soulier-Perkins et al. 2015), and investigations targeted specifically to characterize natural vibroscape are still lacking. Besides the long-held perception that vibrational communication is a highly specialized and rare form of communication effective only at short range, the reason why vibroscape is virtually unexplored is certainly due to the associated technical challenges. The lack of such crucial information hampers further progress in our understanding of the nature of selection imposed on vibrational communication by the environment. However, it should be emphasized that vibroscape is important not only for species using vibrational signals in their intraspecific communication, but for all animals able to detect vibrational signals or cues present in their environment (e.g. Virant-Doberlet et al. 2014; Roberts and Elliott 2017).

In this chapter, we wish to share some of the experiences obtained during our own ongoing vibroscape study in order to stimulate further work. In line with our own research, we will focus on vibroscape in hay meadows. Although studies carried out in other terrestrial habitats or in marine and freshwater sediments will face different technical challenges, some of the issues addressed here apply to other environments as well.

8.1.1 What Is Vibroscape?

Adapting a definition of soundscape (Pijanowski et al. 2011a, b) to vibroscape, we can describe it as the collection of biological, geophysical and anthropogenic vibrations emanating from a given landscape to create unique vibrational patterns across a variety of spatial and temporal scales (Fig. 8.1). The main source of biological vibrations are vibrations emitted by animals, not only during intraspe-

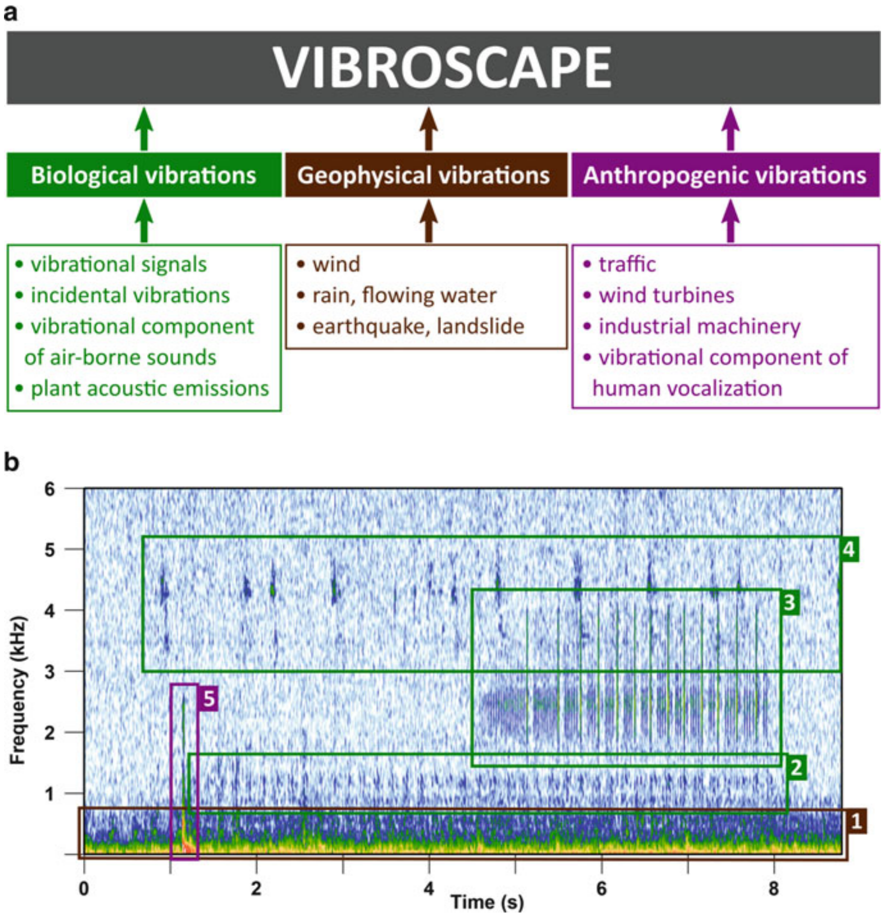

Fig. 8.1 Vibroscape. (**a**) Schematic presentation of vibroscape components and sources of vibrations. (**b**) Visualization in the form of spectrogram of vibroscape, which includes continuous low-frequency vibrations induced by wind (brown, 1), overlapping vibrational signals in two different frequency bands emitted by two unknown insect species (green, 2, 3), vibrational component of a sparrow air-borne song (green, 4) and transient vibration resulting from anthropogenic activity (purple, 5). Spectrogram was generated in Seewave (R package) with Hanning window of 1024 samples with 80% overlap

cific communication, but also as a by-product of other activities (e.g. incidental vibrations induced during walking, feeding and cleaning). In addition, vibrational components of air-borne sounds emitted by insects, birds, mammals or, in the case of marine or freshwater sediment, underwater sounds emitted by crustaceans, fish and mammals are also represented in the vibroscape (Lohrey et al. 2009; Caldwell 2014). Moreover, vibrations resulting from physiological processes in plants (Schöner et al. 2016) can also be considered as part of the vibroscape. Geophysical vibrations are those originating from geophysical, abiotic sources such as earthquake, landslide, wind, rain, thunder, running water, waves and chemical processes in the sediment (Pijanowski et al. 2011a; Desjonquères et al. 2015; Erbe et al. 2015). Anthropogenic vibrations are produced by any human activity, man-made devices like cars, trains, airplanes, boats, wind turbines, industrial and construction machinery (Pijanowski et al. 2011a; Erbe et al. 2015; Roberts and Elliott 2017), as well as vocalizations (e.g. speech) (Joo et al. 2011). In soundscape ecology, the former are also known as technophony (Mullet et al. 2017).

The biological component of vibroscape is by definition also associated with the animal community present at a given location. Adapting a definition of acoustic community (Gasc et al. 2013b; Farina and James 2016; Mullet et al. 2017), we propose to define vibrational community as an aggregation of animals that produce vibrational signals and are active over a specified time. Although by such definition the vibrational community represents only a subset of biological vibrations present in the environment, it allows us to address separately the sources of selection on vibrational communication resulting from species-specific signals and competition for a transmission channel (i.e. resource partitioning of 'vibrational space'), as well as competition for the receiver's attention and 'cocktail party problem' (Virant-Doberlet et al. 2014). At a given location, the vibrational community varies over the day and year, as well as between years. It should be noted that individual perception or experience of the vibrational community depends on the spatial position of the receiver at a given site. Moreover, taking into account a perspective of an individual relying on vibrational communication, the vibrational community may also be divided into heterospecific and conspecific communities, each of them potentially imposing different selection pressures on the evolution of signals and behavioural strategies (Römer 1993; Virant-Doberlet et al. 2014; Greenfield 2015; Schmidt and Balakrishnan 2015).

Vibroscape does not include only vibrations relevant to intraspecific communication, but also vibrations masking and interfering with detection and transmission of relevant information and therefore can be defined as noise (Forrest 1994). Effects of abiotic (geophysical), biotic (biological) and anthropogenic vibrational noise on vibrational communication and behaviour have been documented (McNett et al. 2010; de Groot et al. 2011; Gordon and Uetz 2012; Shier et al. 2012; Roberts et al. 2016). It should be noted that biotic vibrational noise can result from heterospecific and/or conspecific signals and also from air-borne sounds in the environment.

An important concept in vibroscape is signal active space, which has been defined as 'area in which the signal amplitude is sufficiently above the detection threshold of potential receivers to elicit a behavioural response' (Mazzoni et al.

2014). However, in the context of vibroscape, the definition should also take into account that a detection of a vibrational signal may not result only in triggering of an obvious behavioural response (e.g. inducing vibrational reply from a partner), but also in a suppression of signalling activity, when the same signal is perceived by heterospecifics as a biotic noise (Virant-Doberlet et al. 2014). In this respect, the criterion of ‘an effect on behavioural response of the receiver’ would be more appropriate. In general, signal active space depends on the amplitude of the emitted signal, attenuation of the signal during the transmission, amplitude of a background noise and sensitivity of vibroreceptors (Mazzoni et al. 2014). However, in comparison with air-borne sound, the active space of vibrational signals is highly unpredictable, due to complexity of the substrate, filtering properties and amplitude oscillations during the transmission (Michelsen et al. 1982; Barth 1998). The active space of vibrational signals differs enormously, from few cm in fruit flies (Mazzoni et al. 2013) to several km in elephants (Narins et al. 2016). It is generally considered that on plants the active space is limited to a plant on which the animal is signalling; however, it can also extend to neighbouring plants connected by roots and touching leaves or over the soil (Čokl and Virant-Doberlet 2003; Tishechkin 2011) (Fig. 8.2) and even across a several cm wide air gap between overlapping leaves (Eriksson et al. 2011; Kavčič et al. 2013).

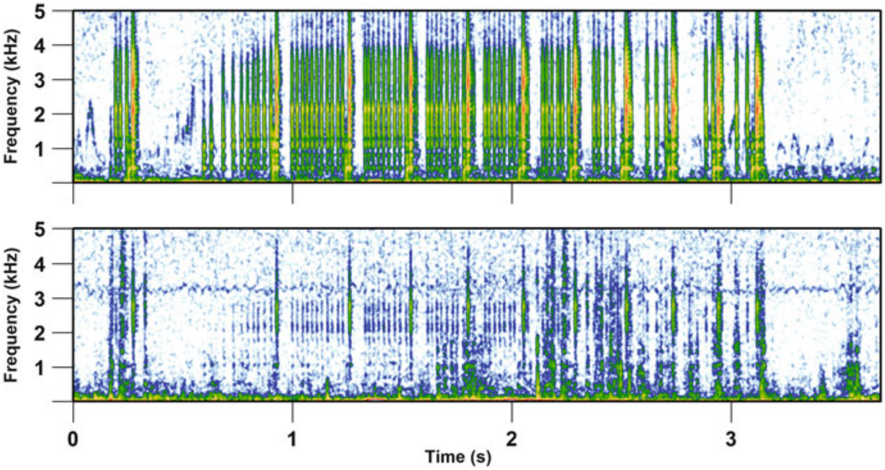

Fig. 8.2 Active space of vibrational signals in the field. One above the other are shown spectrograms of vibrational signals emitted by an unknown species recorded simultaneously from two clover plants growing 3 cm apart. Spectrograms were generated in Seewave (R package) with Hanning windows of 1024 samples with 80% overlap

8.2 Fieldwork

Analogous to field sound recording in soundscape studies, the choice of vibration recording set-up for field use involves three chief considerations: recording system performance, practicality and budgetary constraints. We use the word ‘practicality’ as an umbrella term to refer to several issues, such as portability, reliability of power supply, robustness and security, all of which are important in the field.

8.2.1 Planning the Fieldwork

Primarily, the fieldwork should be planned according to the research objectives; however, planning should also take into account time, financial and technical considerations, as well as staff availability. While for some studies, 1-channel recording obtained by piezoelectric cartridges connected to a portable tape recorder and carried out for a few hours may be sufficient (e.g. Tishechkin 2011), the others may attempt to characterize vibroscape at a larger spatial scale and over longer time. Fieldwork associated with more complex vibroscape studies may need a lot of heavy equipment that also has a high energy demand (Fig. 8.3). Moreover, field recordings usually require a constant presence of a supervisor in order to intervene when the signal is lost (e.g. moving of the plant due to the wind, grazing animals etc.) or in case of rain and thunderstorms. More complex studies certainly require the involvement of several people to share the overseeing in the field, as well as characterizing the vibrational community, the latter also including establishing the reference library of vibrational signals (see Sect. 8.2.5).

As described in more detail here below, most of the technical challenges should be resolved before starting the field recordings. An important decision that has an impact on several issues is the choice of the field site where recordings will be carried out. While in many cases, the research objectives may limit the number of suitable locations, it is worthwhile to take some additional factors into consideration when planning more complex studies. Besides obtaining permission to work at the specific site, an agreement with the owner or manager about the agricultural practice (for example mowing) may prevent unpleasant surprises in studies extending over several months or years. The power supply does not represent a problem at the site with an available grid power, where electricity can be brought directly to the equipment via extension cable. Natural shade at the site may help to avoid overheating of equipment during the hot summer days.

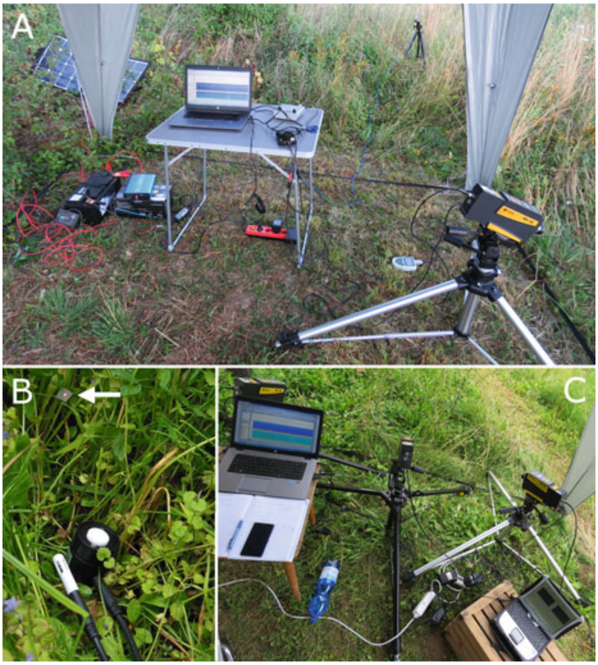

Fig. 8.3 Field equipment used for studying vibroscape in hay meadows. (**a**) Power supply for fully autonomous fieldwork includes solar panel and automotive batteries and enables autonomy up to 24 hours using one portable laser vibrometer, laptop and microphone (in the background). Tent is used to provide protection from the sun and rain. (**b**) Temperature, humidity, pressure and light sensors positioned in the vicinity of the point of registration (arrow) provide automated sampling of environmental parameters. To improve signal-to-noise ratio in vibroscape recording, a small piece of reflective tape is attached to the plant in order to increase reflectance. (**c**) Field set-up using three portable laser vibrometers, a laptop computer and a calibrated data acquisition device (SINUS Soundbook)

8.2.2 Transducers

Vibration transducers are generally limited to one axis of detection (Scheffer and Girdhar 2004), so transducer choice and placing are of utmost importance in designing vibroscape recording experiments (although triaxial accelerometers are not uncommon; Gracewski and Ramoutar 2013). Using more than one transducer in a multichannel set-up will multiply not only the detection area, but also power consumption, data storage requirements and cost.

Cocroft and Rodríguez (2005) list several types of transducers useful for detecting plant-borne insect vibrational signals: laser vibrometers, accelerometers, phonograph cartridges and electrical guitar pickups, each of which could be considered in vibroscape measurements; however, the last type suffers from low sensitivity and is less suitable. To encompass all vibroscape options, geophones should also be added to the list (O'Connell-Rodwell et al. 2000; Hill and Shadley 2001; Roberts et al. 2016). More generally, transducers differ according to the mechanical parameter of the vibration that they respond to displacement, velocity or acceleration of surface motion. These three quantities describe sinusoidal motion differently and can be interconverted (incurring phase shift), but the nature of physical systems means that displacement will normally be the largest at lowest frequencies, and acceleration will be the largest at high frequencies, while velocity is the most general. Measurements of displacement will thus be biased towards low frequencies (up to ~100 Hz) and measurements of acceleration towards high frequencies (from ~2000 Hz up). This becomes important when considering the dynamic range of the measuring device because, for example, an accelerometer's output will be the lowest at low frequencies, so faint low-frequency signals might be lost more quickly in the background noise. Velocimeters are the most versatile, especially within the frequency band 50–2000 Hz (Norton and Karczub 2003), which is the most suitable for a wide range of vibrational emissions encountered in the field.

As a rule of thumb in mechanical engineering, a piezo accelerometer should have no more than 10% of the mass of the structure to which it is attached in order to avoid significant changes to the structure's dynamic response—the so-called mass loading (Gracewski and Ramoutar 2013); however, a more conservative rule might be warranted due to low amplitude of insect-produced vibrations. Cocroft and Rodríguez (2005) thus recommend using accelerometers with at most 5% mass of the structure and they are therefore more suitable for use on woody plants like trees and bushes (e.g. Cocroft 2003) than for herbaceous plants. A variety of accelerometers is commercially available, typically with the frequency range between 1 or 2 Hz and 8 or 10 kHz that is used in engineering, but higher-frequency models can also be obtained (Scheffer and Girdhar 2004), so the choice of the model should be based on expected frequency composition of the studied vibrational environment. An accelerometer should be tightly fastened to the studied surface to avoid decoupling at higher frequencies, either by screws or adhesive (Gracewski and Ramoutar 2013).

Phonograph cartridges are velocity transducers, requiring delicate and stable contact between a stylus and the measured surface. Older-type piezoelectric cartridges should be used for biological measurements because modern electromagnetic variants are much less sensitive (Cocroft and Rodríguez 2005). Despite challenging set-up, their compactness, robustness and low price make them suitable for field recording even in remote, exotic locations (e.g. Soulier-Perkins et al. 2015); however, a pre-amplifier is required for data acquisition. Tishechkin (2007) mitigated the problem of mass loading in his field studies by attaching the cartridge at the base of the focal plant and placing its body on the ground; however, such position may reduce sensitivity because a plant will vibrate less freely near the fixed end. Guitar pickups belong to another class of electromagnetic velocity transducers, which by design do not need external power supply or charge amplifiers, but tend to be bulky and require regular calibration because they contain moving parts (Gracewski and Ramoutar 2013). Velocity transducers for string instruments are cheap and readily available, but their low sensitivity will most likely result in missing many relevant vibrational signals (Cocroft and Rodríguez 2005). On the other hand, industrial-purpose velocity transducers are highly sensitive, but have typically a much narrower rated frequency range (between 10 and 1000 Hz; Scheffer and Girdhar 2004), which, along with their bulk, severely limits their usefulness for biological studies.

Laser vibrometers (laser Doppler interferometers, or LDVs) are the only accessible type of device that avoid the problem of mass loading entirely, by analysing reflection of the laser beam without touching the substrate. Their sensitivity, spatial resolution and frequency range are also superior. These advantages are offset by their cost and complexity, both exceeding mechanical transducers (Gracewski and Ramoutar 2013), which can be a barrier to their usefulness in the field. Nevertheless, some portable models are commercially available and already widely used in biotremology studies. Our experience with the PDV-100 (Polytec GmbH, Waldbronn, Germany) proves that field recording over several days is feasible, with some effort. The main practical issues are power consumption, bulk and sensitivity to environmental conditions. The PDV-100 consumes 15 W power, weighs 2.6 kg without accessories (tripod, cables and connectors) and requires monitoring to prevent signal loss, thus necessitating a portable computer or at least a portable recorder with headphones and constant presence of a supervisor. During field recording in the sunny summer days, when mid-day air temperature reached above 35 °C, the device tended to overheat even when protected from direct sun and had to be turned off to cool down. Caldwell (2014) warns about the possibility of cross-modal contamination by intense sound sources that can vibrate the laser's housing and produce a false signal; although the laser's mass is usually much greater than the measured surface, so acoustic coupling will likely only be an issue when an airborne sound effect needs to be characterized precisely. It is, however, a good idea to place the equipment away from strong sound sources, such as generators, and fix the cables to prevent them from vibrating, regardless of the sensor type used. For similar reasons, the laser vibrometer should be placed in a position protected from wind.

To our knowledge, the research of a ground-borne component of vibroscapes has been applied to both terrestrial and aquatic environments (e.g. O'Connell-Rodwell et al. 2000; Hill and Shadley 2001; Arnason et al. 2002; Lewis et al. 2006; Mitra et al. 2009; Roberts et al. 2016). Geophones can be made waterproof for seabed monitoring; however, Nedelec et al. (2016) make a case for measuring particle motion in underwater environments instead, which can be accomplished with waterproof accelerometers. The line between vibrations in substrate and in liquid media is even more blurred in the water than in the air, so transducer choice and interpreting the measurements should be carefully considered in the planning stage. Several other types of transducers have been successfully employed in field detection of burrowing insects hidden in soil or wood, such as piezoelectric disks, electret probe microphones and accelerometers (Mankin et al. 2000), and also laser vibrometers (Zorović and Čokl 2015). Again, accelerometers and laser vibrometers proved to be the most sensitive. It should be noted, however, that detection of known target species requires less generality (bandwidth) after their vibrations are characterized and can even be accomplished with specific feature extraction from a narrow frequency band (Korinšek et al. 2016), which is not an option in diversity studies.

When setting the recordings in the field, another important decision is from where on the plant one should register vibrational signals. Ideally, the position of a transducer or laser beam focus should be as close as possible to the position of the animal receivers without disturbing their natural behaviour. While in some cases such position may be relatively easy to determine (e.g. for insects forming persistent, visible groups on branches; McNett et al. 2010), this may not be possible in other habitats. In grassland, one is faced with the problem that small animals like insects are hidden in dense vegetation and in many species, males are moving from plant to plant in order to increase the active space of their calls ('fly/jump/walk-call' strategy) (Kuhelj et al. 2015). Here, the registration position may often be a trade-off between signal amplitude, signal-to-noise ratio and stability of recording. The amplitude of the signal is higher closer to the top of the plant (Michelsen et al. 1982); however, so is the amplitude of vibrational noise. Moreover, the top of the plant is more exposed to the wind and often moves out of the laser beam range. To ensure a stable recording, it is usually better to register vibroscape from the position closer to the ground (Fig. 8.3b).

8.2.3 Data Acquisition and Storage

Most biologically relevant substrate vibrations occur in the decahertz up to low-kilohertz range (Čokl and Virant-Doberlet 2003), which is well within the frequency range covered by commercial audio technology, and thus no specialized recording devices are needed. The usual sampling rates in digital recorders (e.g. 44,100 Hz, the standard CD sampling rate) are also sufficient to exceed the Nyquist frequency and avoid aliasing. Depending on portability requirements and power availability, a vibroscape recording set-up might include a portable computer (laptop) with an external data acquisition component or a built-in sound card, or a handheld recorder. The computer's advantage is the possibility of monitoring the recorded data on the screen, with modern devices fast enough to perform FFT calculations and display spectrograms in real-time. It should be taken into account, however, that a mid- to high-performance laptop consumes up to 50 W of power.

There are several calibrated data acquisition devices suitable for field use, such as the LAN-XI (Brüel & Kjær Sound and Vibration Measurement A/S, Nærum, Denmark), VibSoft (Polytec GmbH, Waldbronn, Germany) and Apollo/Soundbook (SINUS Messtechnik GmbH, Leipzig, Germany), although they require specialized recording software installed on a portable computer, which adds to power use and equipment weight. To a biologist, the interface of these programs built for mechanical engineers might seem intimidating, and the time domain measurements are more difficult to implement, but it is possible to set a measurement to store and monitor both the time domain (oscillogram) and frequency spectrum in real time. On the plus side, these devices are versatile, able to process inputs from various different recorders with known voltage response, some of them offering additional slow channel(s) for environmental sensors, which they synchronize with the audio track(s), thus facilitating analysis. If such equipment is available, it is useful to do at least a part of the recording with it (e.g. some hours during a week-long monitoring) to gain insight into absolute amplitude ranges of observed signals. However, long-term recordings are less feasible with calibrated data acquisition devices, because they are memory-intensive, possibly requiring regular breaks in recording to reset the software and clear up the computer's memory. They also produce significantly more data than standard audio recordings, thus making storage and analysis more technically demanding.

When carrying out complex, long-term vibroscape studies, sound files should be automatically saved at regular, short intervals in order to prevent the loss of data due to unpredictable factors (e.g. weather, equipment malfunction). Moreover, short sound files are also more convenient for analysis (see Sect. 8.3).

Data storage is probably the least problematic aspect of field recording, with capacity, portability and robustness of storage media improving rapidly in the current age of solid-state memory devices. Memory cards as large as 512 GB that fit into the palm of a hand and weigh next to nothing are easy to obtain nowadays. Uncompressed Wave (WAV) file size is calculated as

$$\text{size} = \text{sample rate} \times \text{number of channels} \times (\text{bits per sample}/8) \times \text{time in seconds},$$

so a one-channel 48 kbps/16 bit depth Wave file from a digital handheld recorder will take approximately 350 MB of storage space per hour, and a 512 GB memory card will be able to store almost 1500 hours' worth of recordings, which is more than enough for most field needs. However, massive amounts of data from many channels and with higher-than-necessary sample rate might still cause problems during analysis, and the saying that it is easy to collect so much data that computers choke on them (Young 2001) continues to be relevant. It also goes without saying that reliability should be a priority when choosing storage media, and backup storage needs should be considered as well.

8.2.4 Power Supply

Power supply is probably the issue most open to improvisation. Set-ups with mechanical transducers and handheld digital recorders can be powered by standard batteries or specialized battery packs, and time of autonomy should be kept in mind when planning periodic checks of equipment functioning. This should be checked in each piece of equipment's manual, and also tested before the recording season, if possible, to avoid unpleasant surprises in the field. Unfortunately, changing the batteries will usually necessitate at least some minutes' downtime per several hours of recording. The issues are analogous to field sound recording. Further discussion and additional resources that can be consulted in the planning stage are available from Obrist et al. (2010), the Cornell Lab of Ornithology (https://www.macaulaylibrary.org/contribute/audio-recording-gear) and other bioacoustics references.

Using lasers and/or laptops is challenging due to significantly larger power consumption. Modern laptops offer around 4 hours' worth of battery power, which can be maximized by avoiding non-essential consumption (dimming the display and switching it off when not needed, disabling the WI-FI, shutting down all unused programs and background operations), but laptop batteries lose capacity with age. Polytec's battery pack enables a similar time of autonomy for the PDV-100 laser vibrometer. Longer times require bigger batteries where, luckily, both laptops and laser vibrometers operate on 12 V DC power that is provided by automotive batteries, which can be wired directly to the device's input (with appropriate fuses). The so-called 'deep cycle' batteries should be used because regularly draining normal car batteries to less than 85–90% capacity will severely shorten their lifespan. Wiring becomes complicated with more than two devices; however, a quick and dirty solution is to use an inverter with several AC outlet connectors, although an inverter will require some power itself. Additionally, it is important to use a sine-wave inverter, because the cheaper models produce square waves that induce distinct noise in recordings.

Portable solar panels are emerging as a promising option in recent years, and may, in ideal situations, enable full autonomy, at least in sunny weather. The panel can be wired to the battery, which in turn provides power to the recording set-up and stores the excess for night operation (Fig. 8.3a). Consulting an electrical engineer is advisable to calculate requirements, although it should be noted that a battery with enough capacity to power the above-mentioned demanding set-up will weigh 20–30 kg. However, in order to carry out continuous 24-hour recordings over several days, also in cloudy weather, a back-up charged battery is needed.

8.2.5 Other Data Collected in the Field

In order to describe the vibrational community present at the chosen field site, recorded vibrational signals should be ideally linked with species emitting them (see Sect. 8.3.2). In most field situations, animals are not seen while emitting vibrational signals, either due to their small size, habitat complexity or their nocturnal activity. To establish a reference library of vibrational signals, animals should be collected as close as possible to the recording site and their species- and sex-specific vibrational signals recorded in a dedicated set-up, either in the field or in the laboratory (e.g. Tishechkin 2014; Derlink et al. 2018).

In order to correlate vibroscape with the habitat, identification of plant species growing at the recording site is also needed. The area included in the botanical survey depends on the research objective and the type of habitat; however, it should be carried out over a much larger area than is the anticipated active space of recorded vibrational signals, in order to account for mobility of the signalling animals.

Measuring other environmental parameters is also needed for correct interpretation of vibroscape data. For this purpose, a range of sensors can be deployed in the vicinity of the measuring point(s), such as thermometers, anemometers and light and humidity sensors (Fig. 8.3b). Modern digital recorders automate sampling of parameters from various attached sensors and create a text file with time-stamped values. Alternatively, sensors can be attached to slow channels of some specialized data acquisition devices, synchronous with the vibration track (see below). Additionally, a microphone connected in parallel with a vibration transducer enables direct comparison between vibroscape and soundscape, which can improve understanding of their interactions.

8.3 Analyses

An inevitable consequence of shifting the focus from a sender-receiver dyad to the entire community, and moving the studies from the laboratory to the field, is generation of a large amount of raw data (Pijanowski et al. 2011a; Wimmer et al. 2013; Servick 2014). While basic 1-channel recording over a relatively short-time results in a still manageable number of sound files that can be analysed manually with a reasonable effort, the management of a huge amount of files created by more complex, multi-channel continuous recordings is undoubtedly a challenge. During the fieldwork, raw data acquisition can be relatively easy; however, the time and effort needed to screen and analyse these recordings can pose a significant problem, especially with the limited number of experienced observers. It should also be taken into account that prior to the analysis, analogue recordings on cassette tapes have to be converted to a digital format (Gage and Joo 2017).

When approaching the analysis of complex continuous recordings, which result in a large number of individual sound files, the first and crucial decision is how many files can be screened in the available time and with the available financial, technical and expert support, without losing important information. Such a decision can already be made during the planning stage by choosing recording schedules that, instead of a continuous recording, incorporate regularly repeated shorter recordings over a longer period of time (e.g. Farina et al. 2011; Gasc et al. 2013b; Desjonquères et al. 2015; Pieretti et al. 2015) or are focused to a particular time of the day (e.g. Depraetere et al. 2012; Lellouch et al. 2014; Machado et al. 2017). However, we suggest that, at least at present, the best approach in vibroscape studies is to obtain the longest recordings that are sensible and feasible within the particular research objective and then, if needed and justified, select short individual sound files or recording periods for detailed analysis. So far, programmable autonomous vibration recording systems that can be left in the field and can provide continuous recordings for prolonged periods of time, up to several months, are not available and, in comparison with the soundscape research, the cumulative durations of obtained field vibroscape recordings are much shorter. Moreover, the vibroscape is virtually unexplored and we have very little information about temporal changes in vibroscape and vibrational community.

8.3.1 Aural and Visual Inspection of Recordings

The first step in the analysis of vibroscape recordings is identification of recorded vibrations, which is done manually, i.e. by listening to the files as many times as needed and simultaneously visualizing the recordings as oscillograms and spectrograms. Such an approach is common also in soundscape analysis (Depraetere et al. 2012; Lellouch et al. 2014; Rodriguez et al. 2014; Machado et al. 2017), in particular when automated classification of species-specific sounds is not possible (Desjonquères et al. 2015; Ruppé et al. 2015). While we believe that in the future automated signal recognition can also be used in vibroscape analysis (see Chap. 9), in particular when the research objective is primarily focused on a single species, unpredictable changes in signal structure during transmission, and vibrational noise, impose severe technical challenges. When recordings are screened by several people, crosschecking is needed in order to ensure accurate and consistent identification of biological vibrations.

Recordings of the vibroscape are dominated by frequencies below 1000 Hz (Fig. 8.4). The common practice in soundscape analysis is to ignore all frequencies below 2 kHz, since they are considered a background noise (Farina et al. 2011; Depraetere et al. 2012; Towsey et al. 2014; Roca and Proulx 2016; Gage et al. 2017). However, in vibroscape, this frequency band includes most of the relevant vibrations, not only geophysical and anthropogenic vibrations, but also animal vibrational signals used in communication. To reliably separate relevant biological vibrations from the vibrational noise, filtering out at least some of the lower frequencies may be needed. The cut-off frequency should depend on the vibrational community present at the study site. While vibrations below 50 Hz mainly can be attributed to abiotic (geophysical) noise, vibrational signals of stink bugs and lacewings often have dominant frequencies below 100 Hz (Čokl 2008; Henry et al. 2013) and in Auchenorrhycha (leafhoppers, planthoppers and treehoppers), most of the signal energy is usually contained below 1 kHz (e.g. Mazzoni et al. 2010; Derlink et al. 2014; Cocroft and McNett 2006). However, abiotic noise generated by wind is not limited to frequencies below 50 Hz, but rustling leaves and stems can also create vibrational noise in the frequency range extending up to several kHz, although, the amplitude decreases with increasing frequency (Cocroft and Rodríguez 2005).

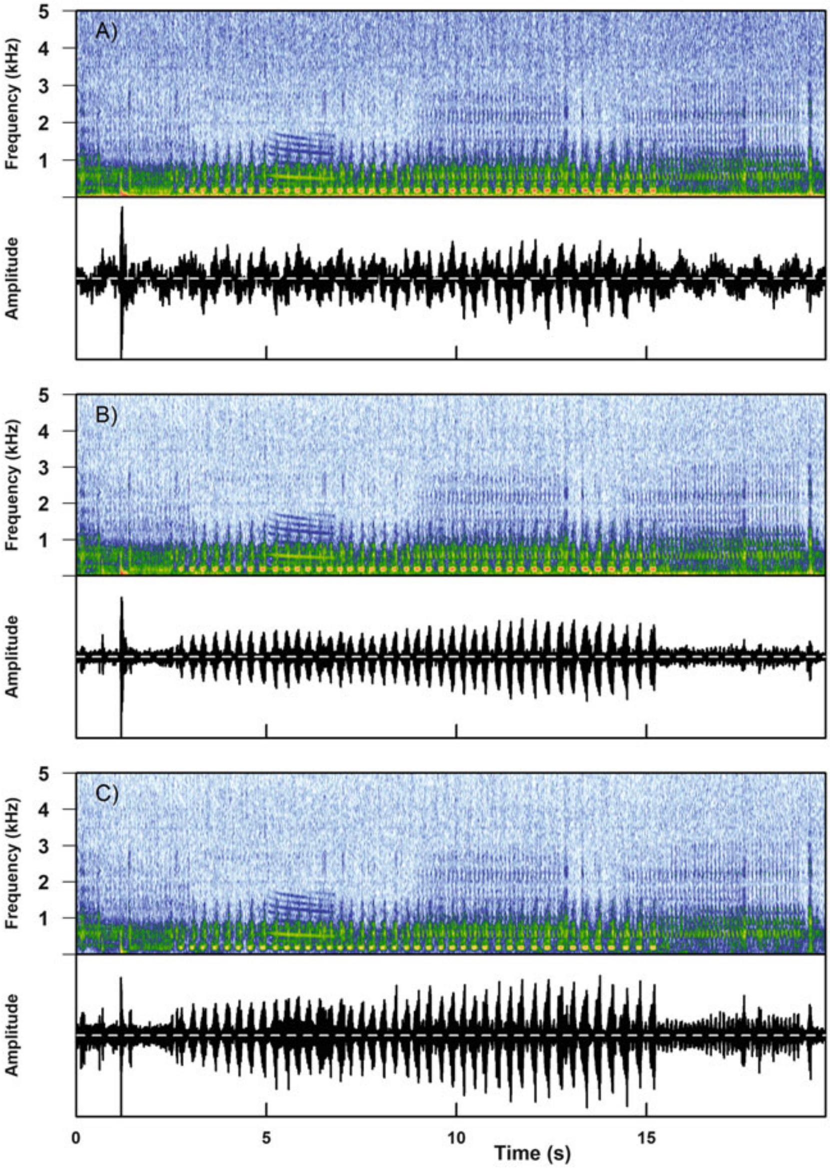

Fig. 8.4 Processing of field recordings. (**a**) Original non-filtered field recording from a clover plant. Spectrogram is shown above the corresponding waveform. The recording includes overlapping vibrational signals emitted by three different species. Vibrational signal with a clear harmonic structure is emitted by unknown species, signal in the time window 2.8–15.3 s with dominant frequency 210 Hz is male advertisement call of the leafhopper *Aphrodes bicincta* 'Dragonja', while the other signals are emitted by an unknown species. (**b**) Application of 50–5000 bandpass Butterworth frequency filter using Seewave, R package. (**c**) Application of 200–5000 bandpass Butterworth frequency filter (Seewave, R package). All spectrograms were generated in Seewave (R package) with Hanning windows of 1024 samples with 80% overlap

8.3.2 Characterization of the Vibrational Community

Regardless of the research objective and the habitat of interest in the vibroscape study, the characterization of the vibrational community is challenging. The main reason is that, due to the enormous diversity and shear number of species relying on vibrational communication, the information on the vibrational repertoire of the great majority of species encountered in the field is not available. Moreover, in dense vegetation small animals like insects emitting vibrational signals are usually hidden to the observer. Furthermore, to an untrained listener, incidental vibrations induced by walking insects often sound like signals intended for communication (Fig. 8.5a). Vibrational signals used in communication are usually characterized by their distinct temporal and spectral properties (Fig. 8.5b–d). In the absence of a reference library, unknown vibrational signals can be assigned to 'vibrational taxonomic units' (VTU), or 'vibration types', as has been done for air-borne sounds in the case of orthopteran communities in the tropics (Riede 1998; Schmidt and Balakrishnan 2015) and in underwater acoustics (Desjonquères et al. 2015; Ruppé et al. 2015). To our knowledge, at present there is only one publicly available archive of vibrational signals, which is dedicated to vibrational signals of Dutch planthoppers (http://www.insectdrummers.com/#Home). A more comprehensive public archive of vibrational signals is clearly needed (see Chap. 23), but nevertheless, establishing individual libraries associated with specific vibroscape projects is still inevitable.

Insect vibrational signals are species-specific (e.g. Henry et al. 2013; Čokl 2008; Tishechkin 2014; Stewart and Sandberg 2006); however, there are several caveats to attributing signals to VTUs that should be taken into account. The vibrational communication strategy used in mating sequences differs among species. The most common pattern is that males spontaneously emit complex advertisement calls that trigger the emission of species- and sex-specific female vibrational reply (e.g. Cocroft and McNett 2006; Percy et al. 2006; Stewart and Sandberg 2006; Derlink et al. 2014; Abt et al. 2018). Consequently, the most commonly encountered vibrational signals are male calls. However, in some species, vibrational signals associated with later stages of the mating sequence differ from those emitted in the beginning (Derlink et al. 2018; Čokl 2008) and specific vibrational signals are also emitted during other social interactions, like rivalry (e.g. Mazzoni et al. 2009; Kuhelj and Virant-Doberlet 2017), as well as food recruitment and parental care (Cocroft and Hamel 2010). While a species-specific vibrational repertoire can be quite rich in itself, in some species regional vibrational dialects have also been described (Virant-Doberlet and Čokl 2004). It should also be emphasized that under complex field conditions, transmission of vibrational signals through plants results in unpredictable degradation of the signal due to frequency filtering, as well as temporal distortions of vibrational signals (e.g. Michelsen et al. 1982; Barth 1998; Polajnar et al. 2012). Consequently, the signal registered far away from the signalling animal may bear little resemblance to the signal found in the library, since

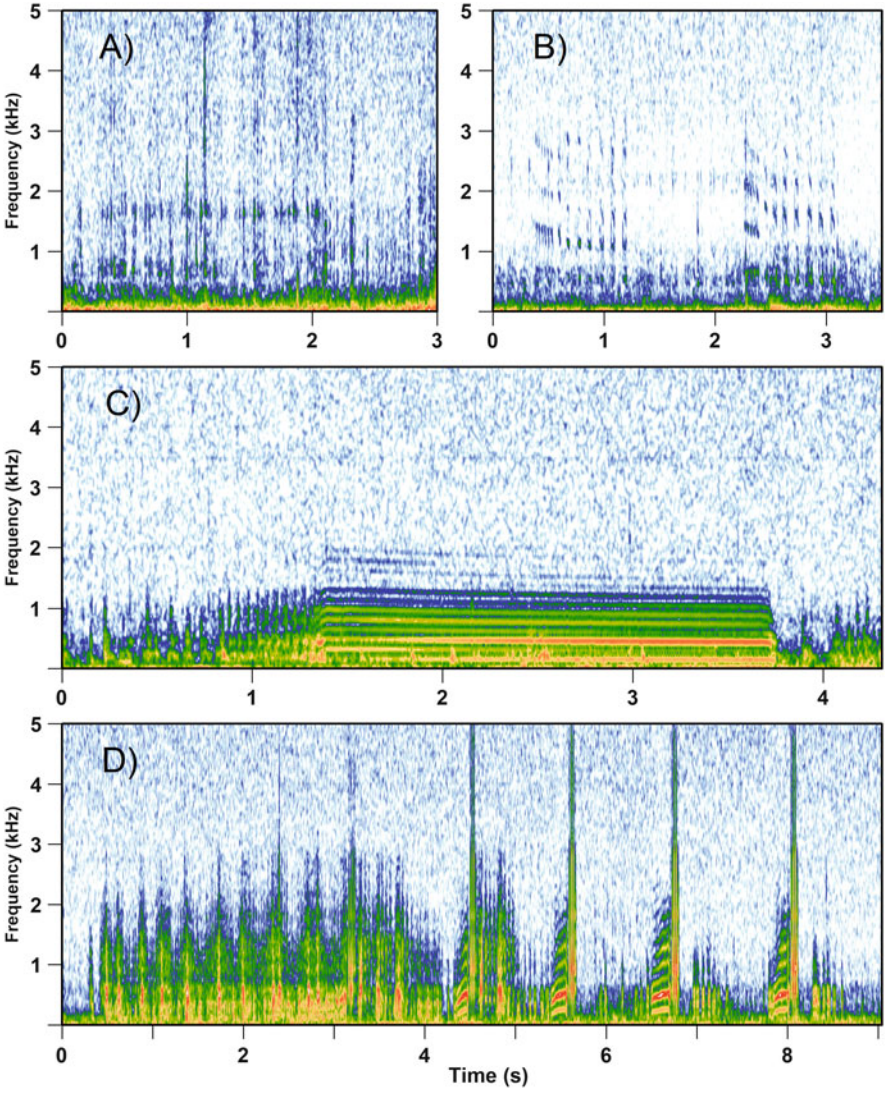

Fig. 8.5 Biological vibrations recorded in the field from a clover plant. (**a**) Incidental vibrations induced by walking. (**b**–**d**) vibrational signals emitted by unknown species. Spectrograms were generated in Seewave (R package) with Hanning windows of 1024 samples with 80% overlap

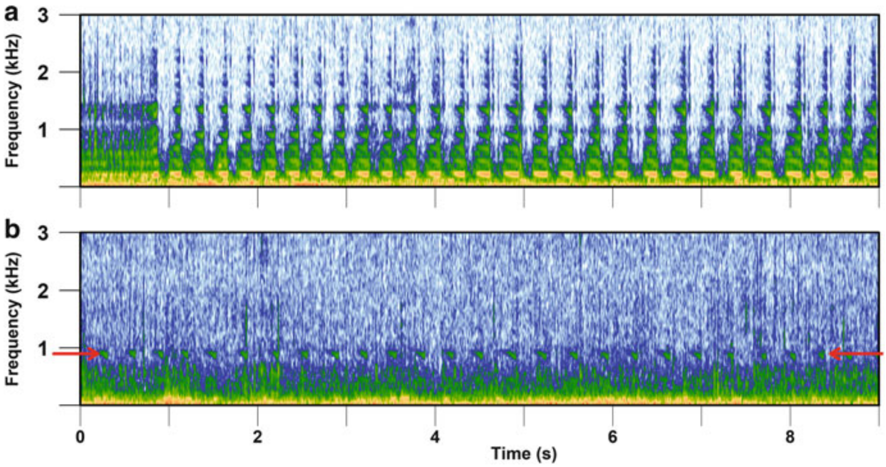

Fig. 8.6 Degradation of vibrational signals during transmission through the environment. (**a**) Male advertisement call of the leafhopper *Aphrodes bicincta* 'Dragonja' recorded in the field from a clover plant. (**b**) Male call (between red arrows) of the same species registered from the same position after a few minutes. Males of this species are using 'fly/jump/walk-call' strategy when moving through the habitat searching for the females. Although we did not see the male emitting these calls, from the complete recorded sequence, as well as from the signal time pattern, it is clear that the calls shown in (**a**) and (**b**) were emitted by the same male—in (**a**) most likely emitted on the focal clover plant and in (**b**) emitted somewhere else in the habitat. Spectrograms were generated in Seewave (R package) with Hanning windows of 1024 samples with 80% overlap

the latter are usually recorded close to the emitter (Fig. 8.6). Furthermore, pulse repetition time is often a species-specific character; however, it can be temperature-dependent (de Vrijer 1984). Because of the above stated difficulties, some care should be taken when dealing with unknown signals in order to not overestimate the number of species forming a vibrational community.

In soundscape studies, acoustic indices are often used to characterize acoustic communities and soundscapes (Sueur et al. 2014; Farina 2014). However, these indices are based on frequency and amplitude analyses and are therefore less appropriate for description of vibroscape. Moreover, they are also affected by signal-to-noise ratio (Desjonquères et al. 2015; Gasc et al. 2015). Nevertheless, simple variables like the number of different vibrational signals/VTUs per unit of time and the total number of vibrational signals/VTUs per unit of time (Desjonquères et al. 2015) can provide relevant information about the diversity and complexity of the vibrational community (Fig. 8.7). In addition, the ratio between the amplitude of the chosen vibrational signal used in communication and the amplitude of other vibrations (i.e. signal-to-noise ratio) may also provide useful information (Desjonquères et al. 2015).

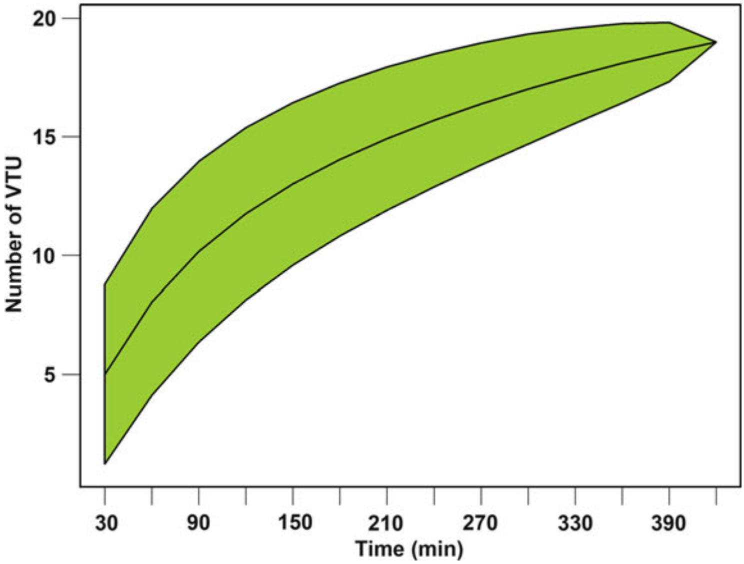

Fig. 8.7 Species accumulation curve of vibrational taxonomic units (VTU) registered in a hay meadow. Included are data from one laser vibrometer obtained during a 7-hour recording in July. Green area around the curve indicates 95% confidence interval. The curve approaches 20 VTUs; however, it does not reach the plateau

8.4 Concluding Remarks

We hope that this chapter will encourage more researchers in the field of biotremology to take their equipment to the field. The evolution of vibrational communication did not involve only an emitter-receiver dyad and did not take place on the vibration-damped table in a sound-proof room. We have no doubt that viewing vibrational communication in a more ecological context will open many important research questions. Although at present vibroscape research is still facing some technical challenges, the availability of equipment and progress in computer technology will hopefully make field studies more accessible in the future. In the present chapter, we borrowed and adapted the definitions from the soundscape research; however, with the development of vibroscape research we will probably have to conceive some new ones. So far, we have hardly opened a window to get a glimpse into the vibratory world and vibroscape is an undiscovered country. There is much opportunity for ground-breaking studies that will change our perception and understanding, not only of substrate-borne communication, but of the world around us.

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Chapter 9
Automated Vibrational Signal Recognition and Playback

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Abstract Behavioural manipulation of insects by exploiting the substrate-borne vibrational communication has gained significant attention in the past years. Advances in understanding mating behaviour, vibration registration and signal processing algorithms allow the design of an efficient low-cost autonomous system. Primary use of such an autonomous system is to study the vibrational communication in insects in which communication is based on rapid duetting interactions. More applied uses involve monitoring the insect population in a particular area, attracting and capturing or repelling the insect. One main habitat used by vibration-producing insects is woody and herbaceous plant tissues, which significantly affect the frequency-temporal parameters of the signals that are being transmitted through such substrates. Furthermore, amplitudes of such signals are typically low and subjected to masking by incidental noise of a biotic and abiotic origin. Despite the described challenges, proof-of-concept solutions exist and are briefly presented in this chapter.

Acronyms

AS	Autonomous system
DCT	Discrete cosine transform
FFT	Fast Fourier transform
FIR	Finite-impulse response
GMM	Gaussian mixture model
LFCC	Linear frequency cepstral coefficients

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LMS	Least mean square
LPC	Linear predictive coding
LPCC	Linear predictive cepstral coefficients
MFCC	Mel-frequency cepstral coefficients
MFSC	Mel-frequency spectral coefficients
MLP	Multilayer perceptron
PNN	Probabilistic neural network
SD	Standard deviation
SVM	Support vector machine
SNR	Signal to noise ratio
VQ	Vector quantization
WPD	Wavelet packet decomposition

9.1 Introduction

In recent years, the availability and widespread use of autonomous sound recorders and the resulting overwhelming amount of acoustic data, as well as the progress in computing and electronics and the development of algorithms for signal recognition, lead to many studies on automated detection and recognition of animal species that produce identifiable sounds in terrestrial and marine environments (Chesmore and Ohya 2004; Marques et al. 2012; Aide et al. 2013; Halkias et al. 2013; Bedoya et al. 2014; Lehmann et al. 2014; Potamitis 2014; Potamitis et al. 2014; Kalan et al. 2015). In comparison with automated recognition of air-borne sounds, automated identification of vibrational signals lags behind and has been mainly limited to few target insect species hidden in soil, plant tissues and man-made structures (reviewed in Mankin et al. 2008, 2011). It is indicative that while automated identification of air-borne sounds was primarily carried out to improve monitoring efficiency in order to provide better conservation measures, the main application for automated detection of vibrational signals was in insect pest management. Most of the studies focused on incidental vibrations induced by moving and feeding insects (Mankin et al. 2007; Pinhas et al. 2008; Potamitis et al. 2009; Mankin et al. 2011; Rach et al. 2013; Bilski et al. 2017) and only recently included also vibrational signals used in sexual communication (Jorge et al. 2013; Lampson et al. 2013; Korinšek et al. 2016; Mankin et al. 2016). This can be attributed to the raised awareness that vibrational communication is widespread among insects (Čokl and Virant-Doberlet 2003; Cocroft and Rodríguez 2005); however, most likely it also reflects the lack of reference libraries of species- and sex-specific vibrational signals needed for training the automated systems, as well as technical challenges associated with identification of signals usually emitted by a highly mobile male and transmitted through different substrates in the presence of high background noise.

While automated recognition systems can undoubtedly provide an invaluable approach in monitoring insect pests (Mankin et al. 2011), such systems also offer an ideal tool to study animal behaviour, in particular, coordinated reciprocal exchange of signals (Hammond et al. 2003; Blumstein et al. 2011; King 2015). In the majority of mating systems based on vibrational communication, mate recognition and location are based on species- and sex-specific signals exchanged in stereotyped duets with a species-specific structure that can differ greatly even among closely related species (Legendre et al. 2012; Derlink 2014; Cocroft et al. 2014; Polajnar et al. 2014; Boumans and Johnsen 2015; Kuhelj et al. 2015). Duetting is a dynamic interaction in which both partners modify their behaviour according to the partner's reply (Kovach et al. 2014). The structure of vibrational duets has only rarely been systematically studied; however, some recent studies revealed tight temporal coordination between the male call and female reply (Rohde et al. 2013; Kuhelj et al. 2015), as well as high plasticity in adapting male signalling behaviour to the female reply (Kuhelj et al. 2016).

Automated interactive recognition and playback systems provide a powerful tool to study rapid duetting interactions in real time (King 2015). Our work in designing an autonomous digital processing system capable of recognizing male vibrational calls and reproducing female replies has been focused on a currently non-described leafhopper species in the genus *Aphrodes* (Korinšek et al. 2016). In this species, a duet structure and male searching behaviour present a significant challenge for an automated system. Sexual communication is initiated by a male advertisement call, which is formed by continuously repeated species-specific elements that have broadband spectral characteristics, and the female reply has to appear in short intervals between these elements (Derlink 2014) (Fig. 9.1). While duetting, the male is approaching a stationary female, thus also inducing incidental vibrations by locomotion that span over a broad frequency range. In this chapter, we wish to provide some guidelines on how to approach designing such automated systems. We hope that this will encourage other researchers to apply such an approach in their own studies, since more detailed studies of vibrational duets may provide invaluable insights into the mechanisms of animal communication in general.

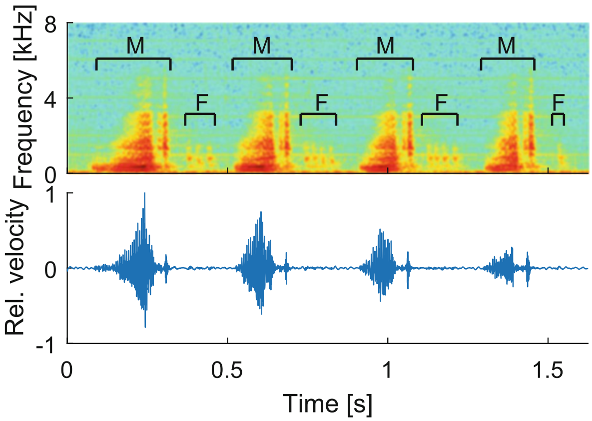

Fig. 9.1 Male-female duet of *Aphrodes bicincta* "Dragonja". M: pulse-chirp dyad in male call; F: female reply. The spectrogram is shown above the corresponding waveform

9.2 Architecture of the Autonomous System

The concept of an Autonomous system (AS) is depicted in (Fig. 9.2). The vibrational signals emitted by the insect are propagated via the substrate and registered by the vibrometer. The analogue signal from the vibrometer is amplified to a level suitable for further processing, filtered to the frequency band of interest and converted into a digital domain by the analogue front-end. The amplification and filtering are typically realized with discrete operational amplifiers (Gutiérrez et al. 2010; Rach et al. 2013; Korinšek 2017). After the analogue-to-digital conversion of the signals, a suitable microprocessor or a microcontroller performs the digital signal processing algorithm to discern the vibrational signals emitted by the insect from the incidental noise. The signal processing algorithm typically comprises four stages: preprocessing, feature extraction, activity detection and classification of the registered signals. The described stages are sufficient for monitoring and classification of species; however, attracting or repelling insects also requires a synchronized playback. In the next sections of this chapter, each block relevant to the AS (Fig. 9.2) will be looked at in a more detailed manner.

9.2.1 *Vibrometers*

Vibrational signals produced by insects typically have low amplitudes and require special vibrometers for registration (Mankin et al. 2011; Cocroft et al. 2014). Laser vibrometry measures a Doppler shift in a reflected laser beam to register the substrate vibrations. In contrast with contact methods, it does not influence the substrate (Cocroft and Rodríguez 2005) and has a high sensitivity in a wide frequency band (Zorović and Čokl 2015). The optics of such a measurement device is fairly complex due to typical realization with a two-beam Michelson interferometer, which also raises the price and the weight of a device. Potential low-cost alternatives are vibrometers based on the self-mixing effect (Giuliani et al. 2003), which occurs in a laser diode. Such an approach significantly reduces the complexity of the optics. By migrating the signal processing analogue circuit into the digital domain, further vibrometer cost reduction can be achieved (Magnani et al. 2012).

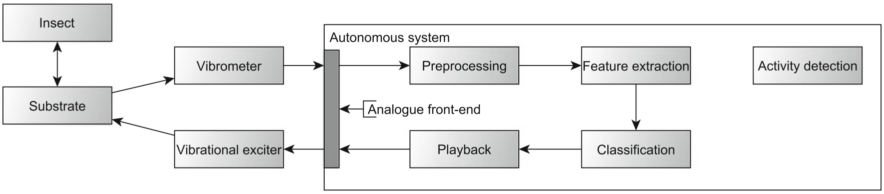

Fig. 9.2 Block diagram of the autonomous system

For a proper optical feedback from the substrate, a reflective tape is usually attached to it. In case of autonomous operation, the movement of the plant needs to be addressed which further increases the complexity of the AS.

Piezoelectric effect-based accelerometers are a low-cost alternative for sensing vibrational signals (Mankin et al. 2000; McNett et al. 2010; Lampson et al. 2013; Bilski et al. 2017) as long as their mass does not exceed a few percent of the substrate mass (Cocroft and Rodríguez 2005). A suitable charge amplifier is required to achieve a sufficient output signal and could be realized in the analogue front-end of an AS. To minimize the playback signal distortions, the frequency characteristics of such a sensor require a proper compensation, especially at higher frequencies where the self-resonances become prominent. Such a compensation could be achieved by pre-filtering the playback signal with an inverse frequency response of the sensor (see Sect. 9.7). The robustness against the movements of the plant when using such a sensor is significantly higher in comparison to optical methods.

Custom-made sensors were developed for detecting the wood boring pests such as the larva of *Rhynchophorus ferrugineus* which infests date palm trees. Such sensors comprise a microphone enclosed in a metallic tube that is pushed into a palm stem (Gutiérrez et al. 2010; Rach et al. 2013). The signal from such a sensor is amplified to a suitable level prior to processing using analogue amplifiers. Despite good sensitivity, the described sensors are not suitable for registering vibrational signals from herbaceous plants.

There are also other sensors such as piezoelectric gramophone cartridges (Tishechkin 2011). Despite the low cost and good sensitivity, the attachment to the plant is difficult (Cocroft and Rodríguez 2005), which limits the on-the-field applications.

In a *A. bicincta* "Dragonja" case study, the laser vibrometer was used to register the vibrational signals from the plant (Korinšek et al. 2016). During the design of the AS analogue front-end, several characteristics such as the noise floor, maximal voltage range and the input impedance must match the laser vibrometer output. Although the signals on the input of the AS were of good quality, a more robust and less expensive sensor such as the piezoelectric accelerometer would be more suitable for the on-the-field application.

9.2.2 Vibrational Exciters

Electrodynamic exciters are often used for vibrational signal playback as they are able to produce high-quality vibrational signals (Cocroft and Rodríguez 2005). Such exciters typically require an amplifier to achieve the full output range; however, they were also successfully driven from a phone output from a sound card in experiments with Hemiptera at 16-bit resolution and 42 kHz sample rate (Mazzoni et al. 2009; de Groot et al. 2011; Eriksson et al. 2012; Derlink et al. 2014; Polajnar et al. 2014; Kuhelj 2015). The AS used in experiments with *A. bicincta* "Dragonja" used an audio codec phone output to drive the electrodynamic exciter (Korinšek et al. 2016). The 32 kHz sample rate and 16-bit resolution were chosen to play the prerecorded female replies, which ensured a good quality of the playback signal at a small microcontroller interrupt load. Electrodynamic exciters were also successfully employed in vineyards to disrupt the mating of *Scaphoideus titanus* (Polajnar et al. 2016), but they may be less suitable for AS applications on smaller herbaceous plants where the contact between the exciter and the plant varies due to the plant movement.

Piezoelectric buzzers have been used as a low-cost alternative for producing vibrational signals (Mankin et al. 2013; Lujo et al. 2016). The reproduction of playback signals is subjected to the frequency characteristics of the buzzer, and a suitable frequency compensation is needed for quality signal reproduction (Cocroft et al. 2014). Playback trials with Psyllidae on a citrus plant have shown that a series of discrete tones produced with a microcontroller and played onto a plant with a buzzer were sufficient to influence animal behaviour (Mankin et al. 2013).

Simultaneous playback on multiple plants via air-borne signal (Rebar et al. 2012) could be used to introduce biotic and abiotic noise into the plant in a controlled manner and study its impact on animal behaviour. For industrial use with AS, it would be possible to detect the insect species in a particular area and then trigger the species-specific disruption playbacks, if required. This would minimize the sound pollution and potentially decrease the negative influence on the more beneficial dwellers on the plants.

9.3 Preprocessing

Signals produced by insects have a low amplitude and a limited bandwidth, which extends to several kHz (Čokl and Virant-Doberlet 2003). The bandwidth defines the AS sampling rate required for proper signal acquisition. The sample rate also defines the amount of memory required for buffering of acquired samples on the AS and the latency of the digital signal processing algorithm. For covering species with different frequency bands, downsampling could be performed in the AS algorithm to minimize the memory required for the signal buffering while maintaining the frequency resolution. A sufficient Signal to noise ratio (SNR), and hence the sensitivity of an analogue front-end, must also be achieved to be able to discern vibrational signals from the incidental noise. Typical sound card resolution used in Hemiptera behavioural experiments was 16 bits (Mazzoni et al. 2009; de Groot et al. 2011; Eriksson et al. 2012; Derlink et al. 2014; Polajnar et al. 2014; Kuhelj 2015), which could be used as orientation for AS design.

Stems of herbaceous (green) plants exhibit low-pass frequency characteristics with discrete resonances (Polajnar et al. 2012) that attenuate the characteristic high-frequency components of signals emitted by a particular species. The $1/f$ noise present in the registered spectrum further contributes to the spectral tilt, defined as the slope of the least squares linear fit to the log power spectrum (Goncharoff et al.

1996). To achieve a better classifier accuracy, the spectral tilt is usually compensated with a high-pass filter (Eq. 9.1); whereas the coefficients k of the filter can be determined statistically from the audio recordings of a particular species, using the first two autocorrelation coefficients (Bou-Ghazale and Hansen 2000). In Eq. 9.1, x and y are the filter input and output signals and n is the sample index.

$$y(n) = kx(n) + (1-k)x(n-1) \tag{9.1}$$

The signal is then split into overlapping frames that are used for the feature extraction. For the spectrum-based features, the frame size is determined as a trade-off between the frequency resolution and the computational load. The frame sizes are typically a power of two for feature extraction algorithms such as Fast Fourier transform (FFT) or the Wavelet packet decomposition (WPD). The temporal resolution of the features is determined by the overlap between the consecutive frames (usually governed by the algorithm processing time). Each frame is subjected to a window function, which minimizes the discontinuities at the edges of the frames and reduces the spectral leakage (Harris 1978). Typically, Hamming (Ganchev and Potamitis 2007; Pinhas et al. 2008; Potamitis et al. 2009) or Hann (Rach et al. 2013; Korinšek et al. 2016) windows were used.

9.3.1 Noise Reduction

In the absence of severe incidental noise, the signals registered from a plant also contain noise from the measurement equipment itself. While the negative impact on recognition accuracy was recognized (Lampson et al. 2013; Rach et al. 2013), solutions other than the cepstral mean subtraction (Ganchev and Potamitis 2007) were not applied. In a study of *A. bicincta* "Dragonja" (Korinšek 2017), a 20 dB difference in SNR was observed between the audio database that was used for the classifier learning and signals recorded during the laboratory behavioural experiments (Fig. 9.3c). To reduce the described noise, several computationally efficient methods exist. In the frequency domain, the methods are typically based on spectral subtraction (Boll 1979) and the minimum-mean square error short-time spectral amplitude estimation (Ephraim and Malah 1984). In the time domain, adaptive filtering methods (Widrow and Hoff 1960) could be used due to low computational load; however, a separate channel with a noisy signal is needed, but often not available. For wavelet-based features, the soft thresholding approach can be used (Donoho 1995). In case of an AS where the computational load is of concern, it is sensible to align the domain of the noise reduction method with the domain of the extracted features.

Most of the described noise reduction methods require an a-priori knowledge of the noise profile to operate correctly. For the AS such a profile could be determined during the calibration phase, which should be performed when there is no animal activity on the plant or its surroundings, and no adverse weather conditions such

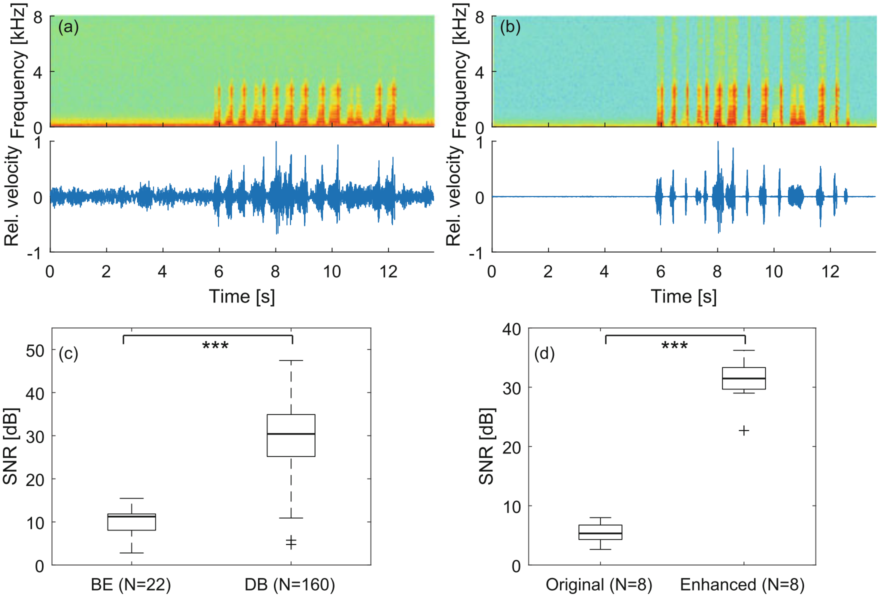

Fig. 9.3 Spectrogram (above) and oscillogram (below) comparison of an example of audio recording from the behavioural experiment before (**a**) and after (**b**) the spectral subtraction. (**c**) The difference in SNR between the audio database (DB) and recordings from the behavioural experiment (BE). Wilcoxon rank-sum test, $***p < 0.001$. (**d**) The difference in SNR before (Original) and after (Enhanced) the spectral subtraction on a subset of recordings from the behavioural experiment. Pairwise T-test, $***p < 0.001$. N = number of recordings. Figures adapted after Korinšek (2017)

as wind or rain (Cocroft and Rodríguez 2005; McNett et al. 2010). An activity detector such as described in Sect. 9.6 could be used for this purpose. If the AS has a wireless link (Rach et al. 2013), information from the local weather stations could be gathered to further improve the calibration window. Such information could be also used to determine if the AS needs to run at all, hence minimizing its power consumption.

In a study of *A. bicincta* "Dragonja", the spectral subtraction method was evaluated (Korinšek 2017). If $P_s(j\omega)$ is the spectrum of the input signal with an additive noise and $\overline{P_n(j\omega)}$ is the average input noise spectrum, then the enhanced signal spectrum $P_e(j\omega)$ can be calculated using Eqs. 9.2 and 9.3 (Berouti et al. 1979). Parameter α governs the amount of band-pass noise in the enhanced spectrum, and parameter β governs the residual noise floor.

$$D(j\omega) = P_s(j\omega) - \alpha\overline{P_n(j\omega)} \tag{9.2}$$

$$P_e(j\omega) = \begin{cases} D(j\omega) & \text{if } D(j\omega) > \beta\overline{P_n(j\omega)} \\ \beta\overline{P_n(j\omega)} & \text{otherwise} \end{cases} \tag{9.3}$$

The parameters where there was no significant distortion in the spectrum were $\alpha = 1$ and $\beta = 0.03$. The initial value of $\overline{P_n(j\omega)}$ was determined during the calibration process using Eq. 9.4 where l denotes the frame index. One thousand noise frames were averaged, the parameter k was 0.99. Equation 9.4 was also used to update the noise during the recognition algorithm execution in conjunction with an activity detector that detects the presence of an input signal or noise.

$$\overline{P_n^{(l)}(j\omega)} = (1-k)P_n^{(l)}(j\omega) + k\overline{P_n^{(l-1)}(j\omega)} \tag{9.4}$$

An activity detector was used (Eq. 9.5) to determine if the frame contained the noise or the signal. To increase the reliability of the detector, at least M consecutive γ values needed to be below the minimal threshold γ_{min} to avoid false positive detections. In this study, the parameters were: $M = 9$, $\gamma_{min} = 3\,\text{dB}$.

$$\gamma = 10\log_{10}\left(\frac{P_s(j\omega)}{\overline{P_n(j\omega)}}\right) \tag{9.5}$$

Simulations of the spectral subtraction method described above using audio files yielded an average 26 dB SNR improvement (Fig. 9.3d) without significant distortions of the enhanced signal (Fig. 9.3a, b). The real-time operation of the AS was also preserved using the described method.

9.4 Feature Extraction

Feature extraction (parameterization) transforms the relevant signal parameters to a compact form that can be presented efficiently to the classifier. Features from existing research involve Linear frequency cepstral coefficients (LFCC) (Ganchev and Potamitis 2007; Potamitis et al. 2009; Lampson et al. 2013), Linear predictive cepstral coefficients (LPCC) (Korinšek et al. 2016), Mel-frequency cepstral coefficients (MFCC) or features based on the wavelet transform (Potamitis et al. 2009; Jorge et al. 2013; Rach et al. 2013), Mel-frequency spectral coefficients (MFSC) (Pinhas et al. 2008) and even the bandwidth limited spectrogram (Mankin et al. 2016). Apart from standard features used in speech recognition, various signal statistics were successfully employed to discriminate the larvae eating from the incidental noise (Hussein et al. 2010; Bilski et al. 2017).

The LFCC and MFCC are spectrum-based features, and their computation comprises four steps (Fig. 9.4). First, the power spectrum is calculated using a FFT

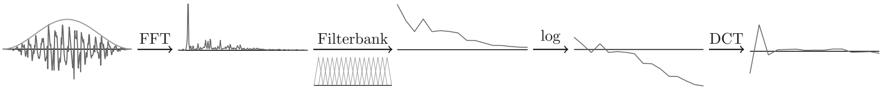

Fig. 9.4 LFCC feature extraction process

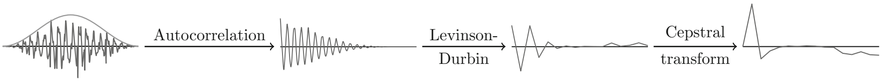

Fig. 9.5 LPCC feature extraction process

algorithm (Van Loan 1992) from a windowed frame obtained during the preprocessing phase (see Sect. 9.3). The envelope of the power spectrum is calculated by multiplying the power spectrum with a series of overlapping triangular band-pass filters. The central frequencies of the filters are distributed linearly over the frequency scale in case of LFCC features, or according to mel scale (Stevens et al. 1937) for MFCC features. The number of filters is smaller than the frame length to reduce the length of the feature vector. The resulting spectral envelope is further subjected to logarithm to compress the dynamic range, and to Discrete cosine transform (DCT) to compact the energies and decorrelate feature vector values (correlation occurs due to overlapping filters). From the resulting vector, the first coefficient, which is dependent on the amplitude of the signal, and the last few, which do not contain relevant information, are usually discarded. The computation of MFSC features is similar to MFCC, omitting the DCT step.

The LPCC features are an alternative to the MFCC or LFCC and are calculated in the time domain. Linear prediction from which the LPCC are derived predicts the current signal sample using a linear combination of past samples. The coefficients of the all-pole prediction filter are calculated by minimizing the mean square error between the actual and the predicted signal sample. The frequency response of such a filter models the spectral envelope of the signal. The procedure of extracting the LPCC features involves three steps (Fig. 9.5). The windowed frame is subjected to autocorrelation, followed by the Levinson–Durbin recursion (Rabiner and Juang 1993), to obtain linear prediction filter coefficients. As the coefficients are highly correlated, a cepstral transformation (Rabiner and Juang 1993) is used to obtain the final LPCC set.

The LFCC, MFCC and LPCC features are widely used in human speech recognition systems (Bimbot et al. 2004; Rabiner and Schafer 2007) and therefore suitable for species that emit syllable like vibrations. In terms of speech modelling accuracy, the LPCC features perform similarly to the MFCC (Bou-Ghazale and Hansen 2000). The computation analyses on the AS for *A. bicincta* “Dragonja” have shown that the LPCC features are computationally less demanding than LFCC for vectors with up to 24 coefficients (Korinšek et al. 2016).

The WPD (Mallat 1989) is an alternative to the features already described and has a benefit of providing a simultaneous localization in time and frequency. Hence, it is suitable for non-stationary signals emitted by insects when walking or feeding. In this method, the input signal is passed through a series of approximation and detail filters. These are, respectively, low-pass and high-pass filters of complementary bandwidths. The outputs of both filters are decimated by the factor two. Due to decimation, both output sub-bands contain half as many samples as the input signal. The process continues recursively for each decomposition level (Fig. 9.6). As the

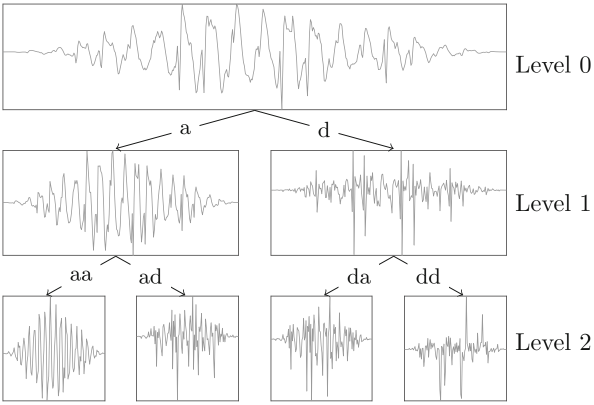

Fig. 9.6 The figure illustrates two level packet wavelet decomposition of the original signal at level 0. At each level of decomposition, the approximation (a) and the detail (d) coefficients are shown as well as their combinations (aa), (ad), (da) and (dd). The number of signal samples at each sub-band is halved

final features, energies of sub-bands that fall into a frequency range of interest at the final decomposition level are calculated (Rach et al. 2013). Another approach is to use decorrelated log energies (Potamitis et al. 2009).

Estimation of the relevant feature vector components can be determined using different metrics (Ganchev and Potamitis 2007; Potamitis et al. 2009) or from the model error curve (Korinšek et al. 2016). Finally, the classifier can be trained with different feature vectors while the optimal confusion matrix is being sought (Pinhas et al. 2008). Extending features with additional parameters, such as the duration or the dominant frequency of the signal emitted by the insect had a positive effect on the classification accuracy (Ganchev and Potamitis 2007; Potamitis et al. 2009).

9.5 Classification

The classification stage categorizes the feature vectors into classes. By training the classifier with a set of training feature vectors with corresponding class labels (supervised learning), it becomes capable of categorizing unseen feature vectors into a predefined set of classes. Adverse effects that increase the variability of feature vectors involve not only differences in signals from members of a single species, but also the position and time-dependent frequency characteristics of the individual substrate. For successful classifier training, large training sets are usually required that contain recordings from different representatives of a species captured on various plants. Recordings of the same species from different geographical locations should also be considered (Čokl and Virant-Doberlet 2003). Different incidental noise profiles also need to be presented to the classifier to increase its robustness.

Table 9.1 Different classification methods used for vibrational signal recognition

Species	Classifier	Recognition accuracy	Reference	Purpose
Euschistus servus	PNN	90.7%	Lampson et al. (2013)	Detection
Hylotrupes bajulus L.	SVM	89.7%	Bilski et al. (2017)	Detection
Nezara viridula	PNN	82.5%	Lampson et al. (2013)	Detection
Rhynchophorus ferrugineus	GMM	100%	Potamitis et al. (2009)	Detection
Sitophilus oryzae	GMM	100%	Potamitis et al. (2009)	Detection
Rhynchophorus ferrugineus	Template matching	90%	Rach et al. (2013)	Detection
Rhynchophorus ferrugineus	VQ	98.9%	Pinhas et al. (2008)	Detection
Diaphorina citri Kuwayama	Template matching	52%	Mankin et al. (2016)	Disruption
Aphrodes bicincta "Dragonja"	MLP	60%	Korinšek et al. (2016)	Attraction

Due to the large feature space, machine learning classification methods are typically used (Table 9.1). It should be noted that there were also successful applications of average template matching classifiers where the distances between the extracted signal features and the predefined feature templates are compared (Table 9.1). Although Table 9.1 contains single species classifiers, taxonomic categorization is also possible using the same algorithms (Ganchev and Potamitis 2007) by extending the number of classes.

The Gaussian mixture model (GMM) (Reynolds and Rose 1995) models the distribution of the feature vectors with a combination of weighted multivariate Gaussian distributions (Fig. 9.7). The multivariate Gaussian distribution is a generalization of a Gaussian distribution for higher dimensional data, and its parameters comprise the covariance matrix and the vector of mean values. The parameters of individual multivariate Gaussians and mixture weights are determined during the training phase by the expectation-maximization algorithm (McLachlan and Peel 2000). During the classification, an unknown feature vector is matched to the model by comparing the computed likelihoods of individual GMMs. The computational demand of the GMM can be significantly reduced by using decorrelated features such as MFCC, LFCC or LPCC (Bimbot et al. 2004). In such a case, the multivariate Gaussian distribution simplifies to a product of several univariate Gaussian distributions. Although this could have a negative impact on the recognition accuracy (Magdon-Ismail and Purnell 2012), it also reduces the amount of memory required to store the model. Typically, two GMMs were used: one for modelling the incidental noise and the second for modelling the vibrational signals emitted by

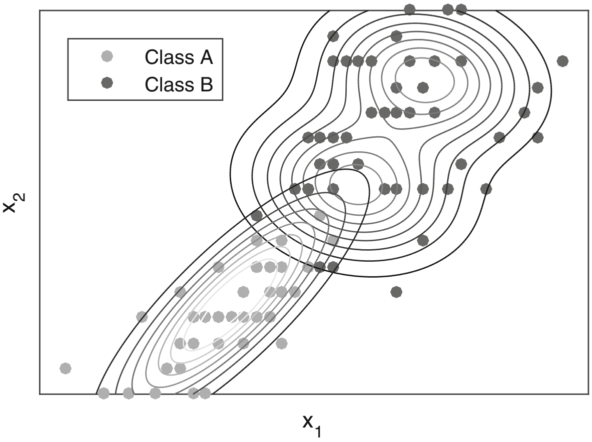

Fig. 9.7 Example of Gaussian mixture modelling. Two clusters, which correspond to classes A and B, comprise several feature vectors (dots) and each feature vector comprises two values x_1 and x_2. Class A is modelled with a single 2-variate Gaussian and class B is modelled with a mixture of two 2-variate Gaussians. The contours depict the individual 2-variate Gaussians

insects (Pinhas et al. 2008; Potamitis et al. 2009; Lampson et al. 2013; Korinšek et al. 2016) (Fig. 9.7). Although the GMM produced perfect results when using high-quality audio recordings (Potamitis et al. 2009), the tests on actual plants turned in favour of other methods (Pinhas et al. 2008; Lampson et al. 2013; Korinšek et al. 2016).

The Support vector machine (SVM) (Cortes and Vapnik 1995) is a binary or two-class classifier that uses the sequential minimum optimization method (Platt 1998) to set the optimal hyperplane that maximizes the margin between feature vectors of two distinct classes (Fig. 9.8). In case of non-linear boundaries between classes, the kernel trick can be used (Cortes and Vapnik 1995) to elevate the SVM operation to higher feature dimensions. For optimal SVM operation, a proper kernel and its parameters need to be chosen which usually involves a trial and error approach. In *Hylotrupes bajulus L.* and *A. bicincta* “Dragonja” studies, the radial basis function kernel produced the best SVM classifier accuracy (Bilski et al. 2017; Korinšek 2017).

The method has a benefit of converging towards a global minimum of the model’s cost function; however, depending on the problem it could happen that the number of support vectors required by the model approaches the number of samples in a training set. As shown in *A. bicincta* “Dragonja” studies, the SVM was 4% better than GMM in terms of recognition accuracy (Korinšek 2017). Although being computationally efficient, the method required a large amount of memory for storing the support vectors, which exceeded the capacities of the AS memory.

The Vector quantization (VQ) (Gray 1984) represents feature vector clusters with corresponding central vectors or centroids. A codebook is used to map the centroids to corresponding classes. During the training phase, the centroids are computed

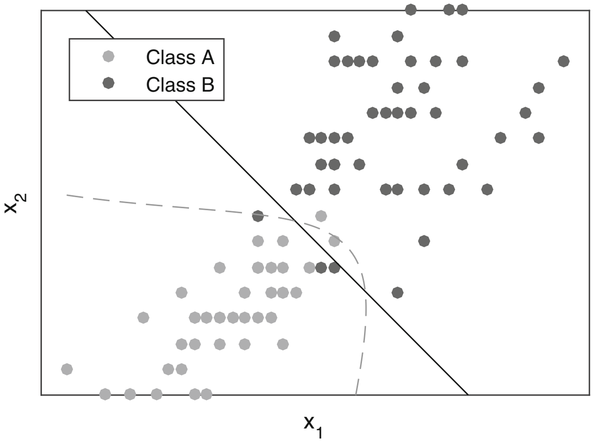

Fig. 9.8 Example of support vector machine modelling. Two clusters, which correspond to classes A and B, comprise several feature vectors (dots) and each feature vector comprises two values x_1 and x_2. The line that separates two classes illustrates an optimal hyperplane. The dotted line depicts a non-linear boundary, which is achieved when applying the kernel trick

with a suitable clustering algorithm (Linde et al. 1980). During classification, a minimal distance between the centroids and the unknown feature vector is sought and the corresponding class is determined from the codebook. The method is computationally less demanding than the GMM, while producing comparable accuracy in discerning the *Rhynchophorus ferrugineus* vibrational signals from the incidental noise (Pinhas et al. 2008).

The Multilayer perceptron (MLP) (Rosenblatt 1958) and the Probabilistic neural network (PNN) (Specht 1990) are representatives of neural network classifiers. The MLP comprises a fully connected network of perceptrons, where each perceptron represents a simple model of a biological neuron (Fig. 9.9) (McCulloch and Pitts 1943). The single perceptron is only capable of solving linearly separable problems; however, the MLP works as a universal function approximator. During the training phase, the weights and the biases of the individual perceptrons are adjusted by a suitable backpropagation method (LeCun et al. 1998). To achieve an optimal classification accuracy, the number of hidden layers, the number of perceptrons in hidden layers and the activation function need to be chosen. Since there is no definitive solution to determine the optimal structure of the MLP, different variations are cross-validated using a subset of the learning database (Bimbot et al. 2004). The PNN or the three layer MLP classifier outperformed the GMM in the ability to discern the different species-specific vibrational signals from the incidental noise by several percents (Lampson et al. 2013; Korinšek et al. 2016). Although the training of the PNN is faster in comparison to MLP, more memory is required to store the model and the classification is slower, hence the latter method is more suitable for the AS.

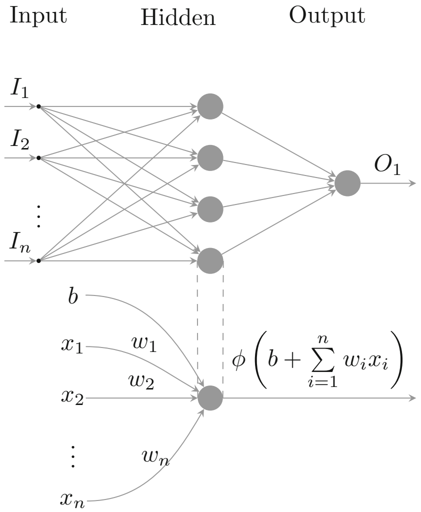

Fig. 9.9 The illustration shows a three layer, fully connected neural network comprised of the input, hidden and the output layer where I_n are the inputs and O_1 is the output. Although the image depicts a single output MLP, several can be added by increasing the number of output layer perceptrons. Each node in the network, depicted as a grey circle is a perceptron with input weights w_n, bias b and the activation function ϕ. The weights and bias are set during the training phase and determine if the perceptron output fires for a particular input feature vector or not

Most methods for species detection presented in Table 9.1 were implemented using high-level languages (Pinhas et al. 2008; Potamitis et al. 2009; Lampson et al. 2013; Bilski et al. 2017) and tested on a personal computer. The presented high-level approach is suitable for detection, but AS-based behavioural studies must follow the species-specific protocol and its real-time constraints. For example, the intervals between the male call and the female reply of *Diaphorina citri* Kuwayama were in a 0.1–0.4 s range (Lujo et al. 2016). In the case of *A. bicincta* “Dragonja”, the interval where the female response is expected was in a 47–175 ms range (Korinšek et al. 2016). In the latter case, the AS completed the signal analysis 4 ms after the end of a male call. Similar constraints were also observed in other Hemiptera (Derlink 2014). The trade-off between the recognition accuracy and the computational time of the classifier needs to be made when designing a low-cost AS to achieve appropriate response latencies. On the other hand, an improvement of recognition accuracy is possible by using different classifiers in parallel and combining their outputs (Ganchev and Potamitis 2007). While the detection or categorization of species requires a high recognition accuracy, this constraint is not always necessary. As shown in the *A. bicincta* “Dragonja” study (Korinšek et al. 2016), the live females had recognition accuracy as low as 8%, while still being able to successfully attract the males.

Preparation of data for the supervised learning of the classifiers involved manual labelling of the classes that correspond to a particular feature set by one or several independent experts (Pinhas et al. 2008; Lampson et al. 2013; Rach et al. 2013; Mankin et al. 2016; Bilski et al. 2017). In case of testing different features with multiple species, such a task is very time consuming and subject to human error. An alternative approach was proposed (Korinšek et al. 2016) that partly automates the training data preparation and could be extended to other species by providing a suitable reference algorithm, designed by an expert.

9.6 Activity Detection

The purpose of the activity detection algorithm is to prevent feeding the noise-based features into the classifier, which could produce false positive recognitions. The activity detector calculates its own set of features to determine if a particular frame contains any acoustic activity or only noise. In previous research, energy-based activity detectors were used (Ganchev and Potamitis 2007; Potamitis et al. 2009; Lampson et al. 2013) that are computationally more efficient than some more robust detectors (Ramírez et al. 2004; Moattar and Homayounpour 2009). The drawback of the energy-based detector is that it may trigger on signals with frequencies outside of the species-specific frequency band. In a laboratory setup, this is limited to the activity of the animals on the plant and the ambient noise, but in the field, this extends to biotic noise (Šturm 2015), due to the activity of other animals on the plant or its vicinity and adverse weather conditions such as wind or rain (Cocroft and Rodríguez 2005; McNett et al. 2010). A bandwidth-limited detector was presented (Korinšek et al. 2016) that could mitigate the adverse conditions; however, extensive field trials are needed to assess the efficiency.

9.7 Playback

The playback could be achieved by converting the digital signal, stored in memory of the AS, to analogue and amplifying it to a suitable level for the vibrational exciter. At first this may seem a simple task in comparison with the automated vibrational signal recognition; however, the effects of the substrate and the playback feedback still need to be considered. For behavioural experiments, the response audio file, latency, duration, amplitude and the number of skipped responses need to be adjustable.

A closed loop formed by the vibrational exciter, plant, vibrometer and the AS can be observed (Fig. 9.2). If a false positive recognition of the registered playback signal occurs, another playback is triggered that could result in system oscillations. To avoid such oscillations, the input of the AS could be muted during the playback. The mute duration should encompass all signal propagation times, including the latencies of AS signal processing buffers.

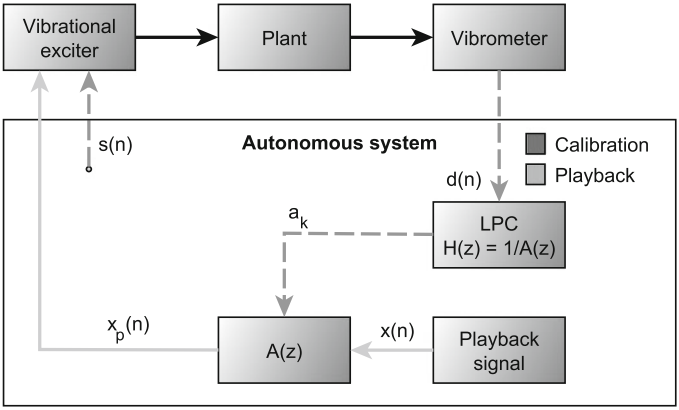

Fig. 9.10 Diagram of the LPC equalizer. By injecting the bandwidth-limited white noise $s(n)$ into the plant via vibrational exciter, it is possible to determine the inverse filter coefficients a_k from the measured signal $d(n)$ using the LPC method. The inverse filter $A(z)$ is applied to the original playback signal $x(n)$ to obtain the $x_p(n)$. Figures adapted after Korinšek (2017)

Herbaceous plant stems exhibit low-pass frequency characteristics with discrete resonances (Polajnar et al. 2012) that influence the parameters of the signal that is being transmitted through the plant (Cocroft and Rodríguez 2005). Apart from the inverse filtering solution in the frequency domain (Hill and Shadley 2001), there are not many applicable engineering solutions that would reduce the effect of the substrate on the transmission of the vibrational signals (Cocroft et al. 2014). To employ the inverse filtering approach on the AS efficiently, less computationally demanding approaches based on adaptive filtering (Madisetti 2009) and the autoregressive model (Rabiner and Juang 1993) were investigated (Korinšek 2017).

If an unknown system is injected with bandwidth-limited white noise, and its output is processed by the Linear predictive coding (LPC) method (see Sect. 9.4), the model of the spectral envelope $H(z)$ of the system can be obtained (Fig. 9.10). The LPC method models the spectral envelope $H(z)$ (Eq. 9.6) as an all-pole filter, and the coefficients a_k define the formants or resonances in the spectrum (Rabiner and Juang 1993). The unknown system in our case is the plant; therefore, the LPC approach should provide a good model for its resonances and the low-pass frequency characteristics.

$$H(z) = \frac{1}{A(z)} = \frac{1}{1 - \sum_{k=1}^{p} a_k z^{-k}} \tag{9.6}$$

The inverse function $A(z)$ represents a Finite-impulse response (FIR) filter in the time domain as seen from Eq. 9.7 and can be applied to the playback signal to achieve the inverse filtering.

$$x_p(n) = 1 - \sum_{k=1}^{p} a_k x(n-k) \tag{9.7}$$

The filter coefficients a_k are normally computed during the calibration phase; whereas the filtering of the playback signal can be done in real time. The group delay of the filter, which corresponds to half of the filter length, needs to be taken into account to achieve a proper playback latency. For greater equalizer robustness, several computations of filter coefficients a_k are performed and the average is used for final filtering of the playback signal.

The Least mean square (LMS) (Widrow and Hoff 1960) is computationally the simplest representative in a family of adaptive filters and can be used for plant equalization (Fig. 9.11). Using the input signal $s(n)$, the adaptive FIR filter iteratively updates its coefficients $\mathbf{h}(n)$ by minimizing the error $e(n)$ between the filter output signal $y(n)$ and the desired signal $d(n)$ according to Eqs. 9.8–9.10.

$$y(n) = \mathbf{h}(n)^{\top}\mathbf{s}(n) \tag{9.8}$$

$$e(n) = d(n) - y(n) \tag{9.9}$$

$$\mathbf{h}(n+1) = \mathbf{h}(n) + \mathbf{s}(n)\mu e(n) \tag{9.10}$$

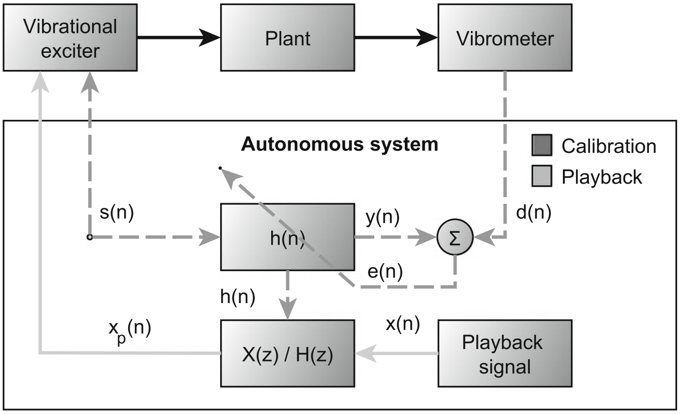

Fig. 9.11 Diagram of the LMS equalizer. The filter adapts its coefficients $\mathbf{h}(n)$, minimizing the error $e(n)$ between the output $y(n)$ and the desired signal $d(n)$. If the $s(n)$ is a bandwidth-limited white noise, the transfer function of the filter $H(z)$ begins to model the transfer function of the plant. The pre-filtered playback signal $x_p(n)$ can be calculated using the inverse of $H(z)$. Figures adapted after Korinšek (2017)

There are several different topologies for using such a filter that allow linear prediction, inverse modelling or system identification (Madisetti 2009). While the inverse modelling approach seems optimal, the required delay of the system is difficult to measure. The identification approach does not suffer from this problem; however, the coefficients of the adaptive filter model the transfer function of the plant instead of its inverse. The inverse filtering of the playback signal $x(n)$ can be calculated using Eq. 9.11. $H(j\omega)$ is the LMS filter frequency response, $X(j\omega)$ is the spectrum of the playback signal $x(n)$ and the $\mathscr{F}^{-1}$ operator denotes the inverse Fourier transform.

$$x_p(t) = \mathscr{F}^{-1}\left\{X(j\omega)H(j\omega)^{-1}\right\} \tag{9.11}$$

Stability of the LMS filter is governed by the step size μ, and the upper limit is defined by the trace of the autocorrelation matrix of the input signal (Madisetti 2009).

Similar to the LPC equalization, the LMS approach comprises the calibration and the playback filtering phase. During calibration, the transfer function of the plant is measured. The duration of the calibration is governed by the convergence of the error signal $e(n)$. From the computation perspective, the LMS equalization slightly surpasses the frequency domain inverse filtering method (Hill and Shadley 2001). The LMS equalizer applies the inverse filtering in the frequency domain, and the real-time filtering of the playback signal on the AS is not possible without increasing the playback latency. To maintain the low latency, the inverse filtering of the playback signal can be done during the calibration phase.

Computer simulations have shown that the LPC equalization method needs fewer filter coefficients (Fig. 9.12a) and equalizes the frequency characteristics of the plant better than the LMS (Fig. 9.12b). Tests on the plant using an AS with the LPC equalization method on a standard test setup (Korinšek 2017) have shown good plant equalization results using 64 filter coefficients (Fig. 9.12c). The delay of the playback signal was only 1 ms at 32 kHz sample rate. A proper level of the playback signal was required for an accurate calibration (Fig. 9.12d). If the level was too low, the incidental noise became dominant and if the level was too high, there was a substantial shaking of the plant, which influenced the laser beam reflection and hence the signal registration. The amplitude of the white noise required for calibration could be adjusted in a reference to the noise floor, provided by the methods described in this chapter (see Sect. 9.3.1).

It should be noted that the described equalization methods not only compensate for the plant frequency response but also for the AS output, the vibrational exciter, the vibrometer and the analogue front-end of the AS. This may produce undesired distortions of the playback signal if the frequency responses are not flat in a band of interest. Tests of LPC and LMS methods were conducted on a single plant, but the proposed methods may be adapted to other similar substrates. The influence of

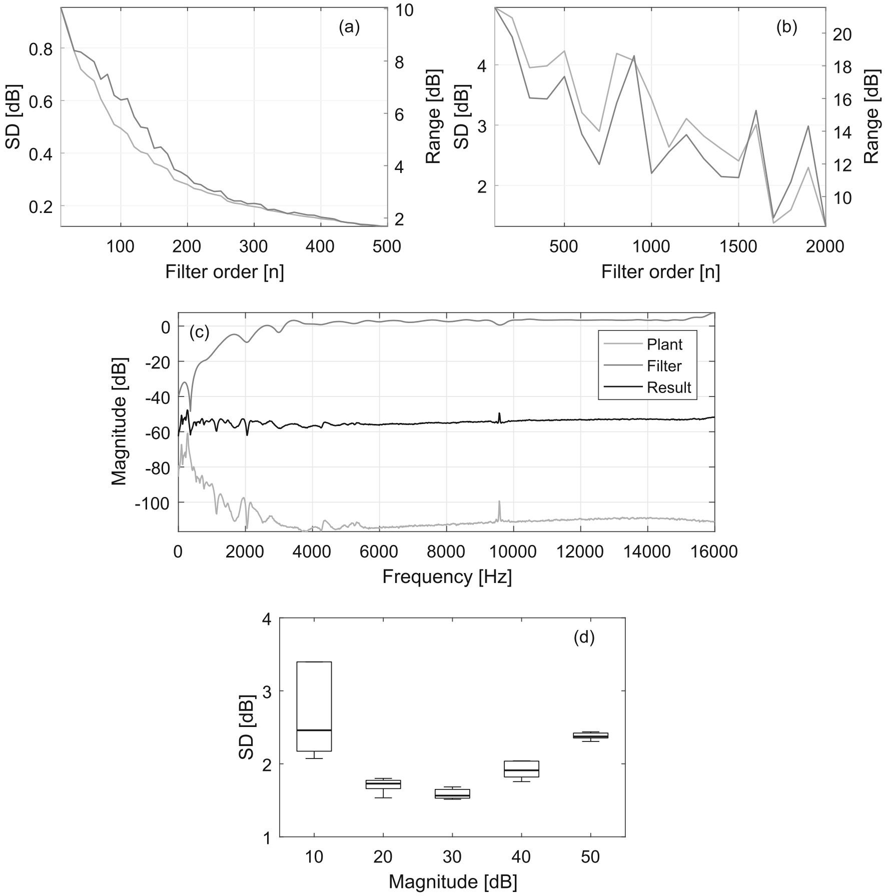

Fig. 9.12 (**a**) The average distribution of the standard deviation SD and the range of the equalized frequency characteristics of the plant at different filter orders using the LPC equalization. The number of simulations per filter order $N = 5$. (**b**) The average distribution of the standard deviation SD and the range of the equalized frequency characteristics of the plant at different filter orders using the LMS equalization. The number of simulations per filter order $N = 5$. (**c**) Test of the LPC equalizer on an actual plant. The graphs display the average frequency characteristics of the plant (plant), the average frequency characteristics of the equalization filter (filter) and the average equalized frequency characteristics (result) using a filter with 64 coefficients. The number of measurements $N = 5$. (**d**) Distribution of the standard deviation SD of the equalized frequency characteristics of the plant at different magnitudes of the playback noise. Number of measurements $N = 5$. Figures adapted after Korinšek (2017)

the equalization on the signals registered at different positions on the plant, and on various plants, still needs to be researched as well as the automated adjustment of the playback signal's amplitude and duration during the AS duetting.

9.8 Conclusion

This chapter presents an overview of some techniques and considerations for designing an AS. While the results of the existing studies look promising, further experiments in an outdoor environment remain a challenge. From the applied perspective, the disruption and detection approaches allow large plant area coverage and are suitable for on-the-field applications. The attraction approach is limited in this regard, but its usefulness is far greater in behavioural experiments. Knowledge of the insect behaviour and the signals they emit are of utmost importance for a successful AS design. Paradoxically, the behavioural study of some insects is not possible without a device that is capable of mimicking one of the participants in a fast alternating duet, while allowing the researcher to adjust different parameters of the experiment in a controlled manner. The technology has matured to the point where the design of such systems is possible (Rach et al. 2013; Korinšek et al. 2016; Mankin et al. 2016), which paves another step towards the understanding of animal behaviour.

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Part IV
Vibration Detection and Orientation

Chapter 10
Mechanisms of Vibration Detection in Mammals

Matthew J. Mason and Léa M. D. Wenger

Abstract Ground-borne vibrations are known to be used for a range of different purposes among mammals, but the sensory mechanisms used in their detection often remain unclear. Potential somatosensory receptors for low-frequency seismic cues include Pacinian and Meissner's corpuscles, while some species such as golden moles are believed to be adapted towards bone-conducted hearing. This chapter outlines the basic physiology underlying vibratory detection by these various means, and considers species in which particular mechanisms are likely to be prominent. Both the somatosensory and the auditory systems have been implicated in the vibratory sensitivity of elephants and spalacid mole rats, which are examined in detail as case studies. It may prove to be the case that interactions between these two modalities at a central level render any clear distinction impossible.

10.1 Introduction

Mammals can detect internal, self-generated vibrations arising from, for example, muscular activity. This kind of sensory feedback contributes to kinaesthesia (Proske 2006). Mammals are also capable of responding to vibrations originating outside the body. Within this exteroceptive category, the vibrations detected include sound waves travelling in air and water, but we shall limit our discussion, and our use of the word 'vibration', to oscillating signals passed to an animal by direct contact with a solid substrate. When transferred through the ground, such signals are referred to as seismic vibrations. Some mammals evidently exploit these vibratory cues to a much greater extent than others, and they will form the focus of this chapter.

Following a brief review of the uses to which vibratory sensitivity are put, we will explore the somatosensory and auditory mechanisms by which seismic vibrations

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can potentially be perceived in mammals, and how the two systems might interact. Elephants and mole rats are believed to use seismic vibrations for communication purposes, but there is as yet no consensus concerning which mechanism is used to detect them. We shall consider what is known about their vibratory reception as two separate case studies. We shall conclude with some suggestions for future research directions.

10.1.1 Use of Vibratory Information by Mammals

Vibrations travelling through the substrate might convey valuable information to a wide range of terrestrial mammals. Potential uses, some of which remain speculative at present, include the following:

- Detection of predators. Vibrations inadvertently made by the approach of another animal could provide a warning of danger (Gregory et al. 1986; Šklíba et al. 2008).
- Detection of prey. Herds of bison on the North American plains were said to be detectable at great distances by human hunters, who would place an ear to the ground to pick up vibrations (Vigne 1832). It has been proposed that felids might use similar vibratory cues to detect prey species (McIntyre 1962; O'Connell-Rodwell et al. 2001; Pawson et al. 2008). Desert golden moles might detect the presence of nearby prey such as termites through the vibrations that these invertebrates produce (Narins et al. 1997).
- Provision of information about the abiotic environment. Elephants respond behaviourally to rainstorms over 100 km away (Garstang et al. 2014), and seismic sensitivity might contribute to this (O'Connell-Rodwell et al. 2001). There have long been claims that some animals are able to predict forthcoming earthquakes, potentially through seismic sensitivity (Buskirk et al. 1981; Kirschvink 2000), but this is highly controversial: a study of satellite-tracked elephants provided no supporting evidence (Wikramanayake et al. 2006). Humans are certainly responsive to 'nuisance' structural vibrations, though (Guignard 1971).
- Provision of navigational cues. As discussed later, desert golden moles and spalacid mole rats appear to use seismic signals for navigational purposes (Narins et al. 1997; Kimchi et al. 2005).
- Vibrations as a channel for intentional communication. Many mammals exhibit foot-stomping or -drumming behaviours (Randall 2010), but other means of generating vibrations for communication purposes include banging the top of the head on the roof of a tunnel (Heth et al. 1987; Rado et al. 1987; Li et al. 2001; Hrouzková et al. 2013), tapping with incisor teeth (Giannoni et al. 1997) and the body slapping of seals (Shipley et al. 1992; Bishop et al. 2015). Although such vibrations are often used as intraspecific communication signals, this is not always the case: kangaroo rats, for example, foot-drum to deter snakes (Randall and Matocq 1997).

Although the availability of sensory cues is limited in tunnels underground, subterranean mammals are regularly exposed to ground vibrations, especially if they use their heads in digging. Seismic signals have been shown to propagate more effectively than airborne signals between subterranean burrow systems of the bathyergid mole rat *Georychus capensis* (Narins et al. 1992). It is therefore not surprising that subterranean species make use of seismic information for a range of purposes, including communication (Mason and Narins 2001, 2010). We shall consider several examples in this chapter.

Zoologists are documenting apparent seismic sensitivity in an increasingly wide range of mammals, but the mechanisms used by these animals to detect vibratory signals often remain unresolved. The somatosensory and auditory systems are both capable of detecting vibratory cues directly. How they achieve this is discussed in detail below.

10.2 Vibration Detection Using the Somatosensory System

Somatosensation is a generic term given to a diverse range of sensory modalities including touch, pain, body position and temperature. Transduction occurs in the peripheral endings of afferent axons, located around the body. These may or may not have associated accessory structures, depending on receptor type. The axons send information to the central nervous system, where it is ultimately processed by the somatosensory cortex.

The quadruplex model of touch sensation in the glabrous (hairless) skin of humans considers perception to be based on four channels of sensory information (Bolanowski et al. 1988; Fig. 10.1). Slowly adapting neurons produce a volley of action potentials in response to the onset of a stimulus, the rate of action potential generation only declining gradually if the stimulus is sustained. Merkel cell–neurite complexes (attached to SAI afferent fibres, detecting skin indentation edges) and Ruffini corpuscles (SAII afferents, detecting skin stretch) represent the transduction elements of the two slowly adapting channels (Johnson 2001). Rapidly adapting (RA) neurons respond to the onset of a stimulus, but their rate of response declines quickly if the stimulus is sustained. RA neurons therefore respond best to changes, and hence are well placed to detect skin vibrations. Meissner's and Pacinian corpuscles represent the transduction elements of the two rapidly adapting channels in humans: Meissner's corpuscles are the end organs of RA (also known as RAI) afferent fibres, while Pacinian corpuscles are the end organs of PC (or RAII) fibres. Collectively, these four mechanosensitive channels respond to vibratory signals from around 0.4 to over 500 Hz (Bolanowski et al. 1988). The transition from Meissner's-mediated to Pacinian-mediated vibratory detection occurs at around 20–25 Hz in humans holding vibratory objects (Brisben et al. 1999), so Pacinian corpuscles are regarded as the key vibratory receptors over most of the detectable range.

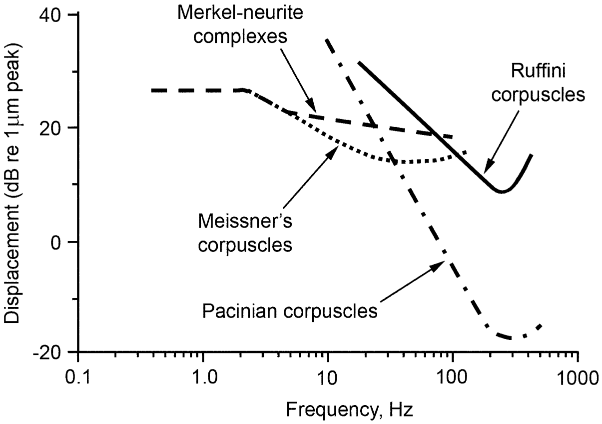

Fig. 10.1 Frequency–threshold characteristics of the four channels of vibrational somatosensation in humans. The curves are based on psychophysical responses obtained from the stimulation of glabrous skin, and have been labelled according to the somatosensory receptors believed responsible for the sensory transduction in each case. Meissner's and Pacinian corpuscles are the lowest threshold receptors over most of the perceptible range. Redrawn after Bolanowski et al. (1988), with the permission of the Acoustical Society of America. See that paper for information about how the original data were obtained

In hairy skin, vibrissal, guard and vellus hairs are collectively supplied by Merkel and Ruffini endings, free nerve endings and lanceolate nerve endings, although the density and pattern of innervation differ by species and hair type (Rice and Munger 1986; Rice et al. 1986). The application of local anaesthetic to hairy skin in humans reduces vibratory sensitivity below around 100 Hz (Merzenich and Harrington 1969; Mahns et al. 2006). This low-frequency sensitivity is conferred by hair follicle afferents. Higher frequency vibratory sensitivity is not affected by the anaesthetic, suggesting that the receptors responsible are more deeply situated: these are thought to be Pacinian corpuscles located in nearby joints or interosseous membranes. Vibratory thresholds in hairy skin may be an order of magnitude higher than in glabrous skin (Merzenich and Harrington 1969; Mahns et al. 2006) because of the deeper location of Pacinian corpuscles and the absence of Meissner's corpuscles.

Skin vibratory threshold at any given frequency will depend on factors including the individual thresholds of each receptor type present, receptor density, the skin area stimulated (influencing spatial summation) and skin temperature (Bolanowski et al. 1988). Lamellated receptors of various types are probably ubiquitous in mammalian skin, being found in monotremes (Proske et al. 1998) and marsupials (Loo and Halata 1985) as well as placental species. All mammals will therefore have some degree of somatosensory sensitivity to vibrations of frequencies from tens to hundreds of hertz, a range appropriate for the detection of biologically relevant seismic cues.

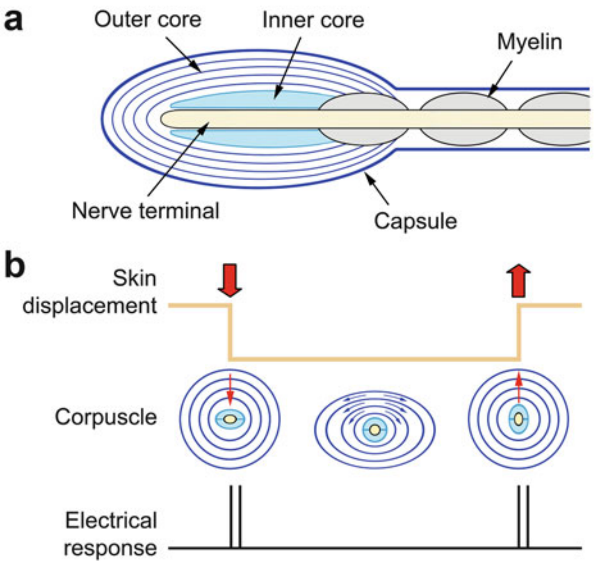

Fig. 10.2 Structure and function of a Pacinian corpuscle. (**a**) Diagrammatic representation of the histological structure of a Pacinian corpuscle in longitudinal section, illustrating its main features. (**b**) How the lamellar structure of a Pacinian corpuscle contributes to its rapidly adapting response, based on the model of Loewenstein and Skalak (1966). Time is represented as progressing from left to right. Left: When the skin is rapidly compressed, pressure (red arrows) passes through the corpuscle, shown in diagrammatic transverse section, to result in distortion of the central nerve terminal. This results in the generation of one or two action potentials, shown as spikes in the lower trace. Centre: With sustained skin indentation, the flow of viscous fluid between the lamellae (blue arrows) allows the nerve terminal to return to its normal shape. No further action potentials are generated. Right: When the external pressure is rapidly removed, the skin springs back to its former position. The central axon is distorted again, and a further one or two action potentials are generated

10.2.1 Pacinian Corpuscles

Pacinian corpuscles, also known as Vater–Pacinian corpuscles, are the largest somatosensory end organs in mammals, typically around 1 mm in length and so easily visible with the naked eye (Munger and Ide 1988). They are found in many places throughout the body, including within the deep dermis and subcutaneous tissues. The following histological description (see Fig. 10.2a) is largely based on the comprehensive review by Bell et al. (1994).

The inner core of a typical Pacinian corpuscle consists of 40–60 lamellae, formed from modified Schwann cells, arranged in two symmetrical halves around the unmyelinated terminal of an otherwise myelinated neuron. Outside the inner core is a ‘growth zone’, and external to that are around 30 lamellae of the outer core, formed from perineurium. The flattened cells forming each outer lamella are connected by means of tight junctions and the whole corpuscle is enclosed within a dense capsule.

Pacinian corpuscles increase in size throughout post-natal life through addition of lamellae (Cauna and Mannan 1959). The largest on record may be an 8-mm long corpuscle, found in the hand of a 65-year-old man (Roset-Llobet and Domenech-Mateu 1991).

Loewenstein and Skalak (1966) developed the classic model describing how the lamellar structure contributes to a Pacinian corpuscle's rapidly adapting response, illustrated diagrammatically in Fig. 10.2b. The lamellae are considered elastic, while the inter-lamellar fluid is viscous. If pressure is rapidly applied, force is transmitted through to the central nerve terminal, leading to distortion of its membrane, the opening of mechanically sensitive ion channels and the development of a depolarization called a generator potential. If the compression is sustained, there is time for the viscous fluid to shift within the corpuscle, and the central axon returns to its resting state. During rapid unloading, stored elastic energy is released and this deforms the axon again (in an orthogonal direction to before), leading to a second generator potential. If large enough, the generator potentials will elicit one or two action potentials during both the onset and offset of the applied force, but there is no sustained response to the static pressure in-between. If pressure is applied slowly, viscous fluid movements will have a 'cushioning' effect and the nerve terminal will not be excited.

The precise nature of the events within the nerve terminal that result in action potential generation are not well understood (see Bell et al. 1994, for a review). Recent models suggest that the orientation of the long axis of the Pacinian corpuscle with respect to the vibrations affects its response (Quindlen et al. 2015), and that the outer lamellae increase the relative strain experienced by the inner core, thus acting as a force amplifier (Quindlen et al. 2016). Increasing the number of layers augments this effect, and shifts the peak frequency response upwards. It follows that having a cluster of different-sized corpuscles would widen the overall frequency response from that area.

Pacinian corpuscles have characteristically U-shaped frequency response curves: they respond to vibrations from below 20 Hz to 1 kHz or above, with greatest sensitivity from 150 to 500 Hz, depending on the threshold criteria used (Sato 1961; Bolanowski and Zwislocki 1984). They are incredibly sensitive, responding to skin indentations as low as 10 nm at 200 Hz under some circumstances in humans (Brisben et al. 1999), but they have very low spatial resolution. Tapping lightly on the experimental table is a technique used by researchers to identify Pacinian responses (Brisben et al. 1999), and even background room vibrations can be enough to generate responses (Hunt 1961). A role for these receptors in exteroception certainly seems possible.

10.2.2 Meissner's Corpuscles

Meissner's corpuscles are found in dermal ridges of glabrous skin of the hands, feet and lips, very close to the base of the epidermis (Munger and Ide 1988). They are much smaller than Pacinian corpuscles, averaging 150 μm in length and 40–70 μm in diameter (Iggo and Andres 1982). They are also much more numerous, with smaller receptive fields, because they are located closer to the surface (Talbot et al. 1968). Originally described in primates, similar corpuscles in other species are sometimes referred to as 'Meissner-like' (Bolanowski and Pawson 2003). There are species differences in the distribution and density of these kinds of receptors (Brenowitz 1980; Bolanowski and Pawson 2003; Hoffmann et al. 2004; Verendeev et al. 2015).

A Meissner's corpuscle consists of a stack of lamellar Schwann cell discs, enclosed within a connective tissue capsule (Takahashi-Iwanaga and Shimoda 2003; Fig. 10.3). Up to nine nerve fibres supply a human corpuscle, winding their way between the discs and ramifying (Cauna 1956). The basement membrane of the epidermis is anchored to the capsule by collagen fibres. Takahashi-Iwanaga and Shimoda (2003) suggest that deformation of the epidermis will pull on the periphery of the corpuscle, which will deform and thereby activate the nerve terminals sandwiched between the Schwann cell layers. Sustained skin deformation allows time for the central portions of the discs to adjust their positions and relieve the tension on the nerve terminals, reducing the response. This would account for the rapidly adapting properties of Meissner's nerve fibres.

In humans, Meissner's corpuscles have relatively flat responses to vibratory frequencies from under 10 to around 100 Hz (Bolanowski et al. 1988; Rowe et al. 2005). They contribute to a sense of 'flutter' (Mountcastle et al. 1990). Meissner's corpuscles are associated with fine tactile discrimination, used, for example, when reading Braille (Phillips et al. 1990) or perhaps when assessing fruit texture (Hoffmann et al. 2004), but Johnson (2001) argues that their main function in humans is the provision of feedback for precision grip control, for example, in responding to slippage of objects between the fingers. Although Meissner's corpuscles have been considered as candidate seismic detectors in mammals (O'Connell-Rodwell 2007), this only seems likely for extremely low frequencies such as the 20 Hz signals said to be used by elephants (see later).

10.2.3 Vibratory Receptors in the Feet and Legs

Although there are species differences, the glabrous skin of fingers, toes and footpads is expected to contain rapidly adapting receptors such as Meissner's and Pacinian corpuscles. Pacinian corpuscles are also found in deeper, musculoskeletal locations such as around tendons, joints, interosseous membranes and in fascial planes between muscles (Adrian and Umrath 1929). These deeper receptors would presumably respond to vibrations arising from, for example, percussive footfalls, sending feedback to the central nervous system. However, because of their location, it has long been considered likely that receptors in the limbs are also used in the detection of ground-borne vibrations (Gray and Matthews 1951; McIntyre 1962; Lewis 1984; Gregory et al. 1986; Bouley et al. 2007).

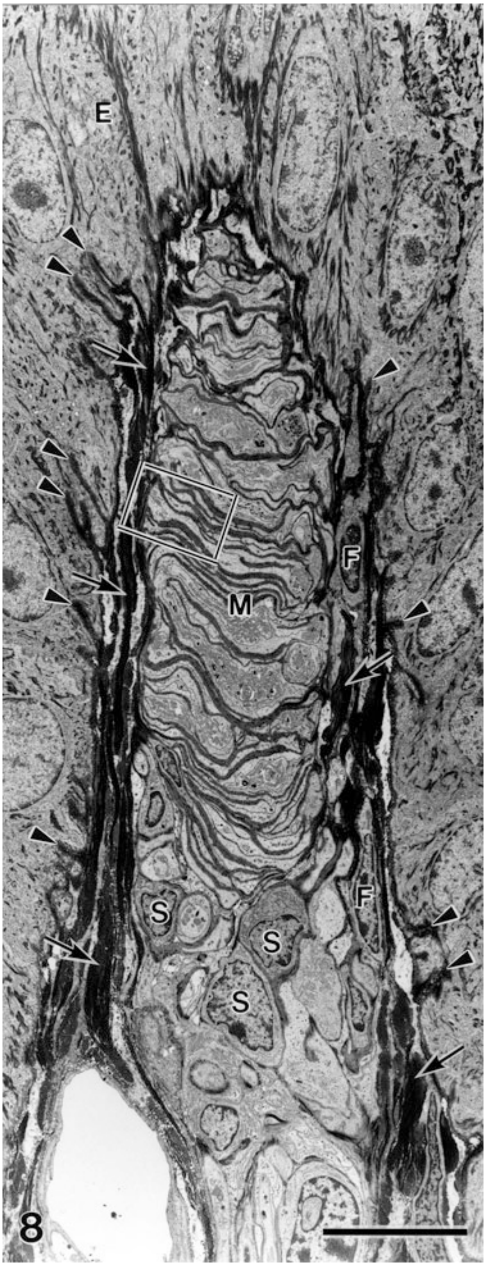

Fig. 10.3 Transmission electron micrograph representing monkey palmar skin. Longitudinal section of a dermal papilla containing a Meissner's corpuscle (M). Dermal collagen fibres stain dark with tannin (arrows). The epidermis (E) displays fine invaginations on the basal aspect (arrowheads). *F* fibroblasts. *S* Schwann cells associating with the Meissner's corpuscle. ×2200. Scale bar 10 μm. From Takahashi-Iwanaga and Shimoda (2003), with permission of Springer. Image kindly supplied by Prof. Hiromi Takahashi-Iwanaga. See original article for close-ups of the area marked with the rectangle

The cat forefoot contains over 660 Pacinian corpuscles, of which 80% are located in the toe region (Kumamoto et al. 1993b). They are found in the dermis and underlying tissue, including in the skin fold over the claw, and are also associated

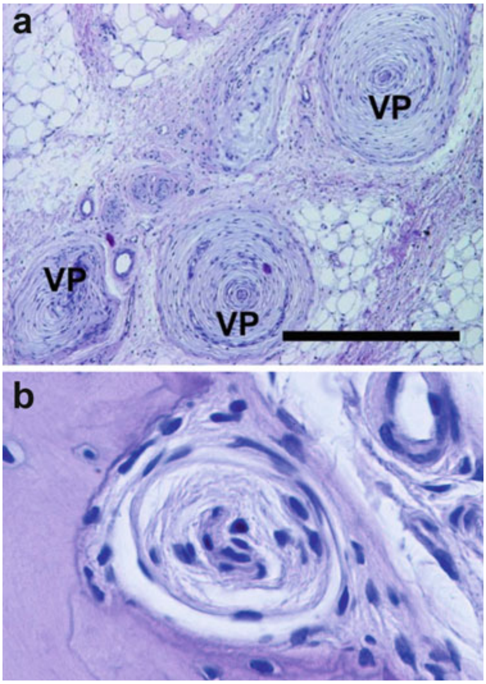

Fig. 10.4 Somatosensory receptors that have been implicated in the detection of seismic signals; not to scale. (**a**) Vater–Pacinian corpuscles (VP) within collagenous tissue of the foot cushion of the African elephant, *Loxodonta africana*, stained with Mayer's haematoxylin/eosin (H&E). Scale bar 500 µm. From Weissengruber et al. (2006), with permission of John Wiley and Sons. (**b**) A much smaller and simpler lamellated corpuscle from the paw of a mole rat *Spalax ehrenbergi* also stained with H&E. These corpuscles are typically 30–60 µm in diameter (Kimchi et al. 2005). Photomicrograph courtesy of Prof. Tali Kimchi

with muscles, tendons and periosteum. Around 300 corpuscles were found in the subcutaneous tissues of adult human hands, their highest density being in the metacarpophalangeal region and proximal phalanges (Stark et al. 1998). Based on counts made in foetuses, Brisben et al. (1999) estimate a total of 2400 in the human hand. Pacinian corpuscles are apparently not found in the dermis of the human foot, but are present in deeper tissues (Bojsen-Moller and Flagstad 1976; Jahss et al. 1992).

Studies of other species have tended to look for Pacinian corpuscles in the skin of the footpads. Pacinian corpuscles have been found in the dermis of the feet/paws of macaque (Kumamoto et al. 1993a), raccoon (Rice and Rasmusson 2000) and elephants (Weissengruber et al. 2006; Bouley et al. 2007), and in the palmar tubercles of the squirrel *Sciurus* (Brenowitz 1980). Simpler lamellated corpuscles were found in the dermis of the paws in the mole rat *Spalax* (Fig. 10.4b), but not in the vole *Microtus* (Kimchi et al. 2005). No Pacinian corpuscles were found in the paw skin of the ground squirrel *Ictidomys* (Brenowitz 1980), nor in the shrew *Suncus* (Kato et al. 1994), but they were found deep to the shrew's flexor tendons. It might be expected that sensitivity to external vibrations is greater in those species with dermal receptors, because of their more superficial location. However, it should be borne in mind that voles, shrews and ground squirrels are all relatively small: deeper lying Pacinian corpuscles might be sufficient if the foot is smaller. A comprehensive and systematic study of the location and number of Pacinian corpuscles in the feet of mammals is needed, taking into account possible effects of body size and phylogeny, before we can reliably conclude that any particular species is unusual. Even then, a high density of receptors does not necessarily relate to seismic exteroception: some animals (such as burrowers) might have a greater need than others for kinaesthetic feedback from their limbs.

10.2.4 Vibratory Receptors in the Nose

Simple, lamellated corpuscles have been described in the glabrous nasal skin of a diverse range of mammals (e.g. Loo and Halata 1985; Silverman et al. 1986; Klauer et al. 1997; Proske et al. 1998). Eimer's organs, found in the snout epidermis of most talpid moles, order Soricomorpha, are much more elaborate sensory structures (Catania 2000). Their function has been investigated most thoroughly in the bizarre star-nosed mole (*Condylura cristata*) from North America.

The star-nosed mole has two sets of 11 moveable, fleshy rays radiating outwards from the tip of its nose, each studded with 750–2000 Eimer's organs (Catania 1995). Each Eimer's organ contains 5–10 free neural processes, one Merkel cell–neurite complex, and in the dermis below, a single lamellated corpuscle (Catania 1995, 1996; Fig. 10.5). It has been estimated that five times more neurons supply the Eimer's organs on the nose of *Condylura* than the mechanoreceptors of the human hand (Catania and Kaas 1996). Some primary afferent fibres supplying the moles' noses are rapidly adapting and maximally sensitive to stimuli applied at 250–300 Hz (Marasco and Catania 2007). Their responses were found to be similar to those of Pacinian corpuscle fibres, although their receptive fields are very small. These are presumably the fibres supplying the lamellated corpuscles. The responses of some of these fibres were directional, in that they responded best to brushing movement of a hand-held probe running over the nose in a particular direction, but they were less strongly directional than some of the other fibre types.

As subterranean mammals, moles are prime candidates for seismic sensitivity, and the dense array of lamellated corpuscles on the snout seems very promising as a detection mechanism. However, unlike many subterranean rodents, talpid moles do not appear to communicate using seismic signals. Instead, the star of *Condylura* is used in the extremely rapid touch exploration of its surroundings. The mole typically touches the substrate 13 times per second with its nose, and if a food item is encountered, the time between identification and consumption can be as low as 120 ms (Catania and Remple 2005). If its invertebrate prey is not directly touched by the snout, it appears not to be detected (Catania and Kaas 1997). There is as yet no evidence to suggest that Eimer's organs are used in the detection of ground-borne vibrations.

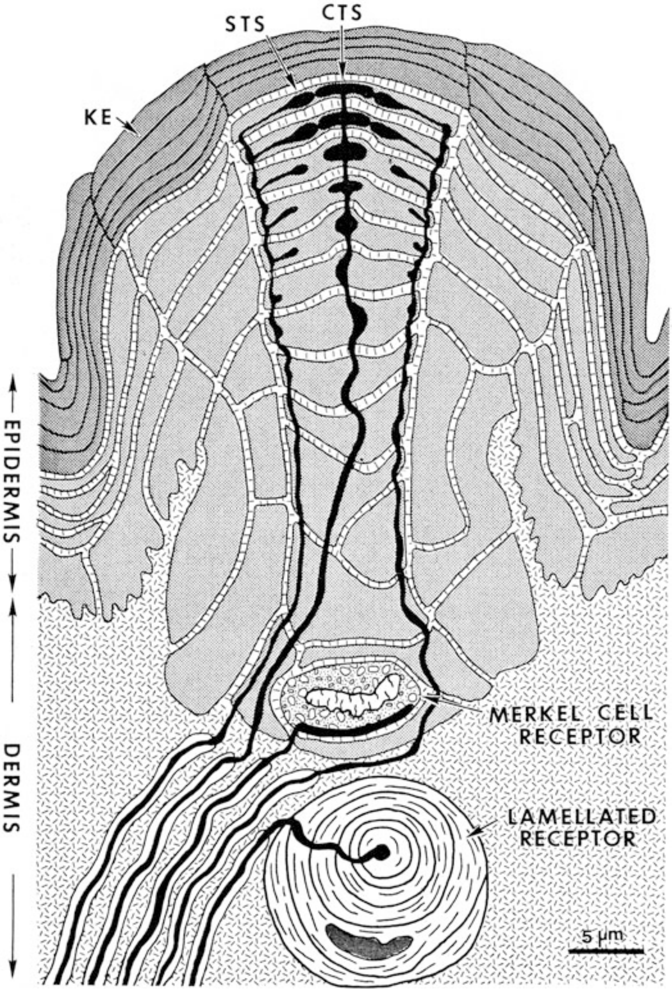

Fig. 10.5 Diagrammatic cross-section of the Eimer's organ of the star-nosed mole, *Condylura cristata*. CTS: terminal swelling of the central neural process; KE: keratinized epidermis; STS: terminal swelling of a satellite neural process. There are five to ten satellite processes in the organ as a whole. The lamellated receptor at the base of the organ is sensitive to vibrations. From Catania (1995), with kind permission of John Wiley and Sons

10.2.5 Vibratory Receptors Elsewhere in the Body

In addition to those associated with the skin and musculoskeletal system, Pacinian corpuscles are found in serous membranes of thorax and abdomen (Adrian and Umrath 1929; Sheehan 1933) and in many other locations around the body, including the walls of various organs such as pancreas and bladder, and the

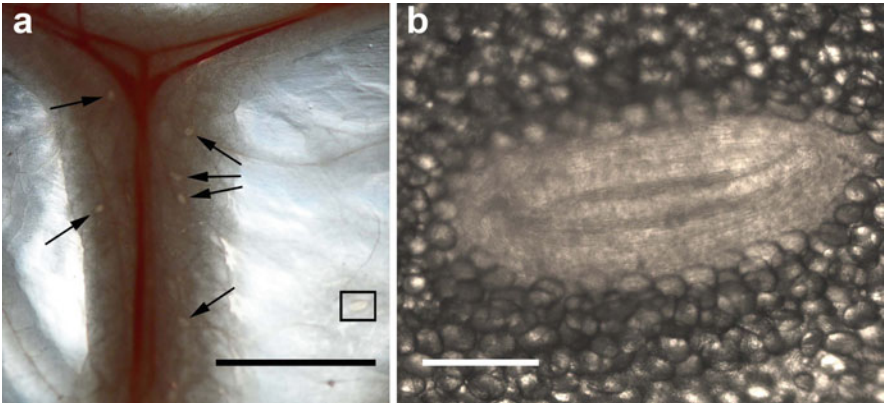

Fig. 10.6 Pacinian corpuscles in domestic cat abdominal mesentery. (**a**) Six Pacinian corpuscles within the fatty tissue surrounding the mesenteric blood vessels, indicated with arrows. These corpuscles were visible to the naked eye. One isolated corpuscle (boxed) lies within the mesentery web. Scale bar 10 mm. (**b**) Photomicrograph of the isolated corpuscle shown in the box in (**a**). Scale bar 0.25 mm. Specimen kindly made available by Ana Ortiz, Alun Williams and Matthew Rhodes, Department of Veterinary Medicine, University of Cambridge

middle ear cavity (reviewed by Bell et al. 1994). The function of visceral Pacinian corpuscles is generally believed to be interoceptive, perhaps relating to sensing organ distension (Shehata 1972; García-Suárez et al. 2010) or vasomotor regulation (Tuttle and McCleary 1975). The numerous Pacinian corpuscles found in cat mesentery (Fig. 10.6) have been the basis of many experimental studies. The turgid corpuscles are easily dissected out, and once isolated have the appearance of tiny, hairless gooseberries. Cats may have an unusual number of mesenteric Pacinian corpuscles, however: no mesenteric corpuscles were found in six other mammalian species, including the subterranean gopher, and there are very few in humans (Roberts 1959).

In humans exposed to low-frequency vibrations, the abdominal viscera will vibrate as a whole within the body with a resonance peak between 4 and 6 Hz (reviewed by von Gierke and Parker 1994). Under such circumstances, mesenteric receptors could act as inertial motion sensors (Lewis 1984). A seismic detection role for the mesenteric Pacinian corpuscles of cats has been suggested (McIntyre 1962; Pawson et al. 2008).

Blurring the distinction between sound and vibration, it is a common experience that very low-frequency airborne tones can sometimes be ‘felt’ deep within the body. Reviewing the literature, Moller and Pedersen (2004) concluded that the ears are the most sensitive detectors of very low-frequency airborne sound (<200 Hz) in humans, but at sound pressure levels 20–25 dB above threshold, vibrations can be perceived elsewhere. Noting the correlation between the responses of accelerometers stuck to human skin and reported sensations, Takahashi (2011) suggested that airborne sound of 50 Hz and below can be detected in the chest and abdomen. Mesenteric Pacinian corpuscles in cats can be excited by tuning forks placed on the pelvis or abdominal wall (Gray and Matthews 1951), raising the possibility that these receptors may be involved.

Experiments performed on both humans and cats have demonstrated somatosensory responses to low-frequency vibrations applied to the teeth (Dong et al. 1993; Robertson et al. 2003; Trulsson et al. 2010). Best sensitivity tends to be well under 100 Hz, although responses extend to higher frequencies. Periodontal ligament receptors, which include slow-adapting, Ruffini-like nerve endings, are among the mechanoreceptors implicated. In the naked mole rat *Heterocephalus glaber*, nearly a third of the enlarged somatosensory cortex is involved in the representation of the incisor teeth (Catania and Remple 2002). Tooth mechanoreceptors are most obviously involved in the control of biting, gnawing and mastication, but it is conceivable that the teeth also contribute to low-frequency vibratory exteroception in some subterranean mammals (Mason and Narins 2010).

10.3 Vibration Detection Using the Auditory System

The peripheral auditory system of mammals comprises the external ear canal, middle ear and inner ear. The tympanic membrane, at the interface of external and middle ears, vibrates in response to airborne sound. These vibrations are transferred via the three auditory ossicles (malleus, incus and stapes) to the oval window, the entrance to the fluid-filled inner ear. The inner ear includes the vestibular system, used in balance control, and also the cochlea. Within the cochlea, hair cells transduce vibrations into electrical impulses, ultimately resulting in signals passing via the auditory nerve to the central auditory regions of the brain.

Kangaroo rats (*Dipodomys spectabilis*) may detect ground-borne vibrations made by a neighbour's foot-drumming indirectly. Seismic vibrations radiate from the burrow walls into underground chambers as low-frequency airborne sound, and it is proposed that this sound is detected by the ears in the normal way (Randall and Lewis 1997). Airborne sound vibrations are not, however, the only possible means of stimulating the cochlea.

10.3.1 Bone-Conducted Hearing

It has long been appreciated that vibrations introduced directly into the skull can be perceived as sound, a form of hearing referred to as bone conduction. Bone conduction tests, commonly involving the application of a tuning fork to parts of the head, are often used in the diagnosis of conductive hearing loss in humans. If the ossicular system is compromised but the inner ear is intact, sound can still be perceived through bone conduction, although there will be significant airborne hearing loss. Bone conduction hearing aids have been developed to help patients with such conditions (Reinfeldt et al. 2015). In sensorineural hearing loss, by contrast, the inner ear or neural auditory pathways are damaged and bone-conducted hearing will be compromised too.

There are many routes by which skull vibrations can reach and stimulate the inner ear, thus there are many different modes of bone conduction (Tonndorf 1972; Stenfelt and Goode 2005). One mechanism of particular relevance to this chapter is ossicular inertial bone conduction. We provide here an intuitive model of how this works; for those seeking mathematical details, Lewis (1984) provides an excellent introduction to the physics of inertial motion sensors.

Let us consider the malleus and incus as one unit, tethered to the wall of the middle ear cavity at the anterior process of the malleus and short process of the incus. The line between these tether points is known as the anatomical axis of the ossicles, and we shall assume that the ossicles are restrained such that they can only rotate about this axis. Given these assumptions, it was pointed out by Bárány (1938) that if the centre of mass of the malleo-incus unit is located precisely on this rotatory axis and the skull is vibrated in the horizontal plane, the ossicles will vibrate together with the skull (Fig. 10.7a). Since there is then no relative movement between stapes and oval window, the response of the cochlea arising from this mode of bone conduction will be zero. Bárány (1938) believed that mammalian ossicular chains, including that of humans, have evolved such that the centre of mass coincides with the rotatory axis. This would minimize transmission of bone-conducted noise from, for example, chewing or talking, which would otherwise interfere with normal hearing. Ossicular inertial bone conduction in humans only

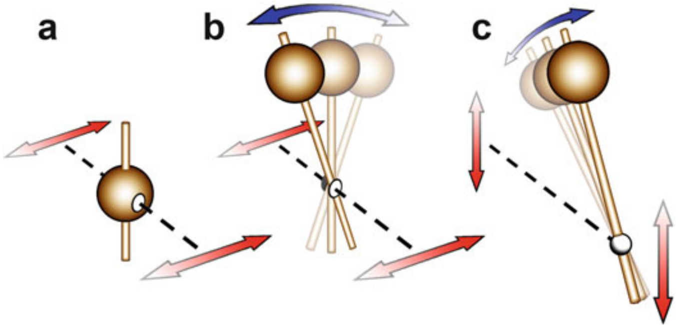

Fig. 10.7 Diagrammatic representations of the movement of mammalian auditory ossicles in response to skull vibrations. Red arrows represent skull vibrations, blue arrows represent relative movements of the ossicles which would translate into a bone-conduction response. (**a**) If the centre of mass of the ossicular chain (brown sphere) coincides with the ossicular rotatory axis (dotted line), the ossicles will vibrate with the skull. There is no relative movement, and hence no ossicular inertial bone conduction. (**b**) If the ossicular centre of mass is shifted dorsally, inertia will lead to relative movement in response to skull vibrations in the horizontal plane. This represents a simple mode of ossicular inertial bone conduction. (**c**) Here, the ossicles are not constrained to rotate about an axis but they are instead tethered at, e.g. the short process of the incus. If their centre of mass is rostro-dorsal to the tether point, these ossicles will be responsive to vertically oriented skull vibrations, as shown, as well as to horizontal vibrations. The ossicles of the golden mole *Chrysochloris* fall into this category

makes a significant contribution to the overall bone conduction response between around 1.5 and 3.5 kHz (Stenfelt 2006), frequencies too high to be useful in the detection of seismic vibrations.

However, if the centre of mass of the ossicles moves away from the rotatory axis, the inertia of the ossicles will cause relative movement between them and the vibrating skull (Fig. 10.7b). The stapes footplate is thus moved within the oval window, and the resulting vibrations of the cochlear fluid can be (frequency and amplitude permitting) processed and perceived as sound. Increasing mass will increase sensitivity, and will shift the peak response to lower frequencies.

10.3.2 Bone Conduction in Golden Moles

The human malleus weighs around 28 mg (Nummela 1995). Remarkably, that of the mouse-sized golden mole *Eremitalpa granti namibensis* weighs twice this (Mason et al. 2006), while the malleus in *Chrysospalax* species can exceed 200 mg (Mason 2003b). It has been proposed that the relatively enormous ossicles of golden moles have evolved specifically to enhance inertial bone conduction (Lombard and Hetherington 1993). This has been achieved not just by expanding malleus volume, but also in some species by increasing bone density (Mason et al. 2006). According to Bárány's (1938) model, increased mass in the ossicular chain will have no effect on bone conduction unless the centre of mass is displaced away from the rotatory axis. This is indeed the case in golden moles, in which the head of the malleus shows the most extreme hypertrophy, moving the centre of mass dorsal to the axis (Mason 2003a). This should render the ossicles responsive to lateral vibrations of the skull (Fig. 10.7b).

This model of inertial bone conduction is based on the notion that the ossicles are stiff, and constrained to rotate about the anatomical axis. However, there is considerable flexibility in elements of the mammalian ossicular chain (reviewed by Mason and Farr 2013), which allows the ossicles to vibrate in different modes according to frequency (Homma et al. 2009). Mason (2003a) proposed an alternative vibratory mode for the ossicles of the golden mole *Chrysochloris*, in which its single, main tether point is at the short process of the incus and the elongated malleus head is supported by a flexible, laminar anterior process. This should render the ossicles sensitive to both lateral and vertical vibrations of the skull (Fig. 10.7c).

The only experimental studies of ossicular vibration in golden moles were performed on post-mortem specimens of *Chrysochloris*. Willi et al. (2006a) found that the enlarged malleus of this species did indeed respond to skull vibrations, over the tested frequency range from 10 to 600 Hz. Both lateral and vertical vibrations of the skull resulted in relative movement of the malleus about a tether point at the short process of the incus, with lateral vibrations yielding the larger response. Resonant frequencies were between 70 and 200 Hz in different ears. In a second study, Willi et al. (2006b) demonstrated that airborne sound from 1 to 6 kHz excited the ossicular apparatus in a different mode, which was expected to minimize rotatory inertia, suggesting that these highly modified ears can respond to both seismic and airborne cues.

Of course, in order to make use of bone-conducted head vibrations, the cochlea of golden moles would have to be sensitive to the frequencies concerned. This has not been studied experimentally and there are no published audiograms for golden moles, so whether these animals really can detect and respond to low-frequency skull vibrations remains to be verified.

10.3.3 Localization of Seismic Cues in Eremitalpa

The Namib desert golden mole *Eremitalpa granti namibensis* finds its prey in isolated grassy tussocks, typically 20–25 m apart. The moles were shown to move from one tussock to the next in a non-random manner (Narins et al. 1997), but being blind and nocturnal they could not use visual cues for this feat of navigation. When the wind blows through the tussocks, ground vibrations are generated, which show a peak difference nearly 30 dB above background noise at around 300 Hz. It was suggested that this phenomenon allows the moles to use the tussocks as ‘seismic beacons’, while at shorter distances they might be able to detect vibrations made by their invertebrate prey within (Narins et al. 1997). To test the theory that the moles can localize tussocks through vibratory cues, Lewis et al. (2006) buried seismic thumpers programmed to reproduce tussock vibratory noise around a sandy arena, and studied the movements of golden moles released in the centre of the arena. Although the results overall were not statistically compelling, some individual moles did approach active thumpers and appeared to investigate them.

Tunnelling in *Eremitalpa* involves compression of the sand with the head and body (Gasc et al. 1986), in the process of which the skull will be exposed to ground vibrations. *Eremitalpa* also runs on the surface, but when it does so it periodically pauses to dip its head and shoulders into the loose sand (Fielden et al. 1992). It is believed that these ‘head dips’ are used to couple the head to the vibrating substrate, so as to make use of bone-conducted hearing (Narins et al. 1997).

Rayleigh waves propagate in sand at velocities of 40–50 m s^{-1} (Brownell 1977). Particle motion in Rayleigh waves follows an elliptical path in the vertical plane: at the top of the ellipse, close to the surface, the horizontal component is directed towards the source. The long axes of the expanded malleus heads are aligned approximately orthogonally to each other in *Eremitalpa* (see Fig. 10.8). Lewis et al. (2006) suggested that Rayleigh waves reaching the mole from a particular direction (other than directly in front or behind) might therefore excite right and left mallei differentially, which could potentially be used by the mole to localize the seismic source. In *Chrysochloris*, the elongated mallei are aligned more or less in parallel, but here again each ear could receive different cues. In response to horizontal vibration of the skull, one malleus would be expected to move medially relative to the skull as the other moves laterally, and this might translate into differences in the motion of right and left stapedes (Willi et al. 2006a).

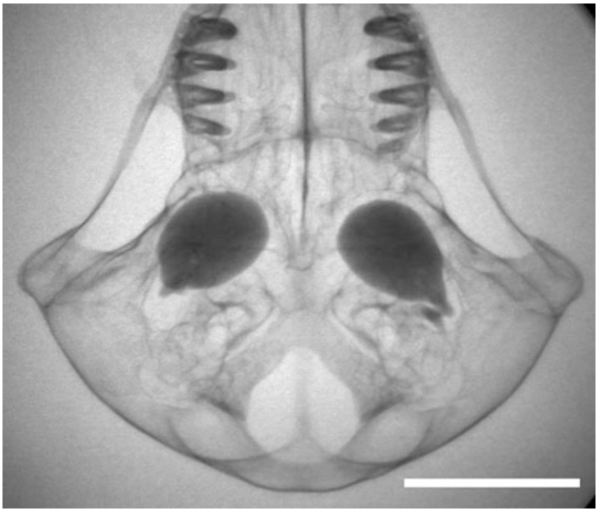

Fig. 10.8 Radiograph of the skull (minus rostral nasal region) of the desert golden mole *Eremitalpa granti granti* (Natural History Museum, London, specimen NHMUK 1939.482). The hypertrophied mallei are readily apparent as dense, black ovoids, with approximately orthogonal long axes. Scale bar 5 mm. Courtesy of the Trustees of the Natural History Museum, London

In a preliminary experiment, differences were found in the horizontal component of malleus velocity in *Chrysochloris*, in response to substrate vibratory cues emanating from different directions (Narins et al. 2016). Intriguingly, malleus velocity was highest in response to ipsilateral stimulation, and a time delay was found when comparing the response of a given ossicle to a seismic source presented at the same azimuth but on different sides of the animal. These results suggest that the middle ear in this species can indeed provide directional cues for seismic localization.

10.3.4 The Inner Ear as a Vibrational Detector

Bone-conducted sound, like air-conducted sound, is normally considered to be transduced by cochlear hair cells. However, there are other end organs in the inner ear capable of responding to vibrations. In frogs, the saccule confers acute low-frequency vibratory sensitivity (Koyama et al. 1982; Narins and Lewis 1984), subserving intraspecific communication in some species (Lewis and Narins 1985).

As in frogs, both the saccule and utricle of mammals, known as the otolith organs, contain otoconial masses made up of dense, inorganic crystals. Linear acceleration of the head creates relative movement between the otoconial mass and the wall of the inner ear, which excites the associated hair cells. This system thereby operates as an inertial motion detector. The otolith organs form part of the vestibular system, which has a role in the sense of balance and orientation. However, otolith organs in a range of mammals, including humans, can also respond to airborne sound and bone-conducted skull vibrations (Curthoys 2017). Recordings from primary afferent fibres in guinea pigs (*Cavia*) have revealed a high sensitivity of certain fibres from both utricle and saccule to bone-conducted vibrations (Curthoys et al. 2016). Responses of these fibres remain phase-locked to the stimulus even at high frequencies (1–2 kHz), at which the 'classical' otoconial inertial system for detecting acceleration should not be functional. It has therefore been proposed that hair cells within the otolith organs can also be activated by pressure waves in the fluid of the vestibule, elicited by airborne or bone-conducted sound stimuli (Curthoys and Grant 2015).

Otoconial masses in mammals are relatively small in comparison with those of frogs and can be invisible in some computed tomography scans of mammalian inner ears (Ekdale 2013). Compared to the majority of mammals, larger otoconial masses have been observed in the wallaby *Petrogale* and certain marine mammals (Gray 1906, 1908). It remains to be seen whether these confer an augmented sensitivity to low-frequency vibrations.

10.4 Interactions Between Touch and Hearing

Interactions between touch and hearing are well-known in humans. Studies have demonstrated improvements in diverse aspects of measured performance when sounds and vibrotactile cues of similar frequency are presented simultaneously (e.g. Ro et al. 2009; Wilson et al. 2010; Roy et al. 2017). Vibrotactile stimulation of the finger tips at 200 Hz can even lead to auditory cortex activation and an impression of sound (Caetano and Jousmäki 2006).

Many parts of the central nervous system involved in decision making will respond to multiple sensory modalities, but, as reviewed by Bizley et al. (2016), exactly where the sensory information is integrated is not always clear. In the gerbil *Meriones* and the vole *Microtus*, labelling experiments have shown direct connections between somatosensory and auditory cortical areas (Budinger et al. 2006; Campi et al. 2010). Budinger et al. linked this finding in the gerbil to its habit of foot-drumming, suggesting the possibility that vibratory and auditory cues generated by the drumming are centrally integrated. Overlap in the processing of touch and hearing complicates the task of revealing the relative roles of each sensory system.

Having reviewed the possible sensory mechanisms for the detection of vibrations in mammals, the case studies which follow examine in detail two groups of animals believed to make particular use of seismic sensitivity.

10.5 Case Study 1: Elephants

As reviewed elsewhere in this book (see Chap. 13), elephants are believed to make use of seismic signals. Elephant vocalization 'rumbles' create not just airborne sounds but also seismic components travelling as Rayleigh waves, both with a main frequency around 20 Hz, and foot stomps create similar seismic waves (O'Connell-Rodwell et al. 2000). There is behavioural evidence to suggest that wild elephants respond to these seismic signals (O'Connell-Rodwell et al. 2006, 2007)—but how are they detected?

10.5.1 Bone-Conducted Hearing in Elephants?

The audiogram of the Asian elephant, *Elephas maximus*, extends from 17 Hz to 10.5 kHz at 60 dB SPL (Heffner and Heffner 1980, 1982). Although sensory mechanisms other than airborne hearing could in principle have been used by the elephant in the detection of the lowest frequencies tested, it is generally accepted that the elephant auditory system is capable of responding to very low-frequency sound. This being the case, bone conduction could potentially be used to detect seismic vibrations at such frequencies.

Reuter et al. (1998) proposed that the 'massive skeleton and pillar-like bones' might be suitable for conducting ground vibrations to the elephant ear. In humans with superior semicircular canal dehiscence, a pathology that enhances bone-conducted hearing, a vibrating, low-frequency tuning fork applied to the ankle can sometimes be heard in the affected ear (Brantberg et al. 2015). Therefore, it would certainly seem possible that elephant ears receive vibratory cues via the skeleton.

Because elephant middle ear ossicles are so large, ossicular inertial bone conduction has been implicated as a means of vibratory detection (Reuter et al. 1998). However, middle ear structures scale with body size in mammals (Nummela 1995; Mason 2001), and so we would expect elephants to have large ossicles. As mentioned earlier, some golden moles have expanded malleus heads, shifting the ossicular mass distribution so as to favour bone-conducted hearing. Published illustrations of elephant ossicles (Hyrtl 1845; Fleischer 1973; Nummela 1995) show no signs of any such adaptations (Fig. 10.9): apart from their large size, elephant ossicles are surprisingly similar to those of humans and many other mammals. Within the inner ears of elephants, the cochleae show low-frequency characteristics but are described as being of a 'generalist' morphology (Ketten et al. 2016). No superior semicircular canal dehiscence or similar anatomical features that might enhance bone conduction were identified in *Elephas* (Brantberg et al. 2015). O'Connell et al. (1999) drew attention to the undivided perilymphatic foramen in elephants: the lack of a discrete cochlear canaliculus is an unusual feature now described in several other afrotherian mammals including golden moles (Mason et al. 2018), but its functional significance remains obscure.

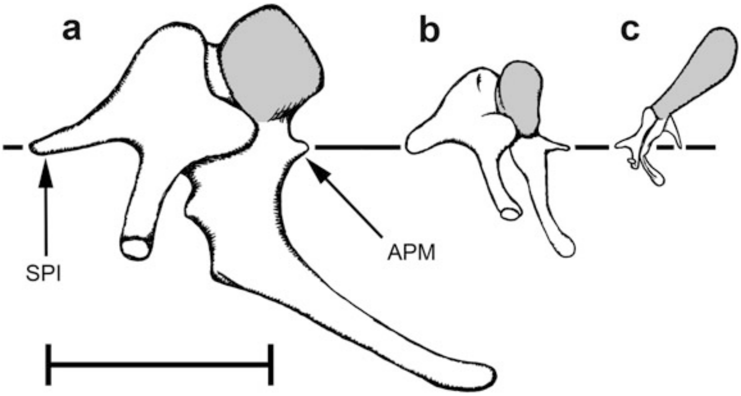

Fig. 10.9 Left malleus and incus of (**a**) African elephant, *Loxodonta africana*; (**b**) human; (**c**) golden mole, *Chrysochloris asiatica*. The head of the malleus in each case is shaded grey. The horizontal line represents the 'anatomical axis' passing between the short process of the incus (SPI) and the anterior process of the malleus (APM). Although the ossicles of the elephant are much larger, they are similar in morphology to human ossicles; the ossicular centre of mass lies close to the axis. In contrast, the expanded malleus head in *Chrysochloris* moves the centre of mass dorsally. Scale bar 10 mm. Illustration of elephant ossicles redrawn from Fleischer (1973), with kind permission of Franckh-Kosmos Verlags-GmbH & Co. KG

Ear canal occlusion augments low-frequency, bone-conducted hearing (Tondorf et al. 1966; Stenfelt et al. 2003). Elephants reportedly possess a sphincter muscle that can close their external auditory meatus (unpublished observations in O'Connell-Rodwell 2007). However, closure is said to be in response to tactile stimulation, indicative of a protective reflex rather than an auditory function.

10.5.2 Somatosensory Detection of Vibrations in Elephants?

In response to seismic cues, elephants can adopt what are interpreted as seismic 'listening' postures, including placing more weight on the front feet and lifting one foot such that it touches the ground only via the toes (Bouley et al. 2007). This has focused attention on the feet themselves in detecting seismic cues.

Elephants have thick, fibrous/fatty cushions at the bases of their feet, formed from modified hypodermis (Weissengruber et al. 2006). Pacinian corpuscles are found both within the fibrous component of the cushions (Fig. 10.4a) and in the dermis, while Meissner's corpuscles are present in the dermal papillae (Weissengruber et al. 2006). Often present in clusters, Pacinian corpuscles are more densely distributed towards the anterior and posterior regions of the feet than in the middle (Bouley et al. 2007). The fat cushions have been interpreted as helping to match the impedance of elephant to that of the ground, for improved transmission of vibratory cues, while the corpuscular receptors have been implicated in the reception of seismic signals

(O'Connell-Rodwell 2007). However, as Weissengruber et al. (2006) point out, similar cushions are found in other mammals too, including cattle and humans, in which they are believed to have a mechanical role in weight support and locomotion. Vibratory receptors are commonly found in mammalian feet, in which they may have a sensory feedback role relating to posture and movement. It is therefore not certain that the receptors in the elephant foot are there for exteroceptive purposes.

10.5.3 Vibratory Localization in Elephants

Distance to a vibratory source could be estimated by comparing the times of arrival of seismic signals with (slower) airborne signals (O'Connell-Rodwell et al. 2000), but azimuthal localization of seismic signals is more difficult to achieve. The wavelength of a 20-Hz vibration in the ground, as generated by elephants, was calculated to be 12.4 m (O'Connell-Rodwell et al. 2000). Although the 2–2.5 m distance between the legs is short compared to this wavelength, O'Connell-Rodwell et al. (2000) suggested that phase differences between somatosensory responses in different limbs might still be detectable. Of course, the elephant would need the central neural machinery to compare somatosensory information coming from different limbs and extract localization cues from this.

The ears of elephants are much closer together than the feet, and at low frequencies (below around 800 Hz in humans: Håkansson et al. 1994) the skull should behave as a rigid body, limiting the possibilities for sound localization through bone-conducted hearing. Auditory localization of seismic cues in elephants could, however, be based on differential ossicular motion in response to the vector components of vibration, as described above for golden moles.

10.5.4 Summary: Seismic Detection in Elephants

Although evidence suggests that elephants do produce and respond to seismic signals, how they are detected remains unknown. Large ear structures and low-frequency hearing are expected for animals of this size. Elephant foot structures have counterparts in other mammals, and vibratory receptors there could be used for locomotory feedback. This does not mean that ears, feet or both are not used to detect ground vibrations, but there is, as yet, no conclusive evidence.

One part of the elephant's body with no close counterpart in other mammals is the trunk. The trunk tip 'finger' of *Elephas* contains free nerve endings, vellus vibrissae (which do not protrude from the skin surface) and receptors including small Pacinian corpuscles and simpler, branched corpuscles in the superficial dermis (Rasmussen and Munger 1996). There are no clearly identifiable Meissner's corpuscles; *Loxodonta* also lacks Meissner's corpuscles in its trunk tip (Hoffmann et al. 2004). If the trunk tip was placed on the ground, its cutaneous receptors might be able to detect seismic vibrations, but it is not clear that elephants routinely do this.

Little attention seems to have been paid to vibratory receptors elsewhere in the elephant's body, including within the trunk itself (as opposed to the skin of its tip). This pendulous appendage can be compared to a 'heavy spring' suspended from its top end, which must presumably oscillate when the elephant is exposed to ground vibrations at appropriate frequencies. Might internal receptors exist that could detect these oscillations? The elephant would have dynamic control of this system through altering the position of the trunk and the tension of the muscles therein. This exciting sensory possibility remains unexplored.

10.6 Case Study 2: The Blind Mole Rat

Blind mole rats of the *Spalax ehrenbergi* superspecies (Rodentia; Spalacidae) have rudimentary eyes located under the skin that serve only for detection of photoperiod (Sanyal et al. 1990). Airborne hearing is restricted to sonic frequencies, with high thresholds even at the most sensitive frequencies, and *Spalax* has very poor sound localization abilities (Heffner and Heffner 1992). Territorial and aggressive, these solitary, subterranean mammals inhabit burrow systems that may be within a metre of a neighbouring system at the closest point, but the tunnels never intersect (Heth 1989). *Spalax* communicates with its neighbours through repeatedly thumping the top of its head on the roof of its burrow (Heth et al. 1987; Rado et al. 1987); the signals typically travel 3–4 m through the ground (Kimchi et al. 2005). The patterns of head thumping vary in rate and duration between chromosomal species (Heth et al. 1991), with the main energy of the seismic vibrations produced lying between 150 and 250 Hz (Rado et al. 1987).

10.6.1 Somatosensory Detection of Vibrations in Spalax?

Nevo et al. (1991) recorded evoked potentials, the brain's electrical response to sensory stimuli, from anaesthetized *Spalax* mole rats in perspex tunnels. Potentials evoked by tapping on the tunnel roof were reduced only slightly when white noise acoustic masking was introduced. No (or very low) evoked potentials were recorded when an adjacent tunnel on a separate table was tapped. Collectively, these results were taken to show that (a) the mole rat is responding largely to vibrations rather than to airborne stimuli associated with the tap, and (b) the mechanism of detection is essentially somatosensory, since the response was barely affected by white noise, which would be expected to mask bone-conducted hearing. In a supplemental experiment, the middle and inner ears of ten mole rats were surgically destroyed. These animals showed similar patterns of evoked potentials to intact animals, and 3–5 weeks later, some still responded to tapping on their tunnels by head thumping.

The fore- and hind paws of *Spalax* each contain 15–20 small, lamellated corpuscles, mostly in the glabrous skin of the toes (Kimchi et al. 2005; Fig. 10.4b). Kimchi et al. did not find similar receptors in voles. These corpuscles are currently the best candidate receptors for somatosensory seismic sensitivity in *Spalax*. Simple sensory corpuscles of lamellated or Meissner type are also found in the tips of dermal papillae within the rhinarium of this mole rat (Klauer et al. 1997). However, similar receptors are found in the nose of domestic rats too (Silverman et al. 1986), and rats are not known to communicate using seismic signals.

10.6.2 Bone-Conducted Hearing in Spalax?

The apparently clear-cut experimental results of Nevo et al. (1991) were strongly challenged by Rado et al. (1998), who performed very similar experiments. Rado et al. found auditory brainstem-evoked responses in *Spalax* occurring within 10 ms of the vibratory stimulus, and then much larger middle latency responses (MLRs) peaking at around 30 ms. Airborne clicks at 120 dB SPL produced responses of similar pattern, but of much smaller amplitude. Vibration-evoked responses were reduced in the presence of masking noise, and almost disappeared in surgically deafened animals. Rado et al. (1998) suggested that Nevo et al. (1991) might have presented their vibratory stimuli at rates high enough to lead to MLR habituation, which would result in a much smaller ‘auditory’ signal after averaging. Deafened animals, once recovered, were found to cease head drumming only over a period of several weeks.

Rado et al. (1998) found the largest responses when the lower jaws of their mole rats were firmly pressed to the floor of the vibrating perspex ‘tunnel’. This is significant in light of earlier observations of ‘jaw listening’ behaviour in *Spalax*, whereby the animal presses its cheek and mandible against the side of a tunnel when a neighbour is head thumping (Rado et al. 1989). Could ‘jaw listening’ mediate bone-conducted hearing?

Subterranean rodents lack notably large ear ossicles (Mason 2001), perhaps because of the vulnerability of an inertial system to gnawing and head knocking (Mason and Narins 2010). Rado et al. (1989) proposed an alternative mechanism for bone-conducted hearing in *Spalax*, involving the transmission of vibrations from the mandible to the incus and stapes, by means of a succession of unusual anatomical features in-between. The related *Eospalax* and *Tachyoryctes* mole rats produce seismic signals by head knocking in a similar way to *Spalax* (Li et al. 2001; Hrouzková et al. 2013), and ‘jaw listening’ has been reported in *Eospalax* (Mason et al. 2010). The anatomical features identified by Rado et al. in *Spalax* are not consistently present in these other genera, leading Mason et al. (2010) to challenge their purported role in bone conduction. Instead, Mason et al. (2010) proposed alternative pathways for bone-conducted hearing in these animals, one involving the cerebrospinal fluid.

10.6.3 Seismic Echolocation

In addition to intraspecific communication, *Spalax* is believed to use head thumps in a form of 'seismic echolocation' (Kimchi et al. 2005). Mole rats are able to choose the most efficient routes for bypassing obstacles interrupting their tunnels, such as ditches or stones (Kimchi and Terkel 2003a, b). This implies that the animals have a means of detecting and evaluating these obstacles. The digging mole rats produce regular, individual head knocks, which generate seismic waves with main energy from 250 to 300 Hz (Kimchi et al. 2005). These researchers proposed that the reflected seismic echoes are used by the animals to assess the obstacles: theoretically, this would be possible for objects over 7 cm in diameter. For an object 30 cm away, the mole rat would have to perceive the reflected echo within 7 ms of a head knock, a delay too small to allow the animal to reposition its head for 'jaw listening' (see earlier). An experiment performed by the same team showed that mole rats in a T-maze correctly identified the left/right location of either a head-thumping conspecific or a mechanical shaker over 80% of the time, but only if the vibrations were generated in the same wooden board that their feet were contacting (Kimchi et al. 2005). Kimchi et al. concluded that somatosensation, using the paw mechanoreceptors described above, must be used in the echolocation process.

10.6.4 Summary: Seismic Detection in Spalax

Based on similar experiments, Nevo et al. (1991) concluded that the somatosensory system is more important in the detection of vibrations by *Spalax*, while Rado et al. (1998) argued for an auditory route. However, it is interesting to note that both studies found a residual impact of the alternative sensory modality. In other words, these research teams agreed that both somatosensory and auditory detection are possible, but differed on their relative importance. Auditory and somatosensory information streams are integrated centrally in humans and other mammals (see earlier), and it would be surprising if this were not also the case in *Spalax*.

In these experiments, responses varied according to the nature of the presented stimuli and the position of the anaesthetized animal in the tunnel. Kimchi et al. (2005) pointed out that the amplitudes of the seismic signals used by mole rats for communication purposes could be 30- to 90-fold weaker than those used for seismic echolocation, owing to the greater distances involved. This implies that the relative importance of each sensory route for a mole rat in the wild could vary under different circumstances.

10.7 Conclusion

Because all mammals have ears and somatosensory receptors, both of which will respond to vibrations, all mammals must be able to perceive external vibrations of sufficient amplitude, within particular frequency bands. This exteroceptive sense takes on particular significance in certain groups, especially subterranean mammals which live in an environment where they are routinely exposed to ground vibrations, but where alternative sensory cues are limited. However, although increasing numbers of mammals are known to make use of seismic cues for a range of purposes, there has been little progress in recent years in understanding how these signals are detected. It is frustrating that this is still not clear even in well-studied species such as elephants and mole rats.

Mammalian biotremology studies have often developed by (a) finding an animal that seems to make use of ground vibrations, most obviously because it is observed to generate them, followed by (b) looking for sensory organs that underpin its supposed seismic sensitivity. The problem with this approach is that all mammals (presumably!) possess rapidly adapting somatosensory receptors such as Pacinian corpuscles, and all ears are capable of bone-conducted hearing. Seek, and ye shall find—but both somatosensory receptors and ears have roles other than the detection of ground vibrations, and so we cannot automatically infer that the receptor mechanism identified must be specialized for that purpose. It is notable that little work has been done comparing sensory thresholds of particular receptors to vibrational amplitudes measured in the field.

Some studies have taken the opposite approach, i.e. to identify unusual sensory structures that could represent adaptations to augment vibratory sensitivity, and then to look more closely at the behaviour of those animals that possess them. In the case of the star-nosed mole, it would appear that the highly sensitive nose is not, in fact, used to detect ground vibrations. However, we believe that it will be productive to apply this approach to other sensory organs. For example, two genera of talpid moles have been identified with grossly enlarged middle ear ossicles (Stroganov 1945; Mason 2006), but almost nothing is known about their habits. The hypertrophied ossicles suggest that bone-conducted hearing is augmented, by analogy with golden moles. These talpids therefore represent prime targets for behavioural studies that might reveal an ecological role for seismic sensitivity. The vestibular system can also respond to low-frequency vibrations: which mammals have the largest otoconial masses, and are they involved in seismic detection?

Surprisingly, there has apparently been no systematic survey of the density and location of Pacinian corpuscles in the feet and legs of mammals. Given that the orientation and size of Pacinian corpuscles are believed to affect their response characteristics (Quindlen et al. 2015, 2016), comparative information about these features would also be valuable. Such a study would allow us to test the hypotheses that animals such as elephants and spalacid mole rats really are specialized in this respect. It might also serve to identify other species previously unsuspected of making use of seismic cues.

Although such future studies could be very revealing, the association (or otherwise) of one particular sensory system with vibratory detection might well represent a misleading oversimplification. The roles of the somatosensory and auditory systems in seismic sensitivity may be conflated through the interaction of these sensory modalities within the central nervous system. It is exciting to contemplate the possibility that this interaction creates a new perception that cannot be identifiable as either touch or hearing.

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Chapter 11
Determining Vibroreceptor Sensitivity in Insects: The Influence of Experimental Parameters and Recording Techniques

Johannes Strauß, Nataša Stritih-Peljhan, and Reinhard Lakes-Harlan

Abstract Vibration detection in insects can be studied behaviourally and neurophysiologically. Specialised vibration receptor organs are often located in the legs. Determining the vibratory threshold is an important parameter to characterise an organs' physiological function. We argue that an experimental setup should consider the sensory organs' functional morphology to measure its maximal vibratory sensitivity. Experimental data show that vibratory thresholds determined by electrophysiological recordings can be influenced by several experimental parameters like leg position, direction of stimulation and attachment of appendages to the stimulator, which affect the mechanical energy reaching the receptor systems. The recording techniques with their different resolutions and the stimulus calibration may also influence the recorded sensitivity. We discuss physiological case studies, mainly from orthopteroid insects, to emphasise the importance of these experimental parameters on absolute sensitivity. We suggest that the experimental parameters with a known influence should be stated in electrophysiological investigations for comparisons of physiological data.

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11.1 Physiological Studies of Insect Vibration Receptor Organs

11.1.1 Vibration Signals in Insect Communication

The detection of vibrational stimuli is likely ubiquitous in arthropods, and numerous species of insects and spiders evolved intra-specific vibrational signalling for mate recognition and localisation (Gogala 1985; Barth 2002a; Greenfield 2002; Virant-Doberlet and Čokl 2004; Cocroft and Rodríguez 2005; Drosopoulos and Claridge 2006; Virant-Doberlet et al. 2006; Cocroft et al. 2014a). Here, we focus on studies of receptor systems detecting vibrational signals in insects. In a recent review, Hill and Wessel (2016) emphasise that usually substrate-borne vibration signals used in animal communication are vibration waves occurring at the boundary, or at a surface, between media. Arthropods predominantly detect such substrate-borne vibrations transmitted at boundaries between two distinct media, in most cases between a solid and air, which include ground substrates such as sand or soil, or different elements of plants like stems or leaves (Hill and Wessel 2016). These vibrations occur in complex waves, including Rayleigh waves and bending waves (Hill 2008; Michelsen 2014). Technically, 'vibration' is a broad term that can include compressional (longitudinal) waves in a certain medium like in the case of airborne sound, the displacement component of near-field sound, direct contact vibrations and surface-borne vibrations like Rayleigh, Love or bending waves (Markl 1983; Gogala 1985; Dambach 1989; Hill and Wessel 2016; Mason and Pollack 2016; Yack 2016). Here, we refer to surface or surface-borne vibrations, and use substrate vibrations equivalently, in line with the biotremological terminology (Hill and Wessel 2016). The experiments discussed below all used stimulations by sinusoidal vibrations as a vibratory stimulus.

11.1.2 Vibroreceptor Organs in Insects: From Neuroanatomy to Sensory Physiology

The vibrational signals and associated vibrational behaviours of signallers and receivers have been widely studied in insects. In addition, several sensilla and organ types are involved in the detection of surface-borne vibrations, especially internal chordotonal or scolopidial sensilla, but also campaniform sensilla, and possibly sensory hairs (Kühne 1982a; Lakes-Harlan and Strauß 2014; Yack 2016). The functional morphology of the sensory organs determines the specific stimulus modality causing mechanical transduction, in response to sound pressure or sound pressure differences (in tympanal organs), particle displacement of sound (e.g. by the antennal Johnston's organ of insects) or surface-borne vibration waves (Römer and Tautz 1992; Field and Matheson 1998; Yack 2004, 2016; Hill 2008; Kamikouchi and Ishikawa 2016). Chordotonal sensilla are units consisting of one to four sensory

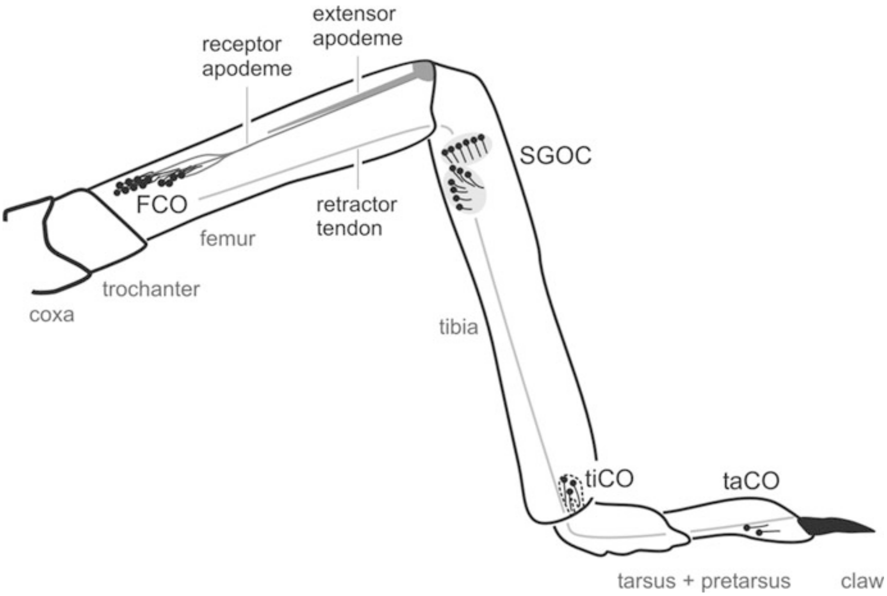

Fig. 11.1 Schematic drawing of chordotonal organs in the leg of an orthopteroid insect. Chordotonal organs shown are the femoral chordotonal organ (FCO), the subgenual organ complex (SGOC), the tibio-tarsal chordotonal organ (tiCO) and the tarsal–pretarsal chordotonal organ (taCO). Sensory organs are attached to apodemes or inserted in cellular masses (grey ovals). Sensory neurons are shown in black, apodemes in dark grey, tendons in grey and connective strands of the tibio-tarsal chordotonal organ (tiCO) in white with hatched line

neurons with additional non-neuronal cells, and these sensory neurons are activated by a mechanical force stretching or tilting the dendrite (Keil 1997; Field and Matheson 1998; Lakes-Harlan and Strauß 2014; Hummel et al. 2016). Different chordotonal organs responsive to surface-borne vibrations are found in the insect body and its appendages, especially the legs (Fig. 11.1). These sensory organs have been studied as crucial receptor elements for vibrational communication, with respect to both functional morphology and sensory physiology (e.g. Autrum and Schneider 1948; Kalmring 1985; Shaw 1994; Čokl et al. 2006; Virant-Doberlet et al. 2006; Lakes-Harlan and Strauß 2014). Generally in physiological investigations, legs are brought distally into contact with a generator of sinusoidal vibrations with variable frequencies and intensities. This can be achieved by animals resting with their legs on a vibrating platform or desk, or by individual legs contacting a mini-shaker. Often, a rod is attached to the mini-shaker that connects to one or more legs (Fig. 11.2). The neurophysiological activation of vibratory receptor neurons is recorded from the sensory nerve proximally in the leg with wire, hook or suction electrodes, or from individual axons near the entrance site of the nerve to the segmental ganglion with glass electrodes (Fig. 11.2). Scolopidial sensilla as well as campaniform sensilla contain primary sensory neurons, which extend

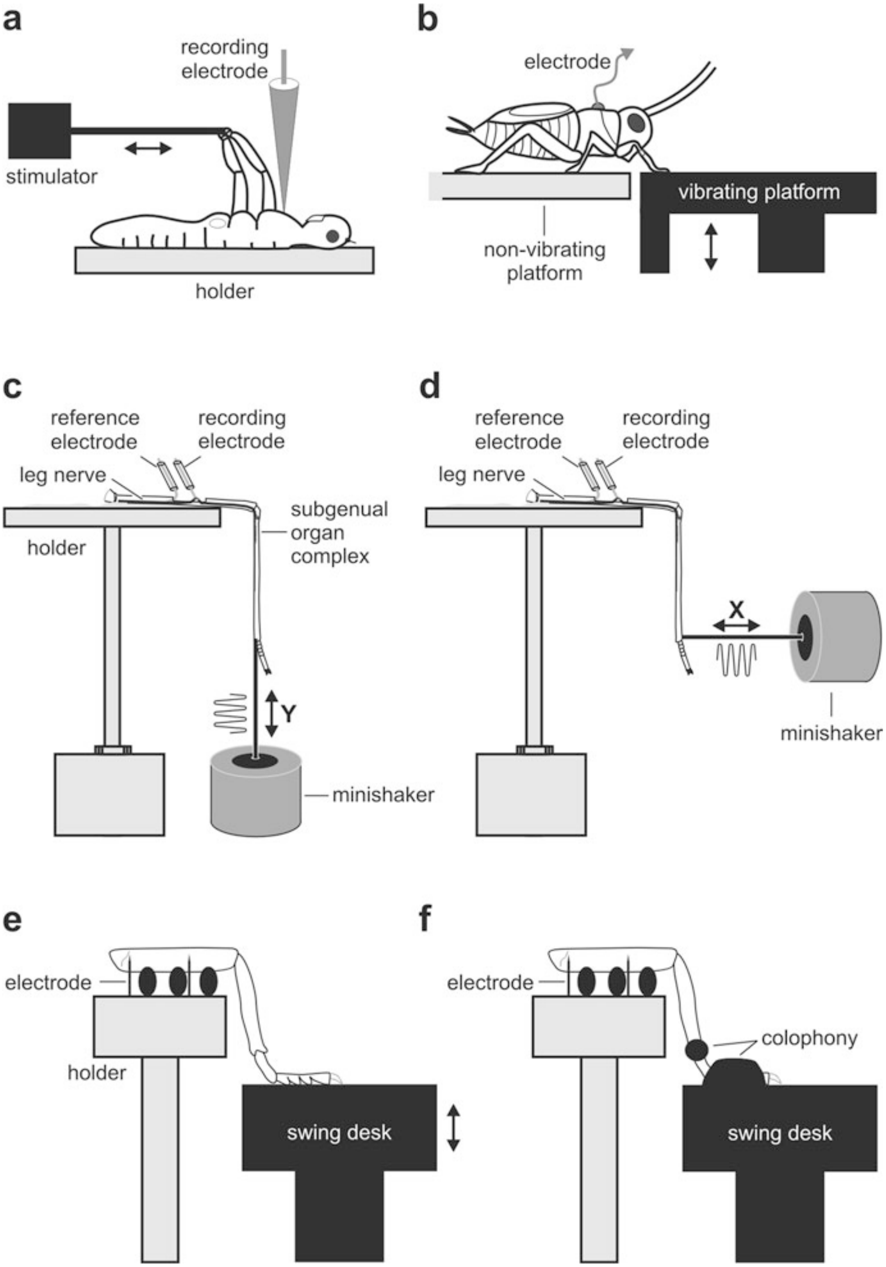

Fig. 11.2 Leg positions and directions of vibrational stimulation during electrophysiological recordings, with double arrows indicating directions of stimulation. Vibrating structures are depicted in black. (**a**) Stimulation of fore- and midlegs of a tettigoniid-mounted ventral side up for simultaneous recordings in the ventral ganglia. Hindlegs have been removed. (**b**) Cricket forelegs are selectively stimulated by a vibrating platform while the other legs rest on a stationary

their axons in these sensory nerves directly to the ganglia of the central nervous system (Pflüger et al. 1988; Schmitz et al. 1991; Field and Matheson 1998). The leg chordotonal organs show a high structural complexity. Some organs are differentiated into morphologically distinct sets of sensilla (scoloparia), or different chordotonal organs with distinct anatomy and innervation are developed in close proximity. The organ most sensitive to substrate vibration is usually the subgenual organ, located in the proximal tibia (Shaw 1994; Field and Matheson 1998; Čokl et al. 2006; Rössler et al. 2006; Čokl and Virant-Doberlet 2009; Lakes-Harlan and Strauß 2014). Remarkably, this organ is not present in Diptera and Coleoptera (Debaisieux 1938; Autrum and Schneider 1948; Lakes and Pollack 1990; Field and Matheson 1998; Takanashi et al. 2016). In several insect groups, the subgenual organ is found with additional chordotonal organs, together termed the subgenual organ complex (Eberhard et al. 2010; Strauß and Lakes-Harlan 2013). Further vibroreceptive organs are the femoral chordotonal organ (FCO; Field and Pflüger 1989; Büschges 1994; Takanashi et al. 2016) and possibly the tarsal or tarso-pretarsal chordotonal organ (Wiese 1972; Perez Goodwyn et al. 2009; Čokl et al. 2006). The FCO is usually the largest chordotonal organ in the insect leg. It is located in the proximal femur and attached by the cuticular receptor apodeme to the femoral–tibial joint (Bässler 1977, 1983; Field and Pflüger 1989). The femoral chordotonal organ in orthopteroid insects usually consists of two scoloparia, of which the dorsal scoloparium responds to sinusoidal vibrations of the tibial receptor apodeme (Field and Pflüger 1989). Importantly, in orthopteroid insects, vibrational signals are likely detected by several elaborate sensory organs located in the femur and the tibia.

The tibio-tarsal scolopidial organ (Mücke 1991; Čokl et al. 2006; Eberhard et al. 2010) or distal tibial chordotonal organ in stick insects (Godden 1972; Strauß and Lakes-Harlan 2017) is proximally often connected to a retractor tendon by connective strands (stick insects: Godden 1972; Bässler 1983), but can also lack specific proximal attachments (cockroaches: Young 1970). This organ consist of only 6–10 sensilla (stick insect: Strauß and Lakes-Harlan 2017; heelwalkers: Eberhard et al. 2010) to 25–30 sensilla (cockroach: Young 1970; locust: Mücke

Fig. 11.2 (continued) platform. Recordings are taken with electrodes from the neck connectives. (**c**, **d**) Stimulation of isolated stick insect legs in different directions. (**e**, **f**) Stimulation of isolated cockroach midlegs by a swing desk with different ways of attachment. Preparations not drawn to scale. Credits: (**a**) modified from Vergleichende funktionelle und anatomische Untersuchungen zum Aufbau der Hör- und Vibrationsbahn im thorakalen Bauchmark von Laubheuschrecken, Sickmann, Copyright 1997, with permissions from Cuvillier; (**b**) redrawn from *J Comp Physiol* 79, M. Dambach, Der Vibrationssinn der Grillen. II. Antworten von Neuronen im Bauchmark, pp. 305–324, 1972, Springer; (**c**, **d**) reprinted from *Comp Physiol Biochem A* 203, J. Strauß and R. Lakes-Harlan, Vibrational sensitivity of the subgenual organ complex in female *Sipyloidea sipylus* stick insects in different experimental paradigms of stimulus direction, leg attachment, and ablation of a connective tibial sense organ, pp. 100–108. Copyright 2017, with permission from Elsevier; (**e**, **f**) reprinted from *Z vergl Physiol* 71, H. Schnorbus, Die subgenualen Sinnesorgane von *Periplaneta americana*: Histologie und Vibrationsschwellen, pp. 14–48, 1971, Springer

1991). Distally, it attaches to the tibio-tarsal joint (Godden 1972; Eberhard et al. 2010) or to the intersegmental tibial–tarsal membrane (in the stink bug *Nezara viridula*; Michel et al. 1983; Čokl et al. 2006; cockroach: Young 1970) by elastic connective strands. This organ is not involved in vibration detection in several insect taxa (Sandeman et al. 1996; Devetak et al. 2004; Eberhard et al. 2010; Strauß and Lakes-Harlan 2017), but responds to low-frequency substrate vibrations in the stink bug *Nezara* (Čokl et al. 2006) and possibly also in the water strider *Notonecta glauca* (Wiese 1972). The tarso-pretarsal chordotonal organ in *Nezara* consists of two scoloparia, one connected to the pretarsal claw and one connected to the retractor tendon (Čokl et al. 2006), and of three scoloparia in the water strider *Aquarius paludum* of which the proximal one attaches to the retractor tendon (Perez Goodwyn et al. 2009). Thus, electrophysiological recordings of neuronal responses at the level of the leg femur or trochanter contain summed action potentials from all these chordotonal organs responsive to vibration stimuli.

Electrophysiological recordings allow us to determine the displacement acting on sensory organs: the displacement component of near-field sound acting on receptor structures (Yack 2016; Kamikouchi and Ishikawa 2016) or minimal displacements of sensory structures by oscillatory vibrations (Shaw 1994; Robert and Göpfert 2002; Hill 2008). Further, sensory threshold curves can be determined over a frequency range for sinusoidal vibrations, with intensities usually expressed as acceleration values, only rarely as displacement (Kalmring et al. 1978; Čokl 1983) or velocity (Zorović et al. 2008). Threshold curves may reveal specific frequencies or frequency ranges of particularly high sensitivity (Schnorbus 1971; Kalmring et al. 1994; Čokl et al. 1995; Rohrseitz and Kilpinen 1997; Stritih and Čokl 2014), and are important for the physiological characterisation of a sensory system.

However, the comparison of physiological data on insect vibration receptors reveals notable differences in sensitivities and ways of experimental approaches between different studies. Here, we review these different experimental approaches and show that many factors cause differences in sensory thresholds. Hence, the measured vibratory thresholds can vary with the setup in stimulation direction, leg orientation and leg attachment, as well as recording techniques, with the values depending crucially on the calibration procedure of the stimuli. To allow for comparisons between such physiological studies, it is important to note these specific experimental conditions.

11.2 Experimental Parameters

In the following sections, we describe and discuss different parameters in experimental setups, which have been used during investigations of insect vibratory receptors, for their influence in vibratory sensitivity.

11.2.1 Leg Orientation and Position During Stimulation

In the vibratory setup, animals and legs can be prepared in different orientations. In combination with intracellular recording from interneurons or sensory afferents, it is most convenient to mount animals with the ventral side up on a holder to gain access to the ventrally located nervous system (Fig. 11.2a; Kalmring and Kühne 1980; Kühne 1982a, b; Čokl et al. 1985, 1995; Sippel et al. 1985; Kalmring et al. 1994; Sickmann 1997; Stritih 2009). Alternatively, animals can also be mounted with the dorsal side up (Čokl 1983; Devetak and Amon 1997; Stein and Sauer 1999; Zorović et al. 2008; Eberhard et al. 2010), usually for recording from sensory units or nerves proximally in the leg. The subgenual organ complex is located in the dorsal haemolymph channel (Eberhard et al. 2010; Strauß et al. 2017), in which the haemolymph flows actively from the distal towards the proximal part of the leg (Wirkner et al. 2013), and turning the leg upside-down might influence this flow and thus possibly vibratory responses. It has so far not been studied in detail if inverting the leg actually affects the threshold for vibratory sensitivity (only the phase sensitivity of the cockroach SGO response was studied by Schnorbus 1971).

There are different possibilities of stimulus presentation in different setups. Recording may be conducted with electrodes from the leg nerve (or neck connectives when recording from interneurons) while the legs are standing freely on a vibrating platform. Such recording was used by Dambach (1972a, b) in crickets, while their legs were in various positions during standing and walking. Using a vibrating platform allows to stimulate also selective legs or leg pairs (Fig. 11.2b), which is also the case in other preparations. It is further possible to record sensory responses to vibrations from isolated legs (Fig. 11.2c–f; Autrum 1941; Autrum and Schneider 1948; Schnorbus 1971; Shaw 1994; Sandeman et al. 1996; Strauß and Lakes-Harlan 2017). Such preparations are specific not only with respect to the leg position, which is often used somewhat differently from that in the living insect (see Fig. 11.2a, b), but also since the leg is isolated from the mechanical response of the rest of the body. It has been shown in various arthropods that body resonance significantly influences leg vibrations (Aicher et al. 1983; Dierkes and Barth 1995; Cocroft et al. 2000; Stritih Peljhan and Strauß 2018), and thereby presumably also the sensitivity of leg vibratory organs.

The leg position in the physiological experiments was often not clearly defined in experimental descriptions, but was referred to as ‘natural’ (e.g. Kühne 1982a; Čokl 1983; Kühne et al. 1984; Lakes-Harlan et al. 1991; Eberhard et al. 2010). Such a description remains unspecific, since an insect leg can assume a range of ‘natural’ positions at different femur–tibia angles and angles between longitudinal leg and body axes, which might differ between insect species or even leg pairs (Dambach 1972a). Some studies have also attached fore- and midlegs jointly to the stimulator (Fig. 11.2a; Kalmring and Kühne 1980; Sippel et al. 1985; Sickmann 1997), which makes it more difficult to maintain legs in a natural position.

The effects of changes in the leg position have rarely been studied, but the existing data show that the response of vibratory sensilla may be position sensitive (honeybee: Sandeman et al. 1996; spider: Finck 1981). In honeybees, a sensory neuron tuned to ~100 Hz was less sensitive by approximately 10 dB when the tibia was flexed rather than extended relative to the femur or at right angles (Sandeman et al. 1996). In these extracellular recordings, the responding mechanosensory unit was not identified, but the authors proposed it originated from a joint chordotonal organ in the leg (Sandeman et al. 1996). A similar influence of leg position was shown for the individual slit sensilla of the lyriform organ, the principle receptor type for substrate vibrations in spiders (Barth 1998, 2002b; Hill 2008). In the orb-weaving spider *Araneus sericatus* (*Larinioides sclopetarius*), physiological responses of individual sensory neurons in the lyriform organ of the patella, tuned to low vibration frequencies below 300 Hz, revealed a decrease in the response threshold of over 40 dB from the maximal leg flexion (decreased sensitivity) to maximal leg extension (increased sensitivity) (Fig. 11.3; Finck 1981). The influence of leg position was found more ambiguous in crickets (Dambach 1972a). Since in the midlegs of a freely walking cricket (*Gryllus bimaculatus*) no marked positional effect was revealed by the summed vibratory response recorded from the leg nerve (Dambach 1972a), the response was judged as being 'scarcely affected by articulations or by vibrating properties of the entire leg' (Dambach 1989). In the cricket hindleg, however, a change in the femur–tibia angle between 80° and 120° influenced the vibratory sensitivity at 400 Hz by 5–7 dB, here increasing it in

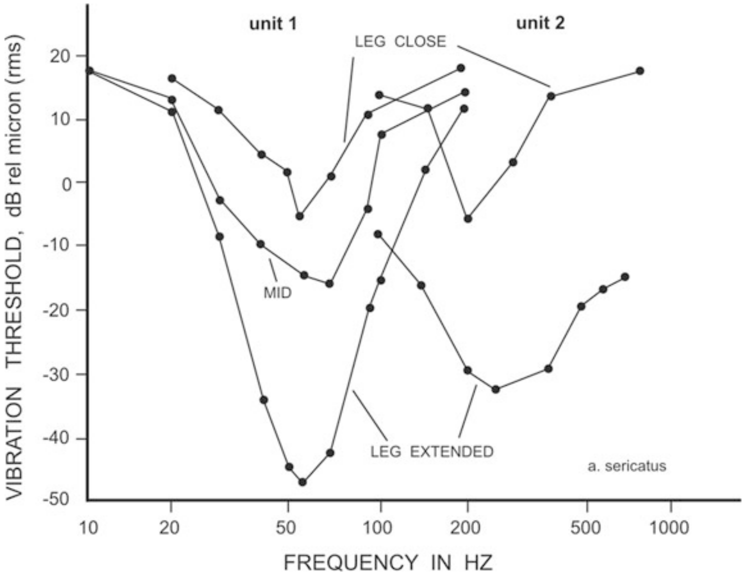

Fig. 11.3 Influence of leg position on the vibratory sensitivity of the patellar lyriform organ in an orb-web spider (*Larinioides sclopetarius* syn. *Araneus sericatus*). Two sensory units with different frequency tunings are recorded, and both respond to changes in leg extension with changes in sensitivity. Reprinted with permission from *J Acoust Soc Am* 70, A. Finck, The lyriform organ of the orb-weaving spider *Araneus sericatus*: Vibrational sensitivity is altered by bending the leg, pp. 231–233. Copyright 1981, Acoustic Society of America

case of flexion and decreasing it in case of extension (Dambach 1972a). However, although the best frequency of the cricket vibratory neuronal response was higher than in spiders and bees, the underlying mechanical basis of the positional influence is not necessarily different between the species. Notably, some papers reporting these effects of leg position on vibratory sensitivity show data from recordings in a single animal (Dambach 1972a; Sandeman et al. 1996), and more systematic and comparative analysis is required.

Similarly, investigations of vibration transmission over the legs of the fiddler crab *Uca pugilator* (Aicher et al. 1983) and the cave cricket *Troglophilus neglectus* (Stritih Peljhan and Strauß 2018) showed a strong positional influence on the mechanical response of the legs and the main body, which may be expected to affect sensitivity of leg vibratory receptors. In *T. neglectus*, the peak frequency of the mechanical leg response increased progressively with the leg flexion up to the femur–tibia angle of 45° (Fig. 11.4a). A close match between the shapes of

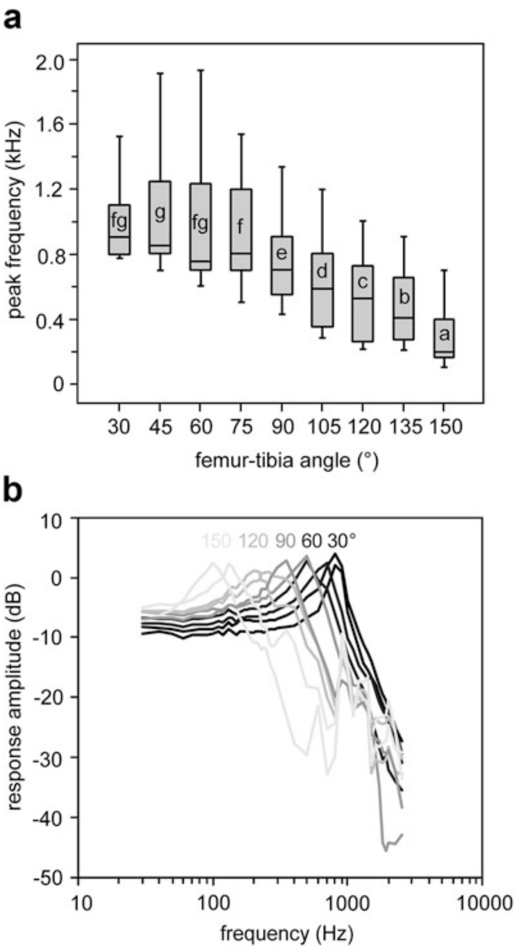

Fig. 11.4 Effect of leg position on the mechanical leg response in the cave cricket *Troglophilus neglectus*. (**a**) Peak response frequency at different femur–tibia angles. Reprinted from *J Comp Physiol A* 204, N. Stritih Peljhan and J. Strauß, The mechanical leg response to vibration stimuli in cave crickets and implications for vibrosensory organ functions, pp. 687–702, Springer. (**b**) Examples of frequency–response functions by one leg in different positions, two individual measurement sets; femur–tibia angles with corresponding responses shown in the same colour (Stritih Peljhan and Strauß 2018, new analysis of data)

the leg frequency–response function and the group of (inversed) receptor threshold curves originating from the SGOC of the species suggests these receptors are mainly responding to leg surface vibration; in turn, they may be highly sensitive to positional change. At best frequencies of these receptors (800–1400 Hz), the amplitudes of the leg mechanical response differed by 20–35 dB between the flexed and extended position, suggesting similar differences for the receptor sensitivity (Fig. 11.4b; Stritih Peljhan and Strauß 2018).

In addition, a further effect of the leg position was reported by the influence on the motor response to substrate vibrations on individual legs in the behavioural context of leg phase transitions (Bässler et al. 2003). Stimulating stick insect (*Carausius morosus* and *Cuniculina impigra*) forelegs in different degrees of anterior extension with substrate vibrations leads to stance–swing transitions if the leg is close to the body, but not if it is extended close to the anterior extreme position during stepping (Bässler et al. 2003). This is likely related to the position of the foreleg in the stepping cycle while differences in vibratory sensitivity resulting from changes in tibia position have not been investigated.

Another influence, closely relating to that of the position, is the tension (stiffness) of the leg articulations, which generally appears as most difficult to control or standardise in an experiment. The first insight into this matter has been given by Shaw (1994), who measured vibratory sensitivity from a leg nerve in the cockroach while changing the ‘flaccidity’ in the femuro-tibial articulation of the leg. Only slightly lifting the femur attached to a stationary platform, relative to the tibia attached to the source of vibratory stimuli, caused an increase in the average sensitivity of the leg vibratory response by about 10 dB; apparently by increasing the stiffness of the joint (Shaw 1994). Similarly, in the cave cricket *T. neglectus* large variation was observed in the mechanical response of the same legs set repeatedly in the same position, as well as an occasional ‘drift’ of the response function to higher or lower frequencies during the test. Both kinds of variation were ascribed to changes in muscle tension influencing leg stiffness (Stritih Peljhan and Strauß 2018). The resulting variation in the leg response amplitude to the same test stimuli was in the range between 10 and 15 dB, which compares to the influence of leg stiffness on the vibratory sensitivity found in the cockroach.

11.2.2 Direction of Leg Stimulation

The direction of leg stimulation, which is closely linked to leg orientation in the experimental setup, influences both the development of the setup and the leg sensory physiology. Usually, researchers have used a specific leg orientation and direction of stimulation within one set of experiments (Kühne 1982a).

The three elementary axes have been tested for the subgenual organ sensitivity of honeybees (Rohrseitz and Kilpinen 1997). Vertical vibrations were induced along the main axis of the leg’s tibia, and horizontal vibrations of the organ were induced parallel to the proximo-distal axis of the femur, or perpendicular to the proximo-

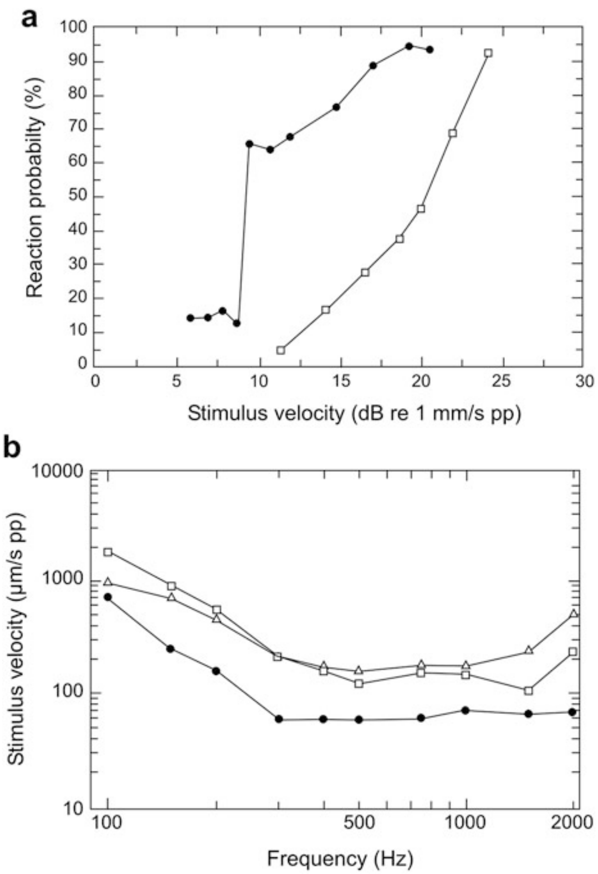

Fig. 11.5 Directional sensitivity in the honeybee *Apis mellifera*. (**a**) Behavioural freezing response to vibrational stimuli in vertical direction (circles) and horizontal direction (squares). (**b**) Sensory thresholds to vibrational stimuli in vertical direction (circles) and horizontal direction (triangles: perpendicular to femur; squares: parallel to femur), recorded as summed nerve response in the midleg femur. Reprinted with permission from *Zoology* 100, K. Rohrseitz and O. Kilpinen, Vibration transmission characteristics of the legs of freely standing honeybees, pp. 80–84, Copyright 1997, Elsevier

distal axis of the femur. This study is so far the most thorough comparison between direction-dependent sensitivities, as it addressed both behavioural and neurophysiological sensitivity. Walking honeybees showed higher rates in freezing responses to vertical vibrations than to horizontal vibrations (Fig. 11.5a). In middle legs, the physiological sensory threshold for vertical stimulation was lower (sensitivity was higher) by about 10 dB than for horizontal stimulation (Fig. 11.5b). A study in stick insects (*Sipyloidea sipylus*) compared the sensitivity between vertical and horizontal vibrational stimuli in all leg pairs (Strauß and Lakes-Harlan 2017). The recorded neuronal activity originated in the subgenual organ complex, as ablation of the distal tibial chordotonal organ did not significantly alter the threshold (Strauß and Lakes-Harlan 2017). Similarly for all stick insect legs, the differences resulted mostly from lower threshold (higher sensitivity) in the response to vertical stimulation (Figs. 11.2c, d and 11.6). These case studies show that the direction of stimulation has a marked influence on sensory physiology. Unfortunately, further studies investigating the physiological and behavioural roles of stimulus direction are so far not available.

For the sensory activation, the stimulus direction is important to consider in the context of differential excitation of sensory organs and their functional morphology in the leg. The subgenual organ is suspended transversely across the haemolymph channel, and is moving most efficiently in the proximo-distal direction of the tibia. Thus, lower thresholds to vertical vibrational stimulation over horizontal stimulation result from displacement of the subgenual organ in the longitudinal direction (see Kilpinen and Storm 1997 on the honeybee subgenual organ). The femoral chordotonal organ, located in the proximal femur (Fig. 11.1), is attached to a receptor apodeme spanning the femur (Bässler 1983). This apodeme is stretched in response to flexion of the tibia, so horizontal movements of the tibia parallel to the femoral axis causes the greatest displacement of the FCO sensilla (e.g. Stein and Sauer 1999). In order to reveal the maximal sensitivity of a specific receptor organ, its functional morphology needs to be considered in the context of the most efficient or 'natural' stimulus direction. The orientation and attachment of sensory organs via ligaments or connective tissue to the leg cuticle, joints or orientation in the haemolymph channel will determine the axis of greater displacements and most efficient stimulation (Field and Matheson 1998; Čokl et al. 2006; Strauß et al. 2017). This applies also for the organs within the subgenual organ complex of orthopteroid insects, which differ in their spatial orientation and attachments (e.g. Lin et al. 1994; Eberhard et al. 2010; Strauß and Stritih 2016; Strauß 2017; Strauß et al. 2017).

11.2.3 Leg Attachment to the Stimulator

For a vibration stimulus transfer, it is very important how firmly the leg is connected to the stimulator. The leg may be either freely standing (e.g. Dambach 1972a; Shaw 1994; Sandeman et al. 1996; Devetak and Amon 1997; Rohrseitz and Kilpinen 1997) or fixed to the stimulator by various adhesive materials, such as glue (e.g. Eberhard et al. 2010), colophony (e.g. Schnorbus 1971; Strauß and Lakes-Harlan 2017), wax (e.g. Lakes-Harlan et al. 1991) or plastiline (e.g. Čokl et al. 1995; Čokl and Virant-Doberlet 1997; Strauß and Lakes-Harlan 2017). Either approach may bring a disadvantage, because freely standing legs imply the risk of movement occurring during recordings, while artificial attachment raises the possibility of influencing leg stiffness and introducing a further mass on the leg, which could affect the vibration transmission. These parameters may change both the amount and composition of the vibratory spectral energy transmitted to the reception site (see Cremer et al. 2005, for the properties of mechanical oscillators).

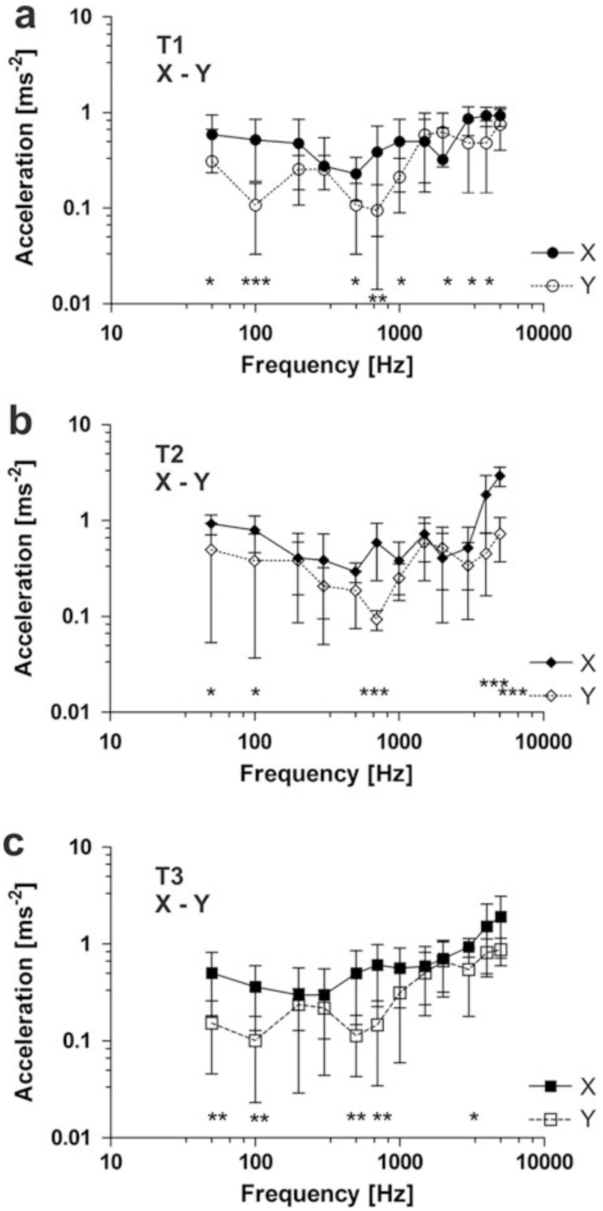

Fig. 11.6 Vibratory thresholds in response to vertical (Y) and horizontal (X) stimulus direction in the stick insect *Sipyloidea sipylus* for (**a**) foreleg T1, (**b**) midleg T2 and (**c**) hindleg T3. Reprinted from *Comp Physiol Biochem A* 203, J. Strauß and R. Lakes-Harlan, Vibrational sensitivity of the subgenual organ complex in female *Sipyloidea sipylus* stick insects in different experimental paradigms of stimulus direction, leg attachment, and ablation of a connective tibial sense organ, pp. 100–108, Copyright 2017, with permission from Elsevier

There are a few studies directly comparing vibratory sensitivity of attached and freely standing legs. In the American cockroach, the sensitivity increased by 20–40 dB at most frequencies compared to freely standing legs when tarsi were attached strongly with the colophony (Schnorbus 1971), and this effect was the strongest in the range below 200 Hz (Fig. 11.7a). Most likely, the stiff colophony enhanced the mechanical coupling, resulting in a better energy transfer from the stimulator to the leg. Similarly, in the stick insect *S. sipylus*, the thresholds recorded from the legs attached with plastiline were consistently lower at frequencies from 200 to 5000 Hz than those recorded from the freely standing legs, though this effect was usually not statistically significant (Fig. 11.7b; Strauß and Lakes-Harlan 2017). The much smaller sensitivity increase in the attached legs observed in the stick insect compared to the cockroach preparation could be expected to result from a weaker coupling of the leg to the stimulator by a much softer plastiline, compared to the colophony. However, a comparison of these attachment materials with different solidity in *S. sipylus* did not reveal any influence on the average sensitivity of the fore- and midlegs (Strauß and Lakes-Harlan 2017). Similar insights were obtained with the mechanical leg response measured in the cave cricket *T. neglectus*, where attaching the leg tarsus with wax–colophony mixture significantly influenced the frequency and amplitude response parameters compared to the free-standing situation (Stritih Peljhan and Strauß 2018). Similarly as in the stick insect, the response hardly changed in the range below 300 Hz following attachment, while at higher frequencies tested up to 2500 Hz, the response amplitude was about 5 dB higher for the attached legs, suggesting an increased vibratory sensitivity.

The influence of damping mass on the frequency tuning has been investigated in the cricket *G. bimaculatus*, by adding the mass of 95.7 mg to a freely standing hindleg (Dambach 1972a). Such additional mass induced a slight increase in sensitivity at 100–500 Hz, while a decrease of up to 10 dB was recorded at 700–2000 Hz. The frequency tuning of the summed leg nerve response with maximal sensitivity at 400–500 Hz, however, was not affected (Dambach 1972a; Dambach and Huber 1974).

With respect to the leg attachment, it may be possible to attach only the tarsus (e.g. Schnorbus 1971; Kalmring et al. 1994; Čokl et al. 1995; Stritih 2009; Eberhard et al. 2010) or also the distal part of the tibia to the stimulator (e.g. Stein and Sauer 1999; Strauß and Lakes-Harlan 2017). Occasionally, this attachment point was not explicitly stated in publications (Kühne 1982a). The best approach would likely be to attach those segments touching the substrate in the natural posture of a particular species. So far, no physiological study compared the influence of the different extent of leg attachment on vibratory sensitivity. However, in the cave cricket *T. neglectus*, we found that such differences largely influence the leg mechanical response to vibration. Attaching more/less of the tarsus, increased/decreased the response amplitude for high frequencies notably, but the response in all situations still reflected the motion of a damped simple harmonic oscillator (expressing a pronounced peak in the response transfer function; Stritih Peljhan and Strauß 2018 and unpublished; see also Cremer et al. 2005). Attaching also the distal part of the tibia to the stimulator, on the other hand, resulted in a nearly flat response of

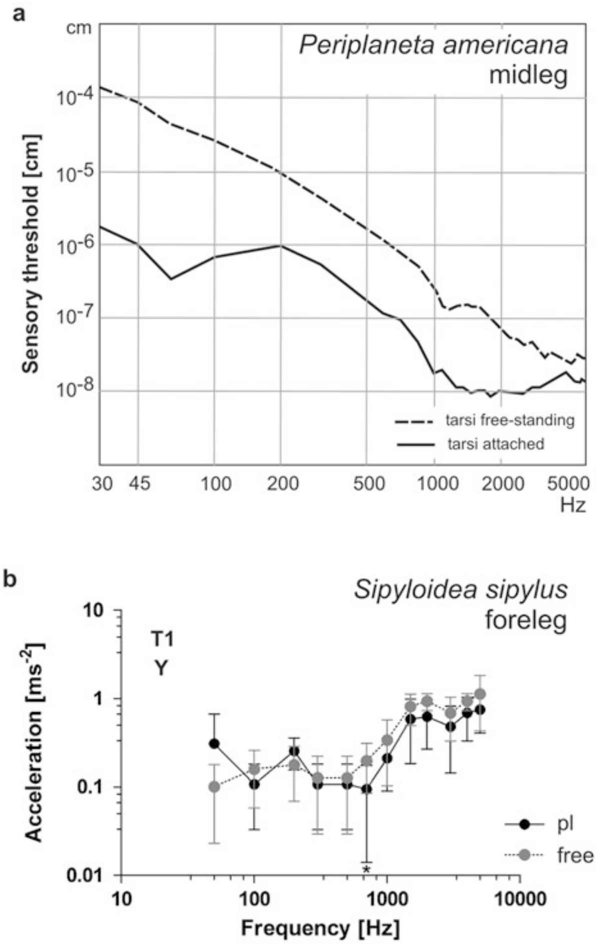

Fig. 11.7 Effect of leg attachments on vibratory sensitivity. (**a**) Comparison of sensory thresholds in isolated midlegs of the cockroach *Periplaneta americana* with tarsi feely contacting the mini-shaker (hatched line) or colophony attachment of the tarsi and tibio-tarsal joint (solid line). Adapted from Schnorbus (1971). (**b**) Comparison of sensory thresholds in the stick insect *Sipyloidea sipylus* foreleg (T1) with tarsi freely resting on the mini-shaker (free; hatched line) or legs attached at the distal-most tibia with plastiline (pl; solid line). Legs were stimulated in vertical (Y) direction. Note that both cases refer to responses of the isolated legs, with the femur attached firmly to the stationary platform (see Fig. 11.2c–f). Reprinted from *Comp Physiol Biochem A* 203, J. Strauß and R. Lakes-Harlan, Vibrational sensitivity of the subgenual organ complex in female *Sipyloidea sipylus* stick insects in different experimental paradigms of stimulus direction, leg attachment, and ablation of a connective tibial sense organ, pp. 100–108, Copyright 2017, with permission from Elsevier

the leg over the tested frequency range, suggesting that the leg follows the motion of the stimulation source directly (Stritih Peljhan and Strauß, unpublished data). These influences may be expected to profoundly influence the sensitivity of the leg vibratory sensilla. Apparently, the way and extent of leg attachment to the stimulator represents another parameter that deserves special attention during physiological experiments.

11.2.4 Electrophysiological Recording Techniques

Neuronal activity can be measured by different techniques. Basically, one can record the neuronal activity in single axons (single-cell extracellular or intracellular recordings) or from nerves containing several axons (extracellular recordings of summed or compound potentials). Both approaches have been applied to mechanosensory organs of arthropods, and to vibrosensory organs, in particular. However, investigations on leg vibroreceptor organs using both techniques for physiological comparisons have so far mainly focused on Orthoptera, with locusts and bushcrickets studied in most detail (Kühne 1982a; Kalmring 1985; Kalmring et al. 1994). Bushcrickets have complex tibial organs with the subgenual organ, the intermediate organ, the accessory organ and the crista acustica (Rössler et al. 2006; Strauß et al. 2016), and sensilla were investigated for physiological responses to sound and vibration (Kalmring et al. 1994).

Recording summed neuronal activity, which is often conducted by hook or suction electrodes from sensory nerves in bioacoustics studies, may be generally expected to reveal somewhat higher thresholds than expressed by the most sensitive axons of the measured receptor population. Due to constraints in the resolution and sensitivity of the detection method, which is visual or combined visual and acoustical, an increase in the response amplitude over the threshold can usually be detected only after a certain proportion of neurons has been activated. This is exemplified by comparative recordings from scolopidial organs in a bushcricket species (*Gampsocleis gratiosa*, Tettigoniinae; Fig. 11.8a), where the lowest vibratory thresholds revealed by summed recordings were 10–15 dB higher than thresholds determined by single-cell recordings (Fig. 11.8b; Kalmring et al. 1994). The same difference in sensitivity was also revealed for auditory receptor neurons by the use of both recording techniques in one species (Kalmring and Jatho 1994; Kalmring et al. 1996). Notably, the summed potentials recorded from the sensory nerve lack a clear frequency tuning, which, however, becomes apparent in single-cell recordings (Kalmring et al. 1994). Such summed tuning curves may be expected to be rather flat since they reflect the activity of the receptors from different organs or sensilla, which are devoted to detection of different frequency ranges, but nevertheless overlap largely (Kalmring et al. 1994; Čokl et al. 1995). Such a lack of clear frequency tuning for vibrosensory organs in the summed recordings was also found in different representatives of atympanate Ensifera and stick insects (Strauß and Lakes-Harlan 2008a, b, 2010, 2017). These summed vibratory tuning curves showed relatively

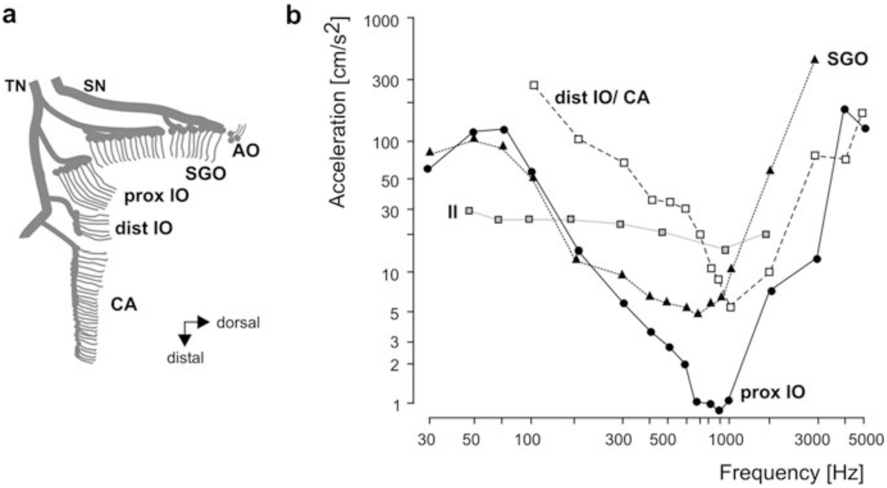

Fig. 11.8 Vibratory thresholds obtained by different recording techniques in the complex tibial organ in the midleg of the tettigoniid *Gampsocleis gratiosa*. (**a**) Schematic of the complex tibial organ in bushcrickets with the subgenual organ (SGO), the accessory organ (AO), the proximal intermediate organ (pIO), the distal intermediate organ (dIO) and the crista acustica (CA) and their innervation by the tympanal nerve (TN) or the subgenual nerve (SN). (**b**) The summed recording of the midleg sensory organs (II, grey squares) shows the averaged vibratory thresholds from the main sensory nerve. The most sensitive vibrational responses of different sensory organs are shown as the lower averaged thresholds recorded from single sensory neurons in the subgenual organ (SGO, solid triangles), the proximal intermediate organ (prox IO, solid circles) and the distal intermediate organ/crista acustica (dist IO/CA, open squares). Additional classes of sensory neurons responding to sinusoidal vibrations with higher thresholds exist in *G. gratiosa*. Data in (**b**) reprinted from *J Exp Zool*, K. Kalmring, W. Rössler, and C. Unrast, Complex tibial organs in the forelegs, midlegs, and hindlegs of the bushcricket *Gampsocleis gratiosa* (Tettigoniidae): comparison of the physiology of the organs, pp. 155–161, Copyright 1994, with permission from John Wiley and Sons

high thresholds at acceleration between 0.01 and 0.1 m/s^2. On the other hand, very low vibratory thresholds of leg sensory organs at intensities about 20–40 dB lower than this (acceleration between 0.01 and 0.0001 m/s^2) have been determined by whole nerve recordings in cockroaches, crickets and bushcrickets (see, e.g., Autrum and Schneider 1948; Howse 1964; Schnorbus 1971; Dambach 1972a; Lakes-Harlan et al. 1991; Eberhard et al. 2010). These large differences, however, could hardly reflect the actual differences in the vibratory sensitivity between the species, but may rather be a consequence of differences in the experimental settings discussed previously, and/or stimulus calibration (see Sect. 11.2.5) applied by different investigators.

11.2.5 Stimulus Calibration

Shaw (1994) in a critical review of some early studies on insect vibrosensation (by Autrum and Schneider 1948; Howse 1964; Schnorbus 1971) scrutinised the extremely high sensitivity reported for the subgenual organs, particularly of the cockroach *Periplaneta americana*, which was supposedly able to detect vibration displacements of subatomic dimensions (down to 0.002 nm, i.e., *ca*. 0.0002 m/s^2 acceleration at the best frequency of 1500 Hz). He suggested that these results were due to erroneous stimulus calibrations based on the linear extrapolation from much higher amplitudes, without actually demonstrating this linearity. Using an optical method that controlled for the stimulus amplitudes directly and in the whole range of tested intensities, Shaw (1994) re-adjusted the sensory thresholds *in P. americana* to 40 dB higher intensities respectively. By using the specialised Brüel and Kjær equipment for vibration measurement and calibration (in particular the mini-shaker type 4810, in concert with a high-sensitivity mini-accelerometer), Čokl and Virant-Doberlet (1997) later confirmed this sensitivity in *P. americana*, reporting for the minimal acceleration thresholds around 0.03 m/s^2 at 1800 Hz. It is thus surprising that with the same equipment, Dambach (1972a) determined in the cricket *G. bimaculatus* vibratory thresholds closely overlapping with those measured in the same species by Autrum and Schneider (1948), which lay in the same range generally criticised by Shaw (1994). Determination of such low thresholds, however, may be valid, as the respective vibration application system, in the ideal circumstances, indeed reaches linearly down to displacement values of 1×10^{-11} m at 1500 Hz (N. Stritih-Peljhan and P. Dolenc, unpublished measurements, conducted in the reference Brüel and Kjær laboratories). It has to be noted, however, that also here extrapolation from high to almost infinitesimal intensities may be problematic, since reliability of the produced stimulus amplitudes relies strongly on the properties of the backup circuitry.

Michelsen (2014) pointed out the importance accounting for additional factors like temperature or electromagnetic fields during calibration, and in particular, for mounting of the accelerometer (Michelsen 2014). It is also important to note that the calibrated output, when measured in a contact way via an accelerometer, is only produced with the accelerometer mounted to the mini-shaker, such as specified, for example, by Dambach (1972a), Čokl and Virant-Doberlet (1997), and Eberhard et al. (2010). After removal of the accelerometer, which provides an additional load to the system, the frequency–intensity characteristics of the output may change. Most studies of the insect vibratory sense, however, do not specify whether this has indeed been considered.

11.3 Conclusion and Outlook

We have summarised case studies on the vibratory sense mainly from insects, and also few other arthropods like spiders and crabs, which show that the experimental determination of vibratory sensitivity can be significantly influenced by the calibration process and the experimental setup parameters under which the recording took place. Changes in these parameters, including leg position, attachment and direction of stimulation, can result in significant differences in the determined sensitivity. Previous case studies are summarised in Table 11.1. This direction-dependent effect

Table 11.1 Experimental Variables in Vibratory Physiological Studies of Insect and Arachnid Leg vibration receptors. Included are studies which compare sensitivities under different settings of one parameter

Parameter	Setup	Species	References
Orientation/position of leg	Hindleg femur–tibia angle	*Gryllus bimaculatus*	Dambach (1972a)
	Foreleg flexed, extended or at right angle to femur	*Apis mellifera*	Sandeman et al. (1996)
	Flexed, middle, extended leg	*Araneus sericatus* (*Larinioides sclopetarius*)	Finck (1981)
Leg stimulation	Vertical vs. horizontal	*Apis mellifera* *Sipyloidea sipylus*	Rohrseitz and Kilpinen (1997) Strauß and Lakes-Harlan (2017)
Leg attachments	Different adhesives	*Sipyloidea sipylus*	Strauß and Lakes-Harlan (2017)
Leg contact with the stimulator	Attached vs. free	*Periplaneta americana* *Sipyloidea sipylus*	Schnorbus (1971) Strauß and Lakes-Harlan (2017)
Recording technique	Summed vs. single-cell recording	*Gampsocleis gratiosa*	Kalmring et al. (1994)

on sensitivity is also relevant to behavioural studies. The directionality of stimulation should be considered for comparisons of vibratory behaviour, for example, in playback experiments (e.g. Cocroft et al. 2014b), or could be compared for different directions in experiments on the role of sensory inputs in locomotor control (Bässler et al. 2003). Hence, particular attention should be given to consistency between preparations of an experimental series on sensory or behavioural physiology. A further significant aspect is the process of calibration of the stimulator output, which may result in strong discrepancies in data obtained by different investigators.

This overview shows that studies addressing and comparing the influence of all these possible variables on vibratory sensitivity in arthropods are so far limited. We argue that it is also very important to note the specific conditions used in a study to give an idea of how the respective data were obtained. These conditions should be considered as an important framework underlying any critical data comparison within and among the species.

Obviously, it may not be possible for all studies to work under strictly identical conditions due to, for example, different resting position of legs in some animals, or due to different sizes of animals and their legs. Therefore, we do not claim that a standardised setting in vibrational research would be essential, but propose that a description of the setup in any experiment should be precise and unambiguous, or that a scheme of the complete setup, including details of the preparation, is provided. This information should include (1) the leg position by the angle between the femur and the tibia, and their vertical inclination, (2) the direction of stimulation or displacement of the leg on the tarsus or tibia, (3) the way and extent of leg attachment to the stimulator and (4) details on the accelerometer measurements and range of calibration measurements.

Hopefully, considering these experimental details will enhance the comparability of physiological data between species. Ultimately, it should also allow some insights into what separates the conditions of the laboratory setup from the situation in the habitat. For example, arthropods would only occasionally position legs with a 90° angle between femur and tibia, which is probably easiest to maintain consistent in the experimental setting, but rather in a different resting or standing position (but see Dambach 1972a for cricket fore- and midlegs in a normal standing position with a 90° ± 10° femur–tibia angle). These considerations could also apply to vibrational behaviour, e.g., to directionality or behavioural thresholds, and thus connect behavioural physiology and neurophysiology. The role of directionality in vibration sensing and behaviour is discussed in detail by Hager and Kirchner (see Chap. 12). Further, the natural situation would include excitation of all six legs with sensory organs in slightly different positions and thus possibly also different sensitivities (for discussion, see Michelsen 2014), as well as an additional input to the leg via the body, especially if it is contacting the substrate (see Stritih Peljhan and Strauß 2018). All these positions should ideally be quantified from natural data and included in comparative physiological studies as well.

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Chapter 12
Directionality in Insect Vibration Sensing: Behavioral Studies of Vibrational Orientation

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Abstract Insects need to orient to various environmental stimuli. Many behavioral studies suggest orientation based on vibrational cues and signals, but they rarely exclude other potential stimuli such as chemical, visual, or airborne sound signals. Here, we review the behavioral evidence for directional vibrational orientation in insects. First, we discuss the potential of vibrational cues and signals for orientation and briefly state the importance of the material properties of the substrate. We then review what is known about vibrotaxis in some particularly well-studied species. Our selection aims to show the different experimental approaches that have been used and, as far as known, which kind of taxis and which kind of vibrational cue are used by the insects to orientate. We show that a growing body of current behavioral studies reveal the remarkable ability of insects to orientate via vibrational cues and signals in various contexts.

12.1 Introduction

Insects need to orient to various environmental stimuli to find mates, food, or to escape predators. In the context of mate location, there should be a high selection pressure on the evolution of mechanisms allowing accurate localization of a potential mate. The same applies in the context of predation, since the survival of predators depends on their ability to catch prey. In the like manner, prey would benefit if predators could be detected, localized, and thereby avoided. In these contexts, different sensory channels such as the visual, olfactory, or mechanical can be employed. Whereas directional hearing, i.e., localization of mechanical signals in air or water, has been studied in vertebrates as well as in arthropods in great detail, localization of sources of surface waves is much less well studied (Cocroft et al. 2014). Solid media are much more variable in parameters affecting signal

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transmission (Elias and Mason 2014). Amplitude differences, time-of-arrival delays or phase angle differences perceived at two or more sensors highly depend on the characteristics of the substrate. In the context of vibrational orientation, the physical properties of the substrate are therefore of fundamental importance. The rich diversity of substrate properties was recently reviewed by Elias and Mason (2014), Michelsen (2014), and Mortimer (2017). Although several behavioral studies demonstrate the ability of insects to localize the source of vibrations (Virant-Doberlet et al. 2006), it is still not well understood how insects can perceive directional information from vibratory signals on solid substrates. Some species seem to solve this task without making any use of directional cues; others, however, localize sources of vibrations using either a klinotactic directional orientation (i.e., temporal comparison of signal parameters) or tropotactic directional orientation (i.e., simultaneous comparison of signals arriving at two sense organs). In this chapter, we review behavioral studies demonstrating the ability of insects to localize the source of vibration and focus particularly on vibrational orientation, i.e., klinotactic and tropotactic orientation.

12.2 Directional Cues for Vibrational Orientation

Insects producing vibrational signals, such as drumming, tremulation, and stridulation, or vibrational cues by walking and feeding induce different vibrations of the substrate with different frequencies and amplitudes (for review, see Hill 2008, 2014). The material's characteristics, like impedance, density, mass, and internal damping, as well as its geometry and boundary condition (Inta et al. 2007; Mortimer 2017) lead to vibrational waves travelling with very different characteristics. This leads to a certain velocity, attenuation, and dispersion of the wave travelling through the substrate. After the vibrational waves have travelled some distance through the substrate a receiver might detect them. Several sense organs are involved in substrate vibration detection in insects: subgenual organs, chordotonal organs and campaniform sensilla (Lakes-Harlan and Strauß 2014). The receiver could use different behavioral strategies to encode directional information. One strategy is to compare measurements over time (klinotaxis). The other behavioral strategy in the context of vibrational orientation is the comparison of the inputs of at least two receptors (tropotaxis). The insect's size is crucial because the distance between the legs, i.e., the receptors, directly influences the magnitude of the differences. For a given insect's size, i.e., two receptors in a given distance to each other, the magnitude of the differences is a function of the substrate's characteristics. Theoretically a vibrational wave should arrive at each receptor at different times and with different intensities. The most obvious directional cues are therefore differences in time of arrival (Δt) and amplitude (Δd) (Virant-Doberlet et al. 2006).

On a physiological level, the temporal resolution of vibrational direction sensing has been studied by Čokl et al. (1985). They showed in *Locusta migratoria* that the response pattern of ventral cord neurons depends on the direction and the time delay of the presented vibrational stimulus. Directional processing occurs at the ventral cord level by integrating the inputs from the vibratory receptors from several legs. Because of the locust's relatively large size, receptors in different legs are at a distance of 5 cm, leading to a time delay between 0.4 and 4 ms (Čokl et al. 1985).

Between different receptors, the insect could compare the first onset of the vibrational wave, the onset of certain frequency components, or other characteristics like the peak amplitude to obtain directional information. For a long time, it has been thought that time-of-arrival differences (Δt) might be too small to be detected on natural substrates because of the high propagation velocity of vibrational waves (Virant-Doberlet et al. 2006). The first arthropods for which it could be clearly demonstrated that time-of-arrival differences are used for tropotactic orientation on solid substrates are the sand scorpion *Paruroctonus mesaensis* and the wandering spider *Cupiennius salei.* The scorpion can detect time delays as small as 0.2 ms (Brownell and Farley 1979) and the spider can detect time delays of 4 ms (Hergenröder and Barth 1983). Recently it was shown for three different insect taxa that time-of-arrival delays are used for vibrotaxis by termites (Hager and Kirchner 2014), hemipterans (Hager et al. 2016; Kirchner et al. 2017) and ants (Hager et al. 2017). The time delays used by insects on solid substrates are in the same range as the time delays detected by scorpions.

Differences in amplitudes expressed as velocity, acceleration, or displacement could be compared between receptors that are spatially arranged on the substrate (tropotaxis), or if the insect moves and probes at different locations (klinotaxis). Vibrational orientation using amplitude gradients has been demonstrated in locusts. Directionality coding of some neurons is improved if, in addition to the time-delayed stimulation, a signal attenuation is simulated. Perception of signal amplitudes and its neuronal comparison leads to directionality-dependent response patterns in ascending neurons (Čokl et al. 1985). Behavioral experiments show that in stinkbugs amplitude differences are sufficient for vibrational orientation (Hager et al. 2016; Kirchner et al. 2017). Whether amplitude differences in the relevant range reliably occur on host plants needs further observation. Recently it was shown for a stinkbug's host plant (*Phaseolus vulgaris*) that only a time delay between the arrival of vibrational waves was a reliable directional cue, since the signal amplitude at the branching point was often higher on the stalk away from the female (Prešern et al. 2018).

Due to frequency-dependent filtering characteristics of some substrates the relative amplitude of different frequency components changes while travelling through the substrate. Assuming the insects' receptors are frequency sensitive in the relevant range, they could compare amplitude ratios between receptors. Moreover, different frequencies travel with different velocities, thus the temporal structure of the substrate vibration changes with distance. For example, a frequency sweep that begins with a high frequency and ends at a low frequency will increase its duration when it travels, but a sweep with increasing frequencies will decrease in duration (Michelsen 2014). Insects on solid substrates may also use phase differences between receptors to solve the orientation task, as it was shown for the backswimmer *Notonecta glauca* (see Sect. 12.6.6; Wiese 1974). Directional information could also be available in mechanical response of the insect body to substrate vibrations, as it was proposed for treehoppers (Cocroft et al. 2000).

12.3 Substrates

The physics of mechanical waves in solids and along media interfaces is quite complicated. Depending on the mechanical properties of the media and on the size and shape of the materials involved, a considerable number of different wave types with quite diverse physical characteristics can occur (Markl 1983). In the following, we summarize briefly what is known about the physical characteristics of solids and the water surface relevant to the context of vibrational orientation. We will focus on the types of waves occurring in the substrates and their propagation velocity, attenuation, and dispersion characteristics. We primarily focus on characteristics that are important to elucidate time-of-arrival and amplitude differences that have the potential to be biologically meaningful. For comprehensive reviews, see Cremer et al. (2005), Markl (1983), Michelsen (2014), and Mortimer (2017).

12.3.1 Plant Stems

In plant stems, vibrations travel as bending waves with a relatively low group propagation velocity. In some plant species, the group propagation velocity is only 36–95 ms^{-1} at low frequencies of 200 Hz and 120–220 ms^{-1} at higher frequencies of 2 kHz (Michelsen et al. 1982). These velocities would lead to time-of-arrival delays between receptors positioned at a 1-cm distance to each other in the range of 0.05–0.27 ms. The energy loss of bending waves in plant stems by friction at frequencies below some kHz is relatively low. Communication is therefore possible over distances of some meters (Michelsen et al. 1982). For some plant species, it was shown that the amplitude of vibrations does not decrease monotonically with distance from the vibration source (Michelsen et al. 1982). Therefore, amplitude gradients are thought to be unreliable cues. However, if measurements are either taken at points with a certain distance between them (by performing klinotaxis), or if measurements are made at special positions on the stem or at the two sites of a node or between the stem and the adjacent petiole of leaves, amplitude differences could be reliable cues (Stritih et al. 2000).

The 2D motion of plant stems changes with distance from the source. Close to the vibration source the motion perpendicular to the stem is ellipsoidal, while further away the motion is circular. An insect standing on a plant stem positions its legs in a three-dimensional array around the stem and could use these differences for orientation (Virant-Doberlet et al. 2006). If vibration perception is influenced by motion along more than one axis, then describing stem motion within a 2D coordinate plane may be important for understanding how vibrations are transmitted and perceived. Sensitivity to orthogonal axes of motion in a vibrational stimulus is important in vibration localization in some scorpions (e.g., Brownell and Farley 1979) and spiders (Barth and Geethabali 1982). To our knowledge, there is only one comprehensive study linking the insect's movement decisions and the complex motion of plant stems (Gibson and Cocroft 2018).

Gibson and Cocroft (2018) studied mate searching in thornbug treehoppers on living plants and mapped search paths of male treehoppers. At each of the males' sampling locations, two-dimensional laser vibrometry was used to measure stem motion produced by female vibrational signals. Thereby, properties of the vibrational signals could be related to the males' movement direction, intersample distance, and accuracy. Males experienced gradients in signal amplitude and in the whirling motion of the plant stem, and these gradients were influenced to varying degrees by source distance and local stem properties. Males changed their sampling behavior during the search, making longer intersample movements farther from the source where uncertainty is higher.

The primary directional cue used by searching males was the direction of wave propagation, and males made more accurate decisions when signal amplitude was higher, when time delays were longer between front and back legs, and when female responses were short in duration (Gibson and Cocroft 2018).

12.3.2 Sand and Soil

Mechanical impacts on a sandy substrate release different types of waves with different properties (Brownell 1977; Aicher and Tautz 1990). In the context of vibrational orientation, Rayleigh surface waves are thought to be particularly interesting. Loose sand conducts Rayleigh surface waves at relatively low velocities of 40–50 ms^{-1} (Brownell 1977). The sand's particle size and frequency of vibrational waves both influence the propagation properties. The damping coefficient at a frequency of 300 Hz varies from 0.26 to 2.61 dB cm^{-1} and is inversely proportional to the size of the sand particle (Devetak et al. 2007). Due to these characteristics, time-of-arrival and amplitude differences occur that have the potential to be biologically meaningful. Generalizations of the soil's physical properties are difficult to make because particle size, degree of heterogeneity, and overall complexity can vary (Hill 2008). Moreover, soils are no static substrates and propagation properties can change from day to day with temperature and moisture content (Hill and Shadley 2001).

12.3.3 Water Surface

Surface waves on the water have quite special physical properties and propagate with relatively low velocity (Markl 1983). Local disturbances of the water surface generate waves that consist of concentric movements of the water particles at the surface. Waves with amplitudes that are much smaller than the water depth are radiated with dispersion. The damping of the waves, which highly depends on frequency, especially causes a loss of high-frequency components during signal propagation (Lang 1980; Bleckmann 1985). Phase velocity reaches its minimum at about 13 Hz, while the minimum of the group velocity is situated at about 6 Hz. At 13 Hz, phase and group velocities are equal and only 0.23 ms^{-1} (Lang 1980). Due to these special physical properties, relatively large time-of-arrival and amplitude differences occur.

12.4 Experimental Methods

Many behavioral studies of insects suggest orientation based on vibrational cues and signals, but they rarely exclude other potential stimuli such as chemical, visual, or airborne sound signals (Virant-Doberlet et al. 2006). In the context of directional vibration sensing, two different experimental designs can be distinguished that allow different conclusions on the insect's orientation abilities. In closed-loop conditions the insect can successively update directional information as it changes its position or orientation relative to the vibration source. In nature and in most arena experiments, insects move freely from a releasing point toward the vibration source and could thereby obtain some kind of amplitude gradient or other characteristics of the vibrational waves that change while travelling through the substrate. In closed-loop conditions, a clear distinction between klinotaxis and tropotaxis is not possible (Gerhardt and Huber 2002). In open-loop conditions, the insect must make decisions without receiving any feedback. Open-loop experiments, therefore, allow observers to discriminate clearly between klinotactic and tropotactic orientation. A very elegant experimental design was first applied by Rupprecht (1968) who glued metal filings to the legs of stoneflies, which allowed him to vibrate single legs independently by means of an electromagnet. By vibrating one leg only he could show that stoneflies turn in the direction of the vibrated leg (Fig. 12.5). This strongly suggests that directional information can be extracted by the stonefly, but does not allow one to draw conclusions about the directional cue that is employed. Wiese (1974) improved this method by vibrating the four legs of the backswimmer that contact the water surface with four electromagnets independently (see Sect. 12.6.6).

12.5 Behavioral Evidence for Vibrational Orientation in Insects

There are several studies indicating that insects can localize the source of vibration. Virant-Doberlet et al. (2006) carefully reviewed behavioral evidence that supports the idea that insects can accurately localize the source of vibration. To localize the source of vibration does not require the insect necessarily to exhibit directional reactions. It could just by chance arrive at the source and then detect it. For example, the drywood termite *Cryptotermes secundus* prefers, in dual choice experiments, wood, i.e., food pieces, that were vibrated over not vibrated pieces (Evans et al. 2007). Clearly the termites detect the vibrations and may show some kind of kinesis, but whether they orientate to the source of vibration, i.e., display a vibrotaxis, remains open. Studies suggest that host-associated vibrations are exploited by parasitic wasps (for review, see Meyhöfer and Casas 1999). *Pimpla turionellae*, for example, employs self-produced vibrations to detect its hosts (Wäckers et al. 1998). However, no study shows vibrotaxis in parasitic wasps.

There are a great number of studies demonstrating that insects arrive at the source of vibration under closed-loop conditions (Virant-Doberlet et al. 2006). As it is often difficult to differentiate whether insects show kinesis or taxis, and closed-loop experiments do not allow one to differentiate between klinotaxis and tropotaxis, we focus on open-loop experiments, which are suitable for distinguishing between klinotaxis and tropotaxis. Table 12.1 provides a summary of the studies demonstrating vibrotropotactic orientation in insects. The studies are compared concerning the species, substrate, behavioral context, and experimental design. So far as it is known, the vibrational cues (Δt and Δd) used for orientation are given.

12.6 Case Studies

In the following, we review what is known about vibrotaxis in some particularly well-studied species. Our selection aims to show the different experimental approaches that have been used and, as far as known, which kind of taxis and which kind of vibrational cue are used by the insects to orientate. Therefore, we first describe the behavioral context and very briefly what is known about the substrate's characteristics relevant to vibrational orientation.

12.6.1 Stinkbugs

The ability of insects to localize the source of vibrations is particularly well studied in the context of mate location behavior in stink bugs. In *Nezara viridula*, the female produces rhythmic calling songs. A male located on the same plant, answers and

Table 12.1 Studies Demonstrating Vibrotropotactic Orientation in Insects

Species	Context	Design	Cue	References
Plant stems				
Atta cephalotes	RC	PB, Y branching	na	Roces et al. (1993)
Atta sexdens	RC	PB, two platforms	$\Delta t = 0.1$ ms	Hager et al. (2017)
Conocephalus nigropleurum	ML	PB, T maze	na	De Luca and Morris (1999)
Euschistus heros	ML	PB, two platforms	$\Delta t = 0.2$ ms $\Delta d = 1$ dB	Kirchner et al. (2017)
Nezara viridula	ML	PB, two platformsLC, branching	$\Delta t = 0.1$ ms $\Delta d = 3$ dB$\Delta t = 0.3$ ms	Hager et al. (2016) Prešern et al. (2018)
Perla marginata	ML	MF, 2D	na	Rupprecht (1968)
Telenomus podisi	HL	PB, Y maze	na	Laumann et al. (2007)
Tettigonia cantans	ML	PB, Y branching	na	Latimer and Schatral (1983)
Soil and sand				
Euroleon nostras	PL	PB, 2D	na	Fertin and Casas (2007), Mencinger-Vračko and Devetak (2008)
Gryllus bimaculatus	ML	PB, Y maze	na	Weidemann and Keuper (1987)
Macrotermes natalensis	AC	PB, two platforms	$\Delta t = 0.2$ ms	Hager and Kirchner (2014)
Water surface				
Gerris remigis	PL	PB, 2D	na	Murphey (1971)
Notonecta glauca	PL	MF, 2D	phase $\Delta t = 8$–16 ms	Wiese (1974)
Notonecta undulata	PL	PB, 2D	na	Murphey (1973)

AC alarm communication, *ML* mate location, *HL* host location, *RC* recruitment communication, *PL* prey location, *PB* playback, *LC* live couple, *MF* magnetic field, Δt time-of-arrival difference, Δd amplitude difference, *na* not available

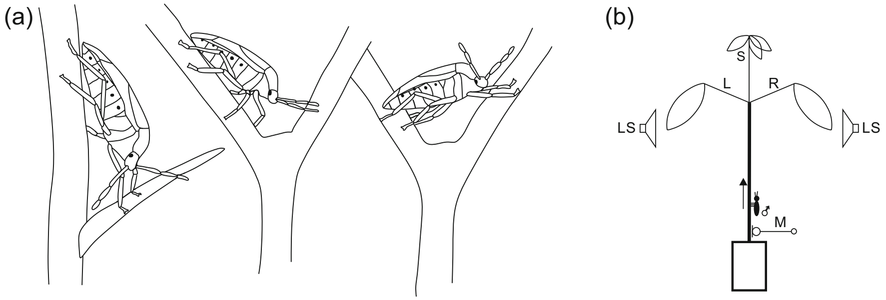


Fig. 12.1 (**a**) Behavior of male *Nezara viridula* at a petiole—the male straddles the forelegs across the fork, places its antennae on the opposite stem, or straddles its legs on the opposite stem (modified from Ota Ota and Čokl 1991). (**b**) Experimental setup used during directionality tests on a bean plant. L: left branch; R: right branch; M: microphone for monitoring the bug's responses; S: middle stem; LS: loudspeaker (modified from Čokl et al. 1999)

searches for the female. When encountering branching points, the male stops and straddles its legs across the fork to compare the vibrations in the two branches (Fig. 12.1) (Ota and Čokl 1991; Čokl et al. 1999). Measurements of vibrational signals on plant stems show significantly different amplitudes and arrival times between the two different branches (Virant-Doberlet and Čokl 2004). It has been shown that differences in amplitude and frequency cause different neuronal responses (Čokl 1983), and Čokl et al. (1999) proposed that time-of-arrival and amplitude differences are used as directional cues. On the host bean plants, the propagation velocities of the bending waves are between 40 ms^{-1} and 80 ms^{-1} (Michelsen et al. 1982; Čokl and Virant-Doberlet 2003). With a leg span of 1 cm this creates a time-of-arrival difference between 0.12 ms and 0.25 ms. As the males straddle their legs across the fork to compare the vibrations while searching for the female, the distance between the legs can reach up to 2 cm. This would increase the time-of-arrival delay to up to 0.5 ms (Čokl and Virant-Doberlet 2003; Virant-Doberlet et al. 2006).

Experiments on natural plants, however, do not allow the examination of whether male *N. viridula* use amplitude or time-of-arrival differences to find the female. This question can be answered by vibrating the legs independently and thereby creating time-of-arrival or amplitude differences between receptors. This method enables us to examine both parameters independently. Stink bugs, standing with the legs of one side of the body on a vibrating bridge and with the legs of the other side of the body on a bridge vibrating a short moment later, turn toward the bridge that vibrates first (Hager et al. 2016). Time delays of 0.1 ms are detected and used for tropotactic orientation (Fig. 12.2a). This clearly shows that the stinkbug's temporal resolution matches with the time delays occurring in natural substrates. In experiments with amplitude differences, stinkbugs turn to the side vibrating more. Amplitude differences of 3 dB are sufficient for tropotactic orientation (Fig. 12.2b). Whether such an amplitude difference reliably occurs on plants is under discussion (Mazzoni et al. 2014; see Sect. 12.4). Furthermore, contrary

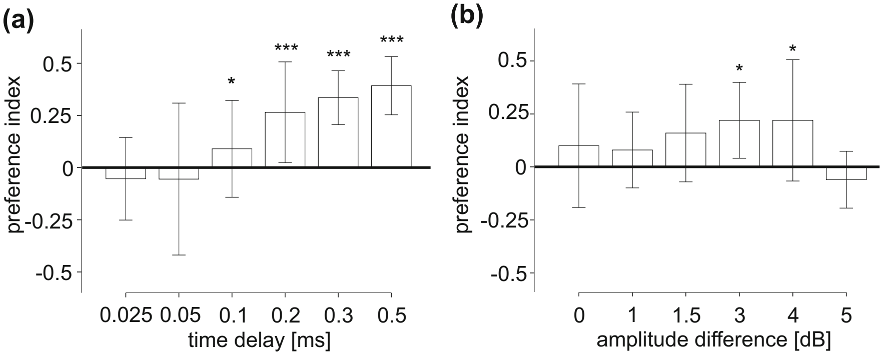


Fig. 12.2 (**a**) Behavioral response of male *Nezara viridula* standing on two bridges that were vibrated independently. Preference indices in relation to the time delay of vibrational stimuli generated with the two bridges. (**b**) Preference indices of *N. viridula* in relation to amplitude differences (Hager et al. 2016)

combinations of a time-of-arrival and amplitude differences were tested. It was possible to counterbalance time-of-arrival differences with amplitude differences (Hager et al. 2016). This could be explained by decreasing latency of the vibratory interneurons with increasing stimulus intensity, as it was found in a cave cricket (Stritih 2009).

Recently a very comprehensive study revealed that on bean plants (*Phaseolus vulgaris*) only time delays are reliable cues (Prešern et al. 2018). At the junction between the main stem and the leaf stalks, the male placed his legs on different sides of the branching and orientation at the branching point was not random. Measurements with laser vibrometers clearly show that only a time delay between the arrival of vibrational wave to receptors located in the legs stretched across the branching was a reliable directional cue underlying orientation, since the signal amplitude at the branching point was often higher on the stalk away from the female (Prešern et al. 2018).

12.6.2 Antlions

Antlions are sit-and-wait predators that dig a funnel-shaped pit into loose sand. They sit on the ground within the trap and wait motionless for their prey to approach. The remarkable ability of directional vibration sensing in antlions was recently reviewed by Devetak (2014). As soon as an antlion detects prey, the head and forelegs are moved to collect sand. Subsequently, the sand is tossed with a violent jerk of the head and prothorax in the direction of the prey; thereby a sand avalanche, which eventually pulls the prey in the trap, is caused (Devetak 1985; Mencinger 1998; Fertin and Casas 2007; Mencinger-Vračko and Devetak 2008).

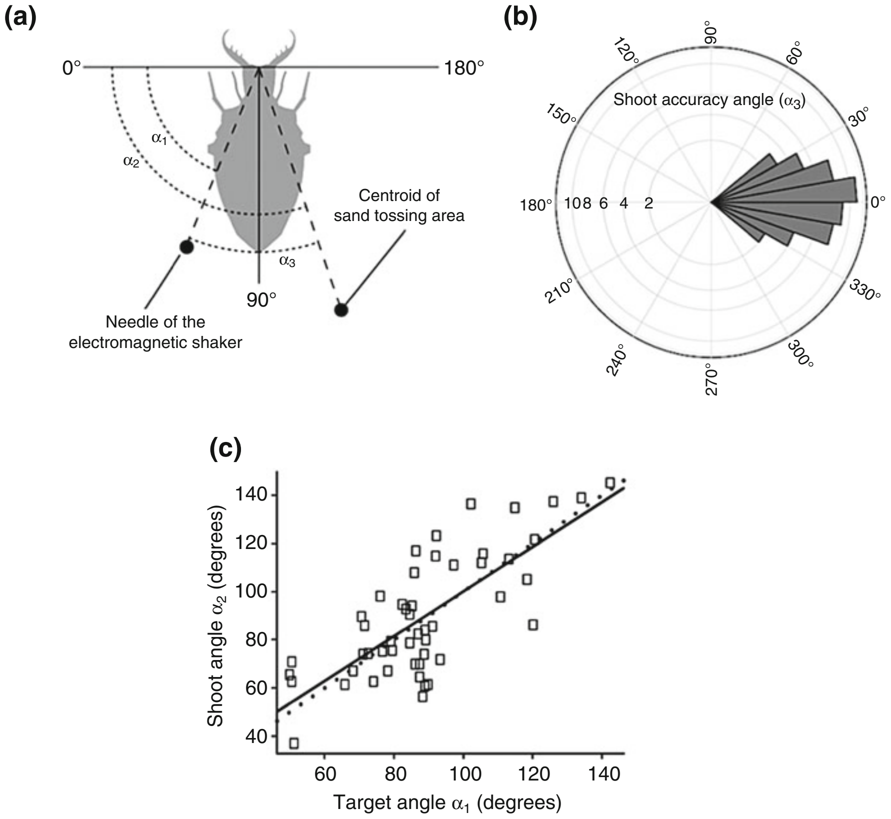


Fig. 12.3 Vibrotropotactic orientation in *Euroleon nostras*. (**a**) Reference frame and angle definition. $\alpha 1$, angle to the tip of the electromagnetic shaker; $\alpha 2$, angle to sand tossing area; $\alpha 3$, angle between tip location and sand tossing area, reflecting the precision of sand tossing. (**b**) Circular distribution of the precision angle of sand tossing ($\alpha 3$). The area of each sector is proportional to its frequency. The scale is indicated on the left half of the circle. (**c**) Angle of sand tossing ($\alpha 2$) as function of the angle of the tip ($\alpha 1$). This response is linear (solid line) and close to the perfect response (dotted line) (Fertin and Casas 2007)

In open-loop experiments, substrate-borne vibrations induced by walking ants were played back with electromagnetic shakers. The angle of sand tossing is a linear function of the angle of the electromagnetic shaker tip with near-perfect correlation—the antlion *Euroleon nostras* throws sand in the direction of the vibration source (Fig. 12.3) (Fertin and Casas 2007). Covering the larval photoreceptors does not affect the antlion's localization ability, thus vision as a directional cue can be excluded (Mencinger-Vračko and Devetak 2008). Antlions usually occupy fine sands or sands with medium particle size (Devetak and Arnett 2015). In those substrates, attenuation with distance is moderate (Devetak et al. 2007). Amplitude differences between receptors might therefore be too small to be detected. Surface

Rayleigh waves in dry loose sand travel with velocities of about 25–35 ms^{-1}, corresponding to time-of-arrival differences in the range of 0.2–0.5 ms, which are most likely in a detectable range (Mencinger-Vračko and Devetak 2008; Devetak 2014). Since it is not possible to investigate the role of amplitude and time-of-arrival differences independently in natural substrates, it remains open which one is the directional cue.

12.6.3 Termites

The termite *Macrotermes natalensis* communicates using vibrational drumming signals transmitted along subterranean galleries (see Chap. 16). When soldiers are attacked by predators, they tend to drum with their heads against the substrate and create a pulsed vibration. Workers respond by a fast retreat into the nest. Soldiers in the vicinity start to drum, themselves, leading to an amplification and propagation of the signal (Hager and Kirchner 2013). Soldiers make use of directional vibration sensing in the context of colony defense. Under closed-loop conditions at the nest surface, soldiers are recruited toward the source of the signal. In arena experiments on natural nest material, soldiers can localize the source of vibration. Experiments under open-loop conditions with two movable platforms allowing one to vibrate the legs of the left and right sides of the body with a time delay show that the difference in time of arrival is a directional cue used for tropotactic orientation (Fig. 12.4). Delays as short as 0.2 ms are sufficient to be detected. Soldiers show positive tropotaxis to the platform vibrating earlier (Hager and Kirchner 2014). The

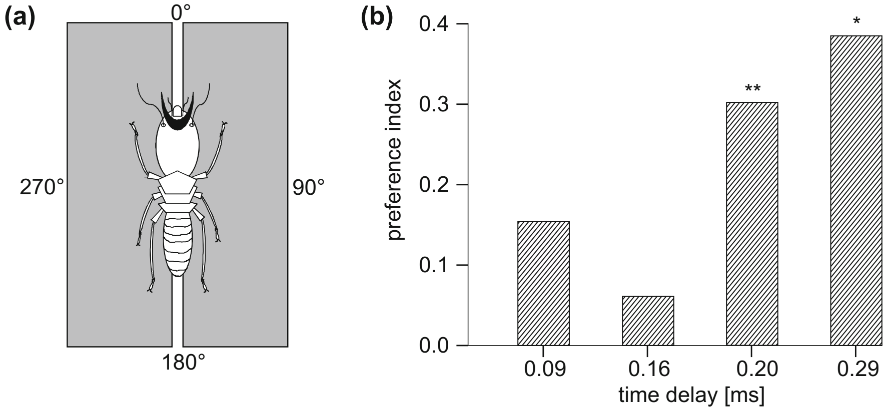


Fig. 12.4 (**a**) Experimental setup for the behavioral test of vibrotropotaxis in *Macrotermes natalensis*. The vibrational stimulus was triggered by an observer when the termite straddled the experimental setup, with the legs of one body side on one platform and the legs of the other body side on the other platform. (**b**) Preference indices of *M. natalensis* in relation to the time delay of vibrational stimuli generated with two movable platforms (Hager and Kirchner 2014)

propagation velocity of the vibrational signal in the termites' nest is approximately 130 ms^{-1}, and with distance between the leg of 16 mm, time-of-arrival delays of 0.12 ms are created (Hager and Kirchner 2013). This is in the same range as the time delays detected by the termites. Whether amplitude differences are used, additionally, for vibrotaxis remains open.

12.6.4 Stoneflies

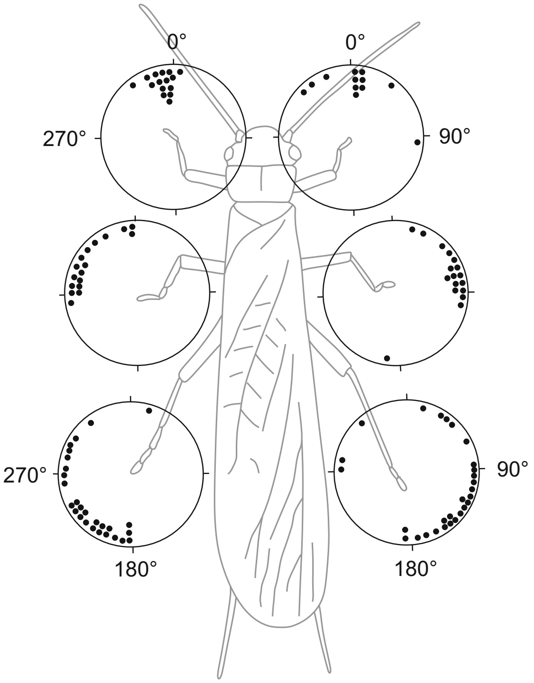
Stoneflies (Plecoptera) of the suborder Arctoperlaria have developed a very diverse and complex system of vibrational communication (Stewart and Sandberg 2006). Vibrational signals are produced by drumming, stridulation, and tremulation with either the unmodified or specialized distal ventral portion of the abdomen. In the context of mate location, a species-specific duet is established: the male call is answered by the female, and in some species the male then replies (Rupprecht 1968, 1969; Stewart and Sandberg 2006). In most species, males search for the stationary females. The transmission range of vibrational signals through dead plants in the medium-sized stonefly *Perlinella drymo* is up to 8 m (Stewart and Zeigler 1984). Several studies demonstrate that once a duet is established males find the female faster, compared to trials in which the females do not reply (Rupprecht 1968; Abbott and Stewart 1993).

In a pioneering study, Rupprecht (1968) carefully described the production, temporal pattern, and behavioral context of drumming signals in European stoneflies (Plecoptera). He could show that drumming signals travel through the substrate and are perceived by the subgenual organ in the legs. Moreover, he demonstrated in *Perla marginata* that substrate vibrations are used for orientation by gluing small iron filings to the tarsi and vibrating single legs with an electromagnet. The stoneflies turn in the direction of the stimulated leg (Fig. 12.5). If one of the front legs is stimulated, the stoneflies move ahead; if one of the hind legs is stimulated, the stoneflies turn around and move backward (Fig. 12.5). By stimulating a middle leg, the stoneflies move in circles (Rupprecht 1968). This is the typical behavior one can observe if one of two receptors is eliminated in insects normally performing tropotactic orientation. This study would probably have gained much more attention, if it had been published in English rather than in German.

12.6.5 Leafcutter Ants

Leafcutter ants communicate with the substrate-borne component of the vibratory emission produced by stridulation. They stridulate by raising and lowering their gaster, so that a cuticular file located on the first gastric tergite is rubbed against a scraper situated on the preceding third abdominal segment (Roces et al. 1993). *Atta sexdens* and *A. cephalotes* workers stridulate when they cut an attractive leaf.

Fig. 12.5 Vibrotropotactic orientation of the stonefly *Perla marginata* after the respective single legs were vibrated independently by gluing metal filings to the legs and vibrating with an electromagnet (modified from Rupprecht 1968)



The vibrations migrate along the body of the leafcutter ant and are transmitted from the ant's head to the substrate. Nearby workers respond to the vibrations transmitted through the plant material by orienting toward the source of the vibration and subsequently join in leafcutting (Roces et al. 1993; Roces and Hölldobler 1996). Workers also stridulate when they are buried by a cave-in of the nest and thereby attract other workers, which subsequently start to dig and rescue the buried ant (Markl 1967). Workers of *Atta vollenweideri* stridulate while engaged in nest digging and attract nestmates to join excavation activity at the same location, thus contribute to the spatial organization of collective nest building (Pielström and Roces 2012).

Open-loop experiments with two movable bridges reveal that time-of-arrival delays of the vibrational signals are used for tropotactic orientation in *A. sexdens* (Fig. 12.6). Ants, standing with the legs of one body side on a vibrating bridge and with the legs of the other body side on a bridge vibrating a short moment later, turn toward the side that vibrates first. With time delays down to 0.1 ms, ants turn more often to the side vibrating first (Hager et al. 2017). It is perfectly possible that time delays in this range can be found in natural substrates; although, leafcutter ants routinely move through different environments while foraging and are found on diverse surfaces such as the nest substrate, the surrounding soil, plant stems, and leaves. The transmission properties may dramatically differ from substrate to substrate. In this context, it would be interesting to analyze the vibrations produced

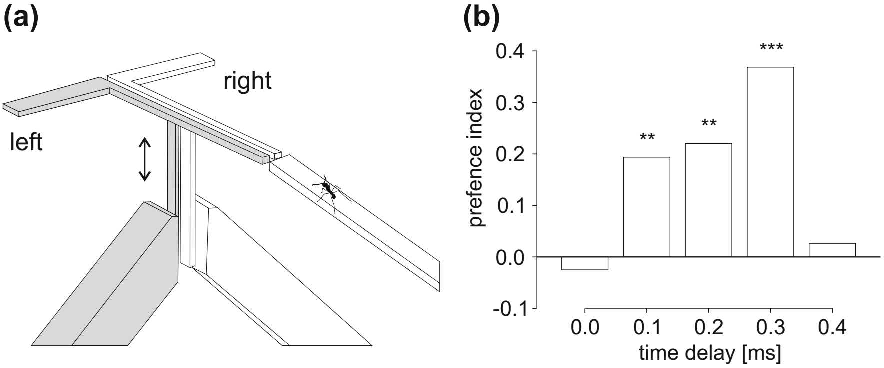


Fig. 12.6 (**a**) Experimental setup to test vibrotropotaxis in ants. Foraging *Atta sexdens* walked over a bridge to enter the experimental setup. Two L-bridges were vibrated independently with short time delays when an ant walked with three legs on one side and with the three other legs on the other side. (**b**) Preference indices of *A. sexdens* in relation to the time delay of the vibrational stimuli generated with the two movable bridges (Hager et al. 2017)

by signaling ants and to answer the question whether leafcutter ants pursue a generalist strategy by producing signals that are effective across the range of substrates they encounter.

12.6.6 Backswimmer

The well-studied backswimmer *Notonecta glauca* makes use of vibrational waves travelling on the surface of water to detect its prey. It swims upside-down and touches the water surface with the legs of the pro- and mesothorax and the tip of its abdomen. The two hind legs are specialized for strong swimming strokes that are directed toward prey that falls in the water. The struggling prey causes concentric boundary waves at the interface between air and water. The waves propagate across the two-dimensional plane and its velocity depends on surface tension, water density, gravity, wavelength, and water depth (Markl 1983). The attenuation of the wave’s amplitude depends on its frequency, with high attenuation above some 10 Hz. For an attenuation of 6 dB, a 5-Hz wave may travel 6 cm, while a 140-Hz wave is already diminished by the same amount over only 0.7 cm distance (Lang 1980). Struggling prey insects on the water surface induce the strongest waves in the frequency range of 10–100 Hz (Wiese 1972). *N. glauca* is sensitive to surface vibrations of 5–300 Hz and the threshold is lowest at around 100 Hz, expressed as displacement, or between 5 and 20 Hz, expressed as acceleration (Markl and Wiese 1969). The dispersive characteristics of water surface waves, the vibrational cues emitted by the prey, and the perception threshold of the predator perfectly match at around 20 Hz.

The backswimmer's orientation toward prey, i.e., the source of vibration, is very precise. If the prey is in front of the backswimmer, it turns instantaneously with about 2° accuracy toward the prey. A source of vibration located behind the backswimmer induces responses with a slightly decreased accuracy of 18° (Markl et al. 1973). Wiese (1972) proposed that time-of-arrival and amplitude differences between receptors are used for tropotactic orientation. Electrophysiological experiments showed that sinusoidal waves in the frequency range of 0.5–150 Hz elicit one response of the phasic receptors per sine cycle. Having in mind that the backswimmer touches the water surface with four receptors in the legs and maybe one in the abdomen, it appears likely that time delays between responses of different receptors are transduced into the adequate turning angle.

Amplitude differences, however, appear unlikely to be compared accurately. This is mainly because the amplitude attenuation of the surface wave over a distance of 10 mm, this corresponds with the distance between the leg positions on the water surface, is much smaller than the perceptual threshold in the relevant frequency range (Wiese 1972). Wiese (1974) conducted an elegant experiment by gluing iron filings to the backswimmer's claws. Four electromagnets were allowed to vibrate the four legs independently (Fig. 12.7a). According to the distance between the insects' legs, i.e., vibration receptors, time delays, i.e., phase shifts of a traveling 20 Hz surface wave, were simulated (Fig. 12.7b). Simulation of surface waves evoked turning reactions well matching the expectations (Fig. 12.7c, d). This experiment clearly shows that time differences caused by phase shifts are used for tropotactic orientation. The time delays are in the range of 8–16 ms (Wiese 1974). Moreover, prey-induced vibrations show characteristic temporal structures and frequencies and the backswimmer makes use of these surface waves to discriminate prey from nonprey (Lang 1980).

12.7 Conclusion

Vibration sensing is at one end of a continuum in the mechanoreceptor-based system for detecting signal sources. This continuum also includes tympanal hearing (Hoy and Robert 1996). Several mechanisms have been identified by which acoustic parameters may be represented in receptor responses, including temporal coding for directional information. Directional sound sources generate intensity differences at the two ears, so that interaural differences in response rate or latency, or both, could encode directional information (Mason and Faure 2004). With the exception of the fly *Ormia ochracea* (the eardrums are mechanically coupled), pressure difference reception has become the standard explanation for directionality in small animals (Michelsen and Larsen 2008). Insect auditory systems have to deal with time delays that are even smaller than those occurring on many substrates used for vibrational orientation. In locusts, the interaural time differences are in the range of 0.01 ms (Mörchen et al. 1978), and they are even less in smaller insects such as the tiny fly *O. ochracea*. As this fly's eardrums are less than 0.5 mm

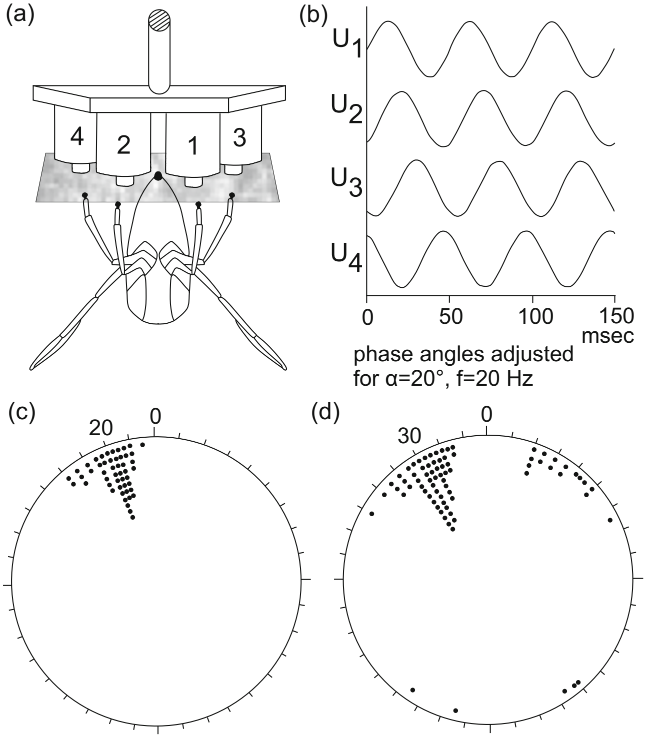


Fig. 12.7 Vibrotropotactic orientation in *Notonecta glauca*. (**a**) Experimental setup to simulate water wave stimuli. Iron filings were glued to the claws and vibrated independently by local alternating magnetic fields. (**b**) The shifting of phase angle corresponds to the travel times of the wave front between the four receptors under stimulation. (**c**) Reactions of *Notonecta* to simulated wave signals for $\alpha = 20°$ (**d**) and for $\alpha = 30°$ (modified from Wiese 1974)

apart, interaural time delays used for orientation are approximately 50 ns (Mason et al. 2001). Insect auditory organs solve the problem either mechanically in the periphery, by translating time delays in amplitude differences, or neuronally through binaural interactions inducing latency differences in the manageable range of some hundred microseconds to a few milliseconds (Mason et al. 2001; Schöneich and Hedwig 2010). The latency of insects' neuronal responses is inversely related to the intensity of the stimuli (Gerhardt and Huber 2002). In the nonhearing cave cricket *Troglophilus neglectus* latency of the vibratory interneurons decreased with increasing stimulus intensity (Stritih 2009). At the integration level, such intensity-dependent time delays could enhance the time delay of arrival of the signal at different legs (Virant-Doberlet et al. 2006). On a physiological level, auditory perception is much better studied than vibrational perception. Since the vibratory mode is ancient, it would not surprise if similarly sophisticated mechanisms have evolved for directional vibration sensing. We can look forward to exciting findings in this field.

As shown here, behavioral studies reveal the remarkable ability of insects to orientate via vibrational cues and signals in various contexts. Future studies should combine behavioral, physiological, and physical aspects to gain a comprehensive understanding of directional vibration sensing. An interesting hypothesis could be tested by vibrating all six legs of free-moving insects, independently with electromagnets, as it was done by Rupprecht (1968). We may be surprised that such a clever method has not been applied with current technical achievements.

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Part V

Biology and Evolution of Vibrational Behavior in Some Well-Studied Taxa

Chapter 13
Vibrational Communication in Elephants: A Case for Bone Conduction

Caitlin O'Connell-Rodwell, Xiying Guan, and Sunil Puria

Abstract We present new physiological data on bone conduction hearing from cadaveric temporal bone ears of an elephant. We discuss the results in the context of the elephant's ability to detect and interpret ground-borne vibrations as signals and compare with similar measurements in a human cadaveric temporal bone ear. Large ossicles are potentially indicative of superior bone conduction hearing, and elephant ossicles are the largest among terrestrial mammals. Using 3D laser vibrometry, we measured stapes velocity in each x, y, z planes and the promontory velocity to determine relative velocity as an indication of vibrational input to the cochlea via the footplate. Since elephant ossicles are at least seven times the mass of human ossicles, we compare the sensitivity of both species to vibrations in the frequency range of 8–10,000 Hz and report that elephants have up to an order of magnitude greater sensitivity below 200 Hz, indicating a heightened sensitivity to bone conduction hearing in comparison to humans.

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13.1 Introduction

The vibration sense is employed by a wide range of taxa as a mechanism of prey detection, predator warning and avoidance, habitat sensing, as well as communication (Hill 2008). Understanding the use of vibrations in communication is an expanding field of research within animal communication.

In small mammals, vibrational signaling and detection is described in a number of small rodents, including the blind mole rat (Rado et al. 1987; Nevo et al. 1991), the cape mole rat (Narins et al. 1992), and the kangaroo rat (Randall 1989, 1997). The golden mole uses a head dipping behavior to navigate the seismic environment and orient toward prey (Narins et al. 1997). Foot drumming in the context of deterring predators or in defense has been described in kangaroo rats, rabbits, skunks, and other small mammals (Randall 2001). The foot thumping behavior of kangaroos (Gregory et al. 1986), body slams of elephant seals (Shipley et al. 1992), and trunk banging in the elephant (for review see O'Connell-Rodwell et al. 2001) indicate that these larger species also make use of percussive vibrations as a threat. Although the propagation of percussive signals by these large mammals has not been measured, a human can generate vibrations by jumping that are measurable at a distance of 1 km (O'Connell-Rodwell et al. 2001; Arnason et al. 2002), showing that large mammal percussive vibrational signals have the potential of propagating long distances. For example, an elephant mock charge ends in a foot-stomping behavior that generates vibrations with energy that could propagate at least as far as sound and models suggest much further (O'Connell-Rodwell et al. 2000a).

In this chapter, we report preliminary physiological measurements on the elephant's sensitivity to bone conduction in the context of vibrational communication. We then compare the sensitivity of elephants to bone conduction relative to humans—a terrestrial large mammal where bone conduction has been a focus of clinical and scientific study, and whose ossicles are only a seventh the size. We also discuss the implications of bone conducted hearing in light of the elephant's ability to detect and interpret ground-borne vibrations as meaningful signals. See O'Connell-Rodwell (2007) and O'Connell-Rodwell and Wood (2010) for a broader, more thorough review of elephant communication via ground vibrations.

13.1.1 Overview of Vibrational Communication in Elephants

Elephant low-frequency (20 Hz) rumble vocalizations are generated at such high amplitudes (on the order of 90–100 decibels SPL at 5 m) that they couple with the ground through the feet and propagate along the surface of the earth in the form of Rayleigh waves, maintaining a separate velocity than their airborne counterparts (O'Connell-Rodwell et al. 2000a). These substrate-borne vibrational cues have the same temporal and frequency structure as the simultaneously propagated bioacoustics signal that propagates in the air, but the distance travelled, and propagation velocities of these signals depend on signal frequency and energy level, geological conditions of the substrate, and frequency-dependent absorption (see O'Connell-Rodwell 2007; O'Connell-Rodwell and Wood 2010 for reviews).

Elephants detect and respond appropriately to seismically transmitted antipredator vocalizations as measured by an increase in vigilance, freezing behavior, a change in orientation, and a decrease in time spent at the waterhole upon presentation of the signal (O'Connell-Rodwell et al. 2006). When played back through the air, these same vocalizations elicit an immediate flight response (O'Connell-Rodwell et al. 2000b). Elephants discriminate between familiar and unfamiliar callers through the ground, demonstrating the ability to distinguish subtle differences in frequency modulation between individual callers (O'Connell-Rodwell et al. 2007).

The interactive pattern of vocalizations that occurs during the "let's go" rumble volley during the time when a family group, or bonded group of males, leaves the waterhole results in a longer repeated signal that would facilitate detection at greater distances than a vocalization generated in isolation. These signals are three times the length of single vocalization (9 vs. 3 s), thus increasing the signal-to-noise level and reducing the noise floor to improve detection both in the air and in the ground (O'Connell-Rodwell et al. 2012).

13.2 Bone Conduction

13.2.1 Introduction

Elephants have two possible pathways for the detection and interpretation of vibrational signals, either through bone conduction to the cochlea, with processing in the auditory cortex, or through vibration-sensitive mechanoreceptors in their feet and trunk that are transmitted to the somatosensory cortex (O'Connell et al. 1999). Animals that use bone conduction to detect seismic signals have enlarged ossicles, the malleus being particularly hypertrophied, which facilitates independent oscillations of the middle ear bones relative to the skull due to inertia (Reuter et al. 1998). When vibrations transmit through the bone, they first couple with the ground via the feet and then travel up through the legs and shoulders and into the middle ear ossicles and cavity, then to the cochlea, or, in the case of some marine mammals and small rodents, straight through the skull, to the cochlea via the ossicles (Rado et al. 1998).

13.2.2 Anatomical Features Suited to Vibration Detection via Bone Conduction

The generation of low-frequency acoustic signals may be facilitated by the elephant's large diaphragm, by a larynx with five rather than the nine bones present in most other mammals (Shoshani 1996) and an unusually large nasal cavity. In addition, all head bones of the African elephant's skull are aerated by sinuses (van der Merwe et al. 1995) and except for the solid mandible, the cranium consists of inflated bones compartmentalized to form diploe (Shoshani 1996). These fatty deposits and aerated skull sinuses in the elephant may facilitate vibration detection.

A novel sphincter-like skeletal muscle surrounding the external auditory meatus of the elephant ear, described in a forthcoming paper from O’Connell-Rodwell and colleagues, contracts upon tactile stimulation, occluding the opening of the ear canal. This occlusion would serve to damp acoustic signals, facilitating better detection in the seismic environment. In addition, pressure builds up in a sealed air canal creating what is known as a “closed acoustic tube” that enhances bone conduction (Stenfelt et al. 2003). This anatomical feature, potentially a remnant of an aquatic ancestry, may facilitate acoustic reception of lower frequencies and/or a bone-conducted pathway for seismic detection.

13.2.3 Behaviors Indicative of Bone Conduction Vibration Detection

Behaviors facilitating bone conduction have been documented in a number of mammalian species, most notably, the blind mole rat exhibits “jaw-listening” behavior, where it places its jaw against a substrate to facilitate vibration detection (Rado et al. 1998). The golden mole, having the largest malleus relative to body size of any animal (Mason and Narins 2002), exhibits freezing and head dipping behavior to better couple the skull to the substrate (Narins et al. 1997).

Elephants also engage in a freezing behavior while detecting vibrational information, such that they lean forward, placing more weight on their larger front feet. Due to the unique graviportal structure of their forelimbs, leaning forward places the foot directly in line with the ear (O’Connell-Rodwell et al. 2006). The elephant, or group of elephants, then continues walking and then freezes again, often mid-stride. This periodic freezing behavior is very similar to the golden mole, with perhaps a similar navigational goal, whereby they may be able to localize the signal source and choose a direction based on information obtained during the freezing and assessment period (Fig. 13.1).

A recurring pattern during playback experiments is that elephants tend to position themselves perpendicular to the source of a seismically transmitted signal. Figure 13.2a–c depict still frames captured during a video recording of a male elephant in musth responding to an estrus call playback broadcast through the air and ground. This perpendicular positioning would create the greatest distance between the ears as receivers, rather than the feet. Positioning in order to obtain the greatest distance between receivers would facilitate localization, and being adjacent would provide a half-meter distance between ears, versus about 2.5 m between front and back feet if the elephant was positioned parallel to the source (O’Connell-Rodwell et al. 2000a). This pattern occurs despite the orientation of the elephant in relation to the signal source at the time of detection.

There should not be directionality attributable to bone conduction hearing, as the ossicles in both ears would receive vibrations from the whole skull and thus should

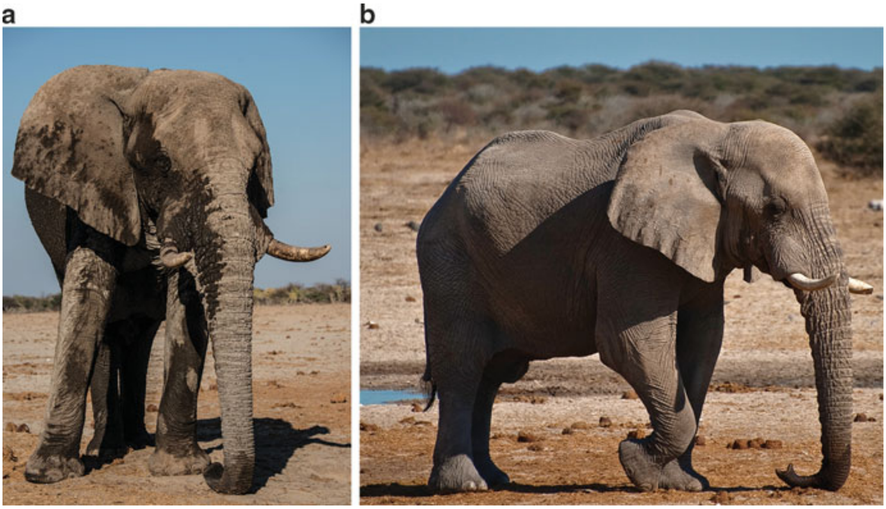

Fig. 13.1 Elephant vibration detection posture. (**a**) Upon signal detection, an elephant appears to focus solely on somatosensory detection via receptors in the trunk. Ears are relaxed, indicating no assessment of the airborne environment. (**b**) Elephant vibration detection posture, where the elephant appears to be using both toenails and trunk to assess a ground-borne signal, its ears not fully extended. This posture suggests an assessment both via bone conduction through the toenails, as well as a somatosensory pathway through Pacinian corpuscles in the trunk. Other posture includes leaning forward on the front legs with ears flat, and sometimes one of the front feet is lifted off the ground (possibly for the purpose of triangulation or better coupling). If focused on an acoustic signal, an elephant holds its ears out and scans its head back and forth in the direction of the sound. Photo credits O'Connell and Rodwell

vibrate at the same time and with the same intensity. This differs from localization of an acoustic signal where the two middle ears in most mammals are isolated, and thus interaural time differences or phase differences at low frequencies and interaural level differences at high frequencies are detectable.

A direct connection between the two tympanic cavities is known only in two subterranean species, the talpid moles and most species of golden mole (Mason 2016). This feature is thought to improve low-frequency hearing and localization through the detection of pressure differences [similar to non-mammalian tetrapods (Christensen-Dalsgaard 2011)]. If the elephant had a direct connection between the two tympanic cavities, detection of low-frequency acoustic signals might be enhanced as it is in these other species, but the possibility of this anatomical feature playing a role in vibrational localization via bone conduction is yet to be determined.

Another noteworthy behavior during seismic detection (in isolation of acoustic detection) is that elephants seem to orientate along compass directions. Upon detection of a signal, some amount of time is spent freezing, leaning forward with a length of the trunk on the ground in a particular direction. A few minutes into the assessment, the elephant shifts about 45° and then resumes the seismic listening posture. This change of compass direction is done several times in at least three

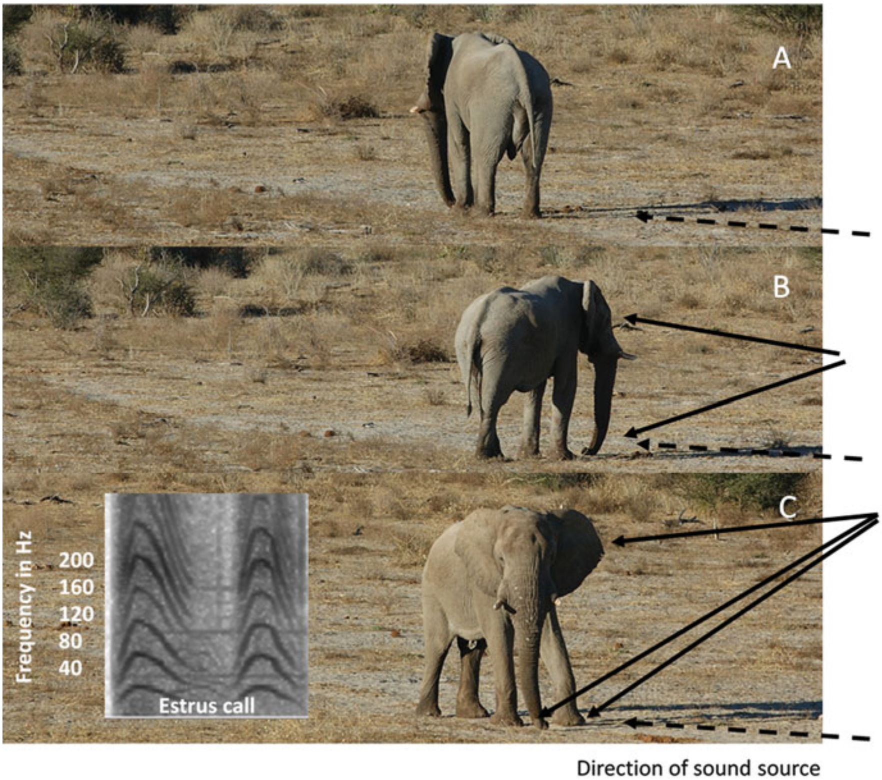

Fig. 13.2 Video stills of an estrus call playback to a male elephant in musth. (**a**) After presentation of the estrus call, the male elephant in musth approaches the signal source and then passes it, walking away along the same compass direction, as if searching for the source in the distance. (**b**) Upon the second presentation of the signal, the elephant turns perpendicular to the signal source, freezing with ears flat to side and trunk on ground. (**c**) After spending time accessing the signal while positioned adjacent to the signal source, the elephant turns and faces the signal source directly. Photo credits O'Connell and Rodwell

different orientations prior to a decision with regard to the direction of departure. This behavior is most often observed when a group of bonded males are making an assessment about a direction of departure, each orientating in a different compass direction at the same time (Fig. 13.3).

Cartilaginous fish such as sharks and rays, as well as a few other fish, have special sensory cells, the ampullae of Lorenzini, capable of detecting electrical and magnetic fields. There is evidence that sharks use this sense to navigate along magnetic fields (Meyer et al. 2005). Another study shows that cattle and deer align along magnetic fields, but there has not been a comprehensive study on large mammals to show the use of magnetic fields in navigation (Begall et al. 2008). Given the elephant's seismic detection behavior, it is worth posing such a question in future studies.

Fig. 13.3 A group of bonded male elephants positioned in different compass directions, each one assessing both the air and the ground for environmental cues as well as possibly seismic information generated by other elephants as to which direction to head after drinking at the waterhole. Usually, the most dominant male decides on a direction and the rest follow him, most often in the opposite direction from the arrival path of a rival male in musth. Photo credits O'Connell and Rodwell

When a playback experiment is presented both in the air and in the ground, simultaneously, the adjacent positioning of ears to the source would suggest that elephants are using interaural time differences to assess the direction of the signal through the air (Fig. 13.2b). However, when the signal is present in both environments, elephants appear to defer to a seismic assessment first (freezing, shifting weight forward, ears flat to the sides, and trunk on ground) and a preference for bone conduction rather than the somatosensory channel (greater distance between ears as receivers vs. feet) prior to scanning the acoustic environment with ears held out and trunk held up to assess olfactory gradients.

Barring some other explanation, perhaps there is some feature of bone conduction that allows elephants to assess directionality and the concept of localization in bone conduction should be revisited. Due to attenuation of vibrations through the skull at higher frequencies (Stenfelt and Goode 2005), it may be possible to lateralize BC vibrations through the skull due to interaural level differences.

Overall, elephants adopt specific vibration detection postures that are suggestive of either pathway of detection, not just bone conduction. During freezing, sometimes weight is positioned on the toenails, which would facilitate bone conduction, while at the same time, placing a length of the trunk on the ground. It is yet to be determined whether the trunk might play any role in bone conduction, but this behavior would facilitate vibration detection through the somatosensory pathway via the dense distribution of vibration-sensitive Pacinian corpuscles present in the foot (Bouley et al. 2007) and trunk (Rasmussen and Munger 1996).

Behavioral responses to seismically generated playback stimuli indicate that elephants often appear to exhibit behaviors indicative of both modes of detection and only sometimes show a preference toward one pathway or the other. Hence, mechanistically, both somatosensory and bone conducted acoustic pathways appear to provide information to the elephant. It is not known whether either pathway might provide a cleaner channel for signal transmission and detection than the other.

While we have examined the somatosensory pathway in depth, elsewhere, here we focus on bone conduction and how vibrational signals might be enhanced via a bone conduction pathway.

13.2.4 Why Mass Matters

Larger mass is positively correlated with better hearing at low frequencies (Hemila et al. 1995), particularly in relation to bone conduction hearing (Stenfelt et al. 2002). Elephant ossicles, the largest among terrestrial mammals, are at least seven times the mass of human ossicles (Doran 1878; Hemila et al. 1995; Fig. 13.4). High-frequency limits are negatively correlated with ossicular mass (Hemila et al. 1995; Coleman and Colbert 2010), such that the larger the mass, i.e., the larger the inertial limitations on motion, the more limited the high-frequency transmission through the middle ear tends to be (Coleman and Boyer 2012), which may explain why elephants cannot hear sounds above 11 kHz, but humans can (Hemila et al. 1995).

We focus our attention on the elephant's middle ear, specifically, due to the assumption that large ossicles would facilitate bone conduction as has been found in other species. Elephants can hear sounds below 20 Hz but not much above 10 kHz,

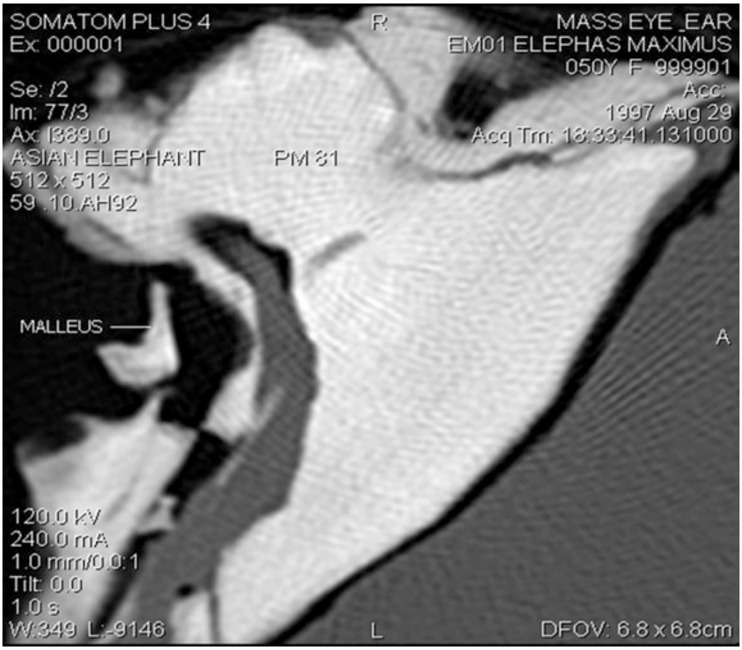

Fig. 13.4 Elephant middle ear ossicles, showing the hypertrophied malleus. CT image courtesy of Darlene Ketten, Mass Eye and Ear Infirmary

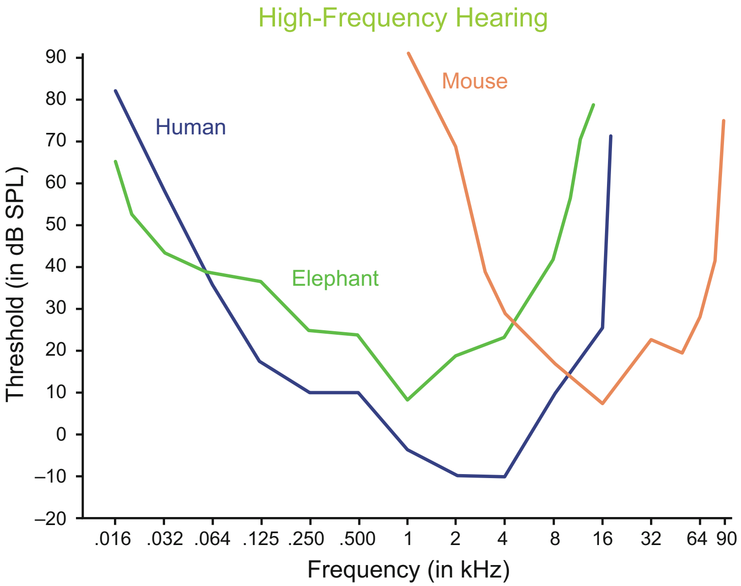

Fig. 13.5 Audiogram for the human, elephant, and mouse (compiled and graphed using Heffner 2004; Heffner and Heffner 1980, 1982)

as compared with human hearing thresholds, which are similar but shifted slightly to the right (Heffner and Heffner 1980), despite such large differences in ossicular shape and size (Nummela 1995). In contrast, these two species differ greatly with the mouse ear, whose frequency thresholds of hearing start and extend much higher [Fig. 13.5 (adapted from Heffner and Heffner 1980, 2007)], making the elephant a more appropriate model for comparison with human hearing, in general.

13.3 Methods

13.3.1 Specimen Preparation

Human ($N = 1$ ear) and African elephant (*Loxodonta africana*) temporal bones ($N = 2$ ears) were harvested and prepared. The adult human specimen was obtained from a donor with no history of otologic disease and was visually screened for middle-ear pathologies upon arrival. The elephant specimen was harvested from a 3-month-old zoo mortality, and both were kept refrigerated and wrapped in saline-soaked gauze until the time of use.

For the human specimen, surrounding soft tissue was removed, and the bony ear canal was shortened to about 1 cm. The facial recess was opened for access to the middle ear. For the elephant specimens, the pinna and soft-tissue section of

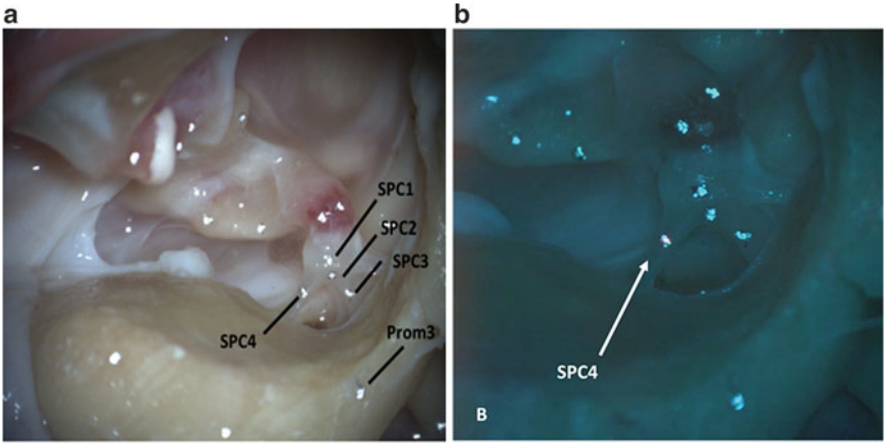

Fig. 13.6 (**a**) Image of an elephant temporal bone specimen fully dissected, the middle-ear cavity viewed through a surgical microscope in the orientation used during measurements, where the umbo, malleus head, IMJ (Incus-Malleus joint), incus body and long process, ISJ (Incus-Stapes joint) and stapes are all visible with retroreflective glass beads applied as the laser targets. The locations along the stapes are labeled here. Four different velocity measurements were made on each ossicle. (**b**) Blow up of same image, showing the laser hitting the glass bead target on SCP4 (anterior crus of the stapes) as seen through the dichroic mirror

the ear canal were removed. The facial recess was opened to expose the middle ear cavity. In the elephant's left ear (ETB1), the large soft structure in the tympanic cavity, which obstructed the malleus and incus heads and the stapes views (except the malleus handle), was removed (Fig. 13.6a).

In the human ear and the elephant's left ear, a number of reflective tape targets (0.2 by 0.2 mm^2) were spread on the ossicular chain for velocity measurement: four on the stapes, four on the incus, and three on the manubrium of the malleus. Figure 13.6b shows the location of the targets in ETB1. In the elephant's right ear (ETB2), four targets were placed only on the malleus handle because the soft septum curtaining the rest of the ossicular chain was left intact.

In all the specimens, three targets were placed on the cochlear promontory. The vibration velocity of the cochlear promontory was collected as a measure of input reference for bone-conduction (BC) and for experimental artifact measurements for air-conduction (AC) stimulations.

13.3.2 Air- and Bone-Conduction Stimulation

To provide AC stimulation, the sound was generated by a loudspeaker (Vifa DPL28, Denmark) coupled to the ear canal via a tube inserted into the ear canal. The gap between the tube and the ear-canal wall was sealed with soft foam. To provide

BC stimulation, the specimen was mounted to a mini shaker (B&K 4810) via a 2-cm long brass rod. Vibration of the shaker mimicked inertial BC stimulation. The orientation of the specimen and the shaker was adjusted to allow access by the 3D LDV to all of the points within the same reference frame.

13.3.3 Measurements of 3D Velocities and Ear Canal Sound Pressure

3D velocities at different locations of the ossicles in response to AC or BC stimulation were measured using a Polytec (Waldbronn, Germany) CLV-3D LDV system, mounted on three motorized and computer-controlled linear translation stages, which allowed the specimen to stay fixed while only the laser was moved to focus on different locations. The motion of these stages, with a resolution of 6.25 μm, was controlled by SyncAV software, which also generated the stimuli and recorded the synchronous responses. The coordinates of each measurement point were obtained and saved by SyncAV. This allowed the 3D LDV to precisely return to any of the previously measured locations.

The three laser beams of the 3D LDV were reflected into both the human and elephant specimens by a dichroic mirror to allow visualization of the experimental field by a Zeiss OPMI-1 operating microscope (Fig. 13.6b). A ThorLabs (Newton, NJ) CMOS USB camera (part no. DCC3240C) connected to the microscope was used to monitor and capture images of the specimens during measurements.

For each measurement location, the velocities in the three orthogonal directions were measured simultaneously. The x-direction approximately aligns with the long process of the incus; y-direction aligns with the piston-motion direction of the stapes; z-direction roughly parallels the anterior-posterior direction.

Ear canal sound pressure near the tympanic membrane during AC or BC stimulation was measured using a Knowles microphone (EK 3103) attached to a probe tube, which was calibrated before measurements. The probe tube was inserted through the sealing foam in the ear canal, and the tip of the probe tube was placed within 2 mm of the tympanic membrane.

Generation of the pure-tone stimulus for the speaker and the shaker and recording of the 3D velocities and ear canal pressures were made using SyncAV (v0.34), a custom LabVIEW (National Instruments, Austin, TX)-based data-acquisition program that performs synchronous averaging between the input channels.

AC or BC drive stimulation consisting of 44 pure tones logarithmically spaced from 3 Hz to 10 kHz were presented using either the speaker or the shaker, while the 3D LDV recorded the vibration velocity at any given location. Meanwhile, the ear canal sound pressure was simultaneously recorded.

Data analysis was performed in MATLAB (Mathworks, Natick, MA). The SyncAV Toolbox, a custom set of scripts designed to interface with SyncAV-generated files, was used to organize the data and for visualization of results, including the three components of the velocity at different locations and the ear canal sound pressure.

13.4 Results

The ossicular component of BC hearing is thought to be due to the differential motion between the stapes footplate and the bony rim of the oval window. Because the stapes is not always accessible (e.g., in ETB2), a proxy for the stapes motion is the umbo motion. We calculated the differential velocity of the stapes and the umbo with respect to the cochlear promontory near the oval window for each specimen. To compare the results across ears, the differential velocities were normalized by the promontory velocity in z direction, which is the dominant motion direction of the entire specimen in the current configuration. Results are depicted in Fig. 13.7 for the 8 Hz–10 kHz frequency range, where the signal-to-noise ratios of each of the measured velocities were 13 dB, or greater.

13.4.1 Relative Umbo Velocity in Elephant and Human Ears

Figure 13.7 displays the x (A), y (B), and z (C) components of the magnitude of the relative umbo velocities in elephant and human ears stimulated by BC. The relative umbo velocities, in the left and right elephant ears, across frequencies are similar in all three directions. Despite some local resonances, the relative velocity generally increases with a slope of about +15 dB/decade in the y and z directions and of almost +20 dB/decade in the x direction in the 10–1000 Hz range. Above 1 kHz, the velocities appear to plateau.

In the human ear, the three components of the relative umbo velocities also show some common frequency-dependencies: (1) below 100 Hz the velocity stays low and flat, (2) in the 100–3000 Hz range, the velocities increase rapidly with a slope of as much as 40 dB/decade, and (3) at above about 3000 Hz, the velocities appear to plateau.

Comparison of the relative velocities between the two species for BC stimulation indicates that the umbo of the elephant vibrates with greater amplitude than that of the human from 8 Hz to about 2000 Hz. In the x and y directions, the differences are about 16 dB on average, while for the z direction the differences are about 12 dB on average. Above about 2000 Hz, differences between the elephant and human umbo motions are minor.

13.4.2 Relative Stapes Velocity in Elephant and Human Ears

Figure 13.7d–f show the relative velocity of the stapes in the 8–10,000 Hz frequency range for the three directions in the elephant and the human ears. Similar to our analysis of the umbo velocity, we calculated the differential velocity of the stapes

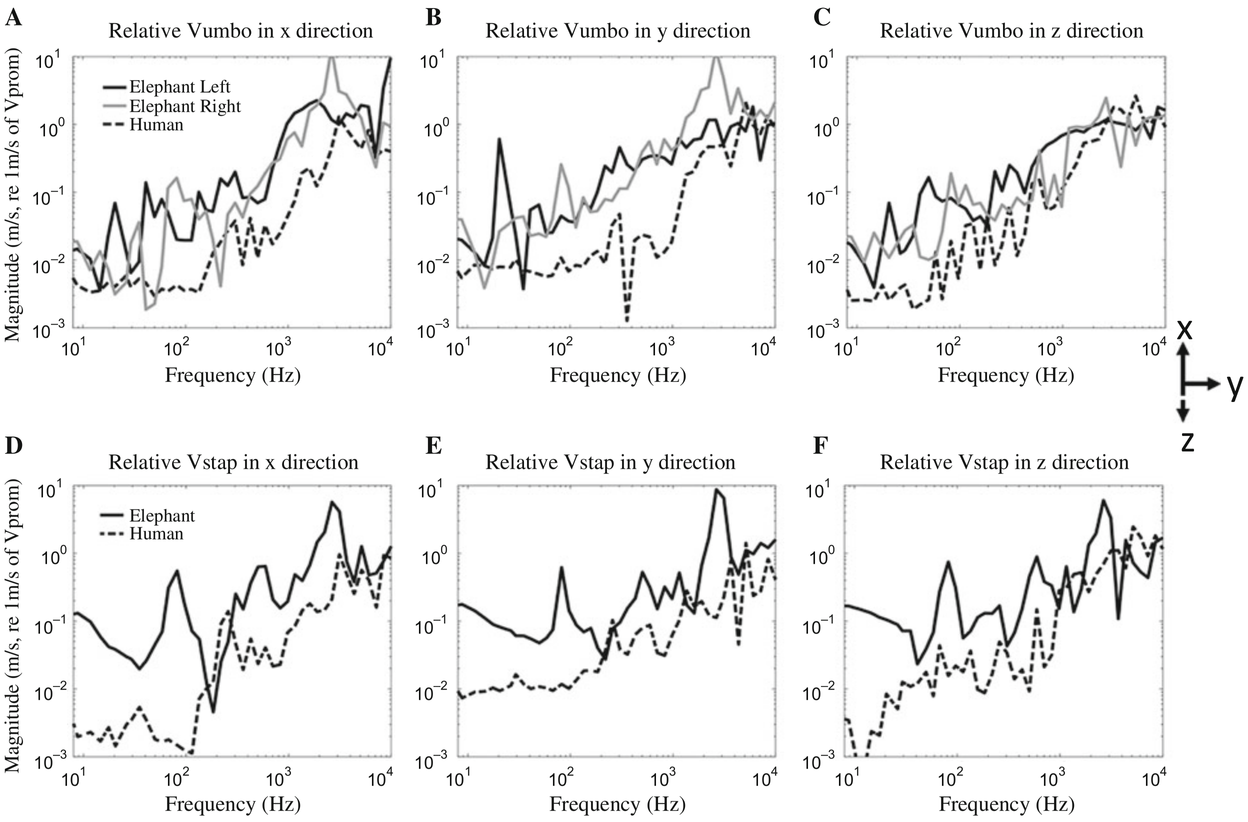

Fig. 13.7 (continued)

in each of the three orthogonal directions and normalized them by the promontory velocity in the *y*-direction.

A striking finding is that at frequencies below 3 kHz, the relative velocity of the stapes in all directions in the elephant is generally greater than that in the human ear. Between 8 Hz and 100 Hz, the difference between the two species is more prominent: the relative velocity of the elephant is greater than that of the human by up to ~40 dB in the *x* and *z* directions and by 20 dB on average in the *y* direction.

The elephant stapes velocity manifests large resonant and anti-resonant peaks in all three components. However, the overall amplitudes across the frequencies are similar among the three components. In each direction, the relative velocity is in general greater at higher frequencies.

In the human ear, the shapes of the three components of the relative stapes velocities across frequency more or less resemble those of the umbo velocity: they are flat at low frequencies, increase with frequency over 100–2000 Hz, and do not change much at higher frequencies. Below about 100 Hz, the velocity in the *x* direction is about 2–5 times lower than that in the *y* and *z* directions.

If we assume that the piston direction of the footplate via the stapes (the *y*-direction) is representative of the ossicular contribution to BC hearing, the result (Fig. 13.7e) suggests that the sensitivity of the elephant middle ear is superior to that of the human middle ear for the bone conduction pathway below approximately 200 Hz.

13.5 Discussion

The up to an order of magnitude increase in sensitivity to bone conduction of elephants (relative to humans) below about 200 Hz (Fig. 13.7) was unexpected, but makes sense in light of previous research showing the elephant's use of vibrations in communication. The difference in sensitivity in two species with similar auditory thresholds highlights why inter-species hearing and vibration sensitivity comparisons are important. Of particular interest are comparisons of species that have similar thresholds but are slightly offset on either end of the frequency spectrum. The fact that elephants have higher sensitivity to bone conduction at the low-frequency threshold relative to humans, and yet a slightly lower frequency limit at the high-frequency threshold of human hearing, could be instructive as a model

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Fig. 13.7 (continued) Measurement of velocity of the umbo and stapes in *x*, *y*, and *z* directions upon vibration stimulation of both the elephant and human middle ear. (**a**), (**b**) and (**c**) depict *x*, *y*, *z* directions in the umbo. (**d**), (**e**) and (**f**) depict *x*, *y*, *z* directions in the stapes. Motions were normalized against the stationary promontory region of the temporal bone. These data demonstrate the elephant's ability to detect vibrations via bone conduction in the frequency range of their vocalizations (20 Hz) and that they have much greater sensitivity to bone conduction in the low frequencies (below 200 Hz) relative to humans

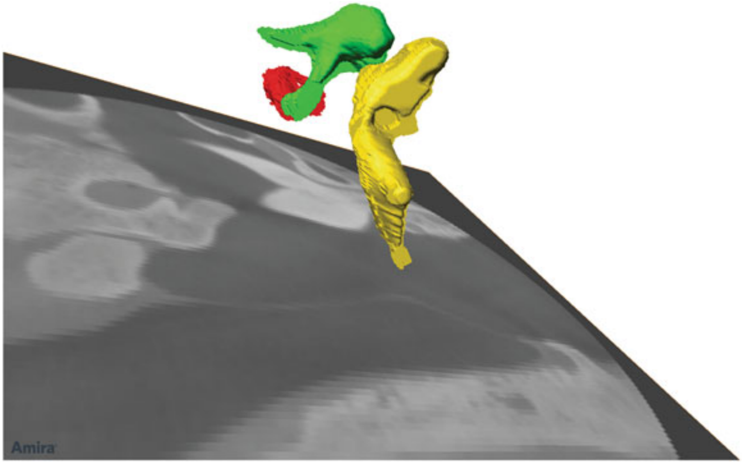

Fig. 13.8 Cone beam CT scan of elephant ossicles (0.09–0.4 mm), showing the shape and relationship among all through middle ear bones. Prior to performing a micro-CT image on this specimen for improved resolution, the current image indicates that the malleus-incus joint may behave differently than in humans and that the increased mass of elephant ossicles may dictate flexibility of motion overall

to understand what factors actually pose limits to human hearing thresholds at both ends of their hearing range.

In future studies, we plan to overlay the x, y, z velocity data from the laser vibrometry onto micro-CT scans of the malleus, incus, and stapes in both elephants and humans to visually compare the relative motion of each ossicle at low and high frequencies under various conditions, including fusing joints. The cone-CT scan of elephant ossicles depicted in Fig. 13.8, shows the shape and relationship between all three middle ear bones in elephants and indicates that the malleus-incus joint may behave differently in elephants than humans, and possibly than previously described, and that the increased mass of elephant ossicles most likely adds to the flexibility of the joints.

The range of frequency modulation within an elephant acoustic alarm call is approximately 15–19 Hz (O'Connell-Rodwell et al. 2007). The minimum perceptible frequency change (Δf) is related to the critical bandwidth (CBW) in the following way: $\text{CBW} = \Delta f * 20$. Therefore, if this equation holds true for elephants, an estimated Δf of 0.75 to 0.95 Hz would allow them to detect very small changes in frequency modulation across calls transmitted through the ground, which would explain their ability to discriminate differences between two callers emitting calls within the same call type (O'Connell-Rodwell et al. 2007).

13.6 Conclusions

The generation of seismic signals in elephants may be a byproduct of vocal communication, but in some situations, may have a larger zone of audibility than its acoustic counterpart. Having the potential to detect the same signal by two different modalities would improve its chances of detection.

The simultaneous monitoring of both airborne and seismic vocalizations can provide cues about the distance of the vocalizing animal, because seismic signals most often travel at a different velocity than their airborne counterparts, which produces a time-of-arrival difference cue that increases with distance from the source (O'Connell-Rodwell et al. 2000a, 2001; Arnason et al. 2002). Seismic communication could supplement airborne communication or be especially beneficial when airborne conditions are not ideal for transmission. In addition, since seismically transmitted signals are less susceptible to the environmental influences that limit airborne transmission, and geometric spreading also produces less attenuation for seismic than airborne vocalizations ($1/\sqrt{r}$ for seismic as opposed to $1/r$ for acoustic), seismically transmitted vocalizations are potentially detectable at greater distances than airborne vocalizations (Arnason et al. 2002), depending on signal strength, soil velocity, and frequency-dependent absorption (O'Connell-Rodwell et al. 2001; Gunther et al. 2004).

The sophistication with which elephants can detect vibrational cues indicates that the ground may be a very important resource for elephants to send and receive signals and assess their environment. With a better understanding of the sender–receiver process, vibrational communication could be viewed as increasing the biological distance to an elephant's already long-distance acoustic communication ability.

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Chapter 14
Seismic Communication in the Amphibia with Special Emphases on the Anura

Peter M. Narins

Abstract Amphibians have been defined as quadrupedal vertebrates having two occipital condyles on the skull and no more than one sacral vertebra. Although this morphologically based definition continues to be valid and accurate, we now know that, in addition, all amphibians studied to date exhibit extreme sensitivity to substrate-borne vibrations. In this chapter, the pathways through which seismic signals are transferred to the inner ear for detection and processing, as well as the most common methods of seismic signal generation in amphibians, are reviewed. Several well-studied examples of amphibians that use vibrational signals for communication are presented, and the case is made for the continued study of seismic signaling in the vertebrates.

14.1 Introduction

Terrestrial seismic communication is the exchange of information between an emitter and a receiver using self-generated vibrational signals transmitted via a substrate such as the soil, a plant stem, or even a blade of grass. The physical characteristics of the substrate can impose important influences on the properties of the received signal including filtering, dispersion, and attenuation. In fact, seismic communication may be defined as the change in behavior exhibited by the receiver as the direct result of having detected a substrate-modified, information-laden signal from the emitter. The receiver may use the information in the signal in reaching a decision about its response, which can ultimately affect the fitness of both the sender and the receiver (Skyrms 2010; Wiley 2013).

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This type of signaling is advantageous since it can occur during the day or night, the signals are effective over a short range and have short persistence—and are thus in little danger of detection by distant predators—and they are relatively unaffected by an inhomogeneous medium. Disadvantages of terrestrial seismic signaling include difficulty in localizing the emitter due to the relatively long wavelengths of the vibrational signals, the physiological limits on the upper rate of seismic signal generation, and the physical constraint that for highest efficiency, emitter and receiver should share a common substrate.

Terrestrial seismic communication in the vertebrates has been the subject of several comprehensive publications (Narins 2001; Hill 2008; Cocroft et al. 2014; Narins et al. 2016). In this chapter, I will review the evidence, both behavioral and neurophysiological, for terrestrial seismic communication in amphibians.

14.1.1 Vibration Pathways to the Ear in Amphibians

Terrestrial frogs have at least two parallel pathways for conducting acoustic energy into the inner ear for processing (Purgue and Narins 2000; Lewis et al. 2001; Mason 2007; Fig. 14.1a). The first is the *airborne* pathway via the tympanic membrane, or in the case of the "earless frogs," via the skin overlying the middle ear structures (Lindquist et al. 1998; Hetherington and Lindquist 1999) and into the fluids of the inner ear capsule via the stapes and its footplate, which abuts against the rostral portion of the oval window, the entrance to the inner ear (Mason and Narins 2002; Fig. 14.1b).

In the second, *substrate-borne* pathway, vibrations are conducted from the substrate, up through the forelimbs to the suprascapular cartilage, then via the opercularis muscle to the cartilaginous operculum, which abuts against the caudal portion of the oval window, and into the fluid-filled inner ear (Lewis et al. 2001; Mason et al. 2003; Fig. 14.1b). It is this second pathway—the pathway through which substrate vibrations are guided to the inner ear for detection and analysis, as well as the generation of vibratory signals for communication—that will be the focus of this chapter.

In the field, vertebrate vibrational signals have been measured using a variety of sensors (Wood and O'Connell-Rodwell 2010) including accelerometers (Barnett et al. 1999), geophones (Narins et al. 1997; Lewis et al. 2001; O'Connell-Rodwell et al. 2000, 2006), or laser Doppler vibrometers (Narins 1992).

14.1.2 Signal Production

Two mechanisms for generating seismic signals have been described among terrestrial anurans: thumping and toe-twitching.

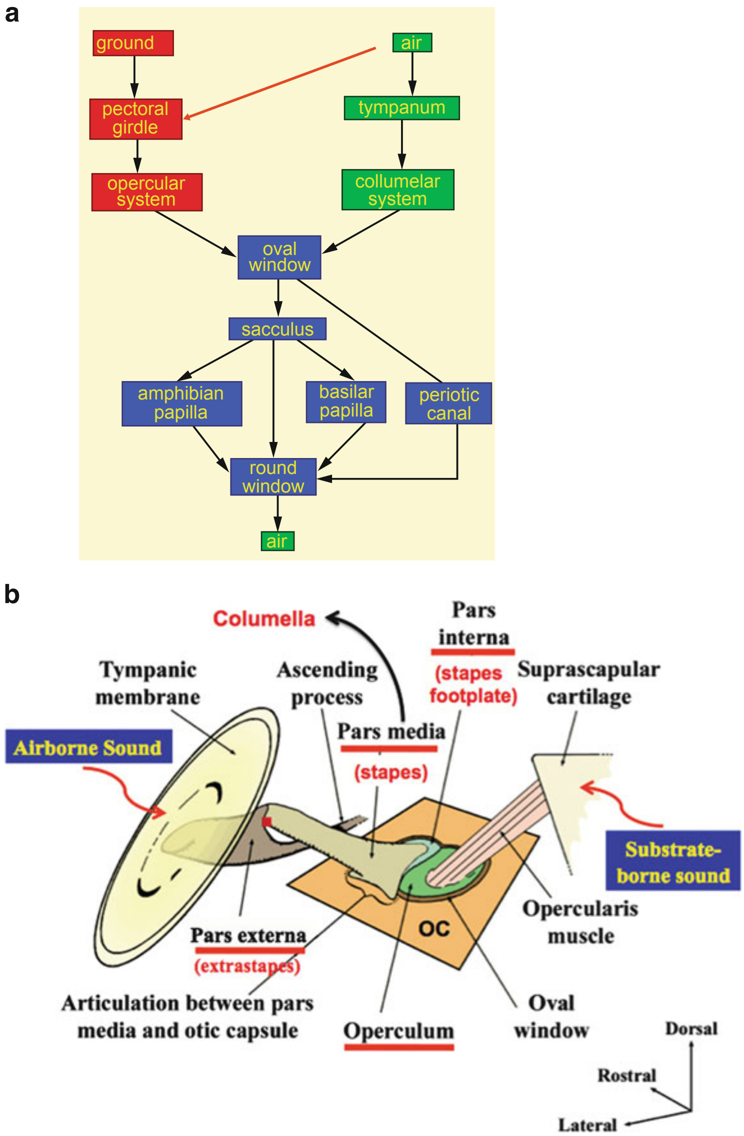

Fig. 14.1 (**a**) Putative diagram of the acoustic signal pathways into and through the frog ear. Redrawn from Lewis et al. (2001), with permission from Oxford. (**b**) Schematic diagram of the middle ear of the bullfrog (*Rana catesbeiana*) showing the two pathways for entry into the frog inner ear via the oval window: (1) airborne vibrations through the stapes and stapes footplate and (2) substrate-borne vibrations through the suprascapular cartilage and the opercularis muscle. Modified from Mason et al. (2003), with permission from Karger AG

14.1.2.1 Thumping

This mode of vibration production has been described in two species of leptodactylid frogs, *Leptodactylus albilabris* (Lewis and Narins 1985) and *L. syphax* (Cardoso and Heyer 1995). Males of *L. albilabris* call from muddy ground with the posterior half of the body buried in the substrate. The emission of each advertisement call involves a fast expansion of their large subgular vocal sac, which strikes the substrate producing a surface (vertically polarized Rayleigh) wave (Narins 1990).

Thumps are also produced by calling males in *L. syphax* over muddy substrate (Cardoso and Heyer 1995), but there are two important differences between seismic generation in this species and *L. albilabris*: (1) Males of *L. syphax* do not produce the thump with the vocal sac, but rather by beating the forefeet on the ground; and (2) the thump is produced independently of the vocal output. While neither the spectrum nor the propagation of the putative seismic signals have been characterized in *L. syphax*, foot thumping is a reasonably vigorous movement that produces an audible “click” with a broad frequency spectrum between ~100 and ~2500 Hz (Gridi-Papp and Narins 2010).

14.1.2.2 Toe Twitching

The behavior of lifting and dropping one or more of the toes repeatedly, without moving the foot (toe twitching) while perched on the substrate, is widespread among frogs and has been suggested to have a role in visual luring of prey or intraspecific communication (Narins 1995; Bertoluci 2002; Hartmann et al. 2005; Narvaes and Rodrigues 2005; Toledo et al. 2007; Grafe 2008; Hagman and Shine 2008; Sloggett and Zeilstra 2008). Toe twitching has been shown to function as an effective visual lure in cane toads (*Chaunus marinus*), attracting smaller anurans as prey (Hagman and Shine 2008). While the visual signal produced by toe twitching can have a luring effect on prey that are themselves visual predators, toe twitching has also been documented in several frogs that consume mostly herbivorous invertebrates. An alternative explanation for the role of toe twitching is the production of seismic signals that could play a role in intraspecific communication (Narins 1995; Hartmann et al. 2005) or stimulate nearby prey to move (Sloggett and Zeilstra 2008).

Increased prey motion should enhance the ability of anurans to visually detect and locate the prey (Lettvin et al. 1959). This hypothesis might be tested by recording the seismic stimuli produced by toe twitching and then delivering the vibration stimulus to the substrate (e.g., with a mechanical vibration exciter) in the absence of the frog, to determine if the seismic stimulus alone increases prey motion or if it has any attractive effect (Gridi-Papp and Narins 2010).

The available evidence for seismic sensitivity in amphibians has been previously summarized in several reviews (Narins 1990, 2001; Narins et al. 2009; Gridi-Papp and Narins 2010; Narins and Clark 2016). A few salient examples follow.

14.2 Selected Examples of Studies of the Vibration Sense in Amphibians

14.2.1 The Caribbean White-Lipped Frog, Leptodactylus albilabris

I first became aware of the acute vibration sense of amphibians in 1973 during my initial field trip to the island of Puerto Rico to carry out my dissertation research on the acoustic communication behavior of the arboreal frog, the Puerto Rican Coqui (*Eleutherodactylus coqui*). One night during the early course of these studies, I heard an unfamiliar frog call emanating from a spot no more than a few meters from my feet, and I was curious to capture and examine it. I carefully approached this nearby male, but no sooner had I taken one step toward it, the calling abruptly ceased. Only after I remained motionless for several minutes, did the frog resume calling. Nevertheless, despite my best effort to approach quietly, each footstep silenced the frog. When I finally did get to the spot where I thought the frog was hiding, repeated attempts to grab it produced only handfuls of mud, devoid of frog. This happened repeatedly, to the point of frustration, but that night's experience left an indelible first impression on me while learning firsthand of the "zone of silence that surrounds herpetologists."

After a succession of abortive attempts to spot this elusive creature, I eventually succeeded—through no brilliant gymnastic feats of my own—but rather by exploiting a tactical error made by this particular individual in choosing his calling site. That evening, the male in question was vocalizing from under a pile of *Cecropia* leaves that had fallen into one of the many concrete culverts constructed in the forest to divert excess rainwater to the roads. Carefully removing the leaves revealed the frog in plain sight; however, with no access to its usual escape maneuver of burrowing lightning quick into the muddy soil, this frog was an easy catch. Although this was my first glimpse of the Caribbean white-lipped frog (*Leptodactylus albilabris*), the quantitative study of the vibration sensitivity of this remarkable animal would wait nearly a decade for our collaboration with the Lewis laboratory at UC Berkeley to flourish.

Caribbean white-lipped frogs are found throughout much of Puerto Rico and the nearby islands of Culebra and Vieques (Rivero 1978). Male Caribbean white-lipped frogs are nocturnally active in the Puerto Rican rainforests, and often vocalize from cryptic calling sites in the moist substrate—usually from beneath dense vegetation, under logs, or hidden near the edges of rivulets—to attract females (Lopez et al. 1988). Males produce two distinct types of vocalizations, which have been identified as "chirps" and "chuckles" (Lewis and Narins 1985; Lopez et al. 1988; Moore et al. 1989; Fig. 14.2). Chirps (peak energy at ca. 2.4 kHz) are produced at the rate of ca. 4 notes/s during bouts lasting several minutes and serve as the species advertisement call. In contrast, chuckles are longer than individual chirps, typically descending in pitch from 2.3–1.0 kHz, and are thought to be involved in male-male aggressive interactions (Lewis and Narins 1985).

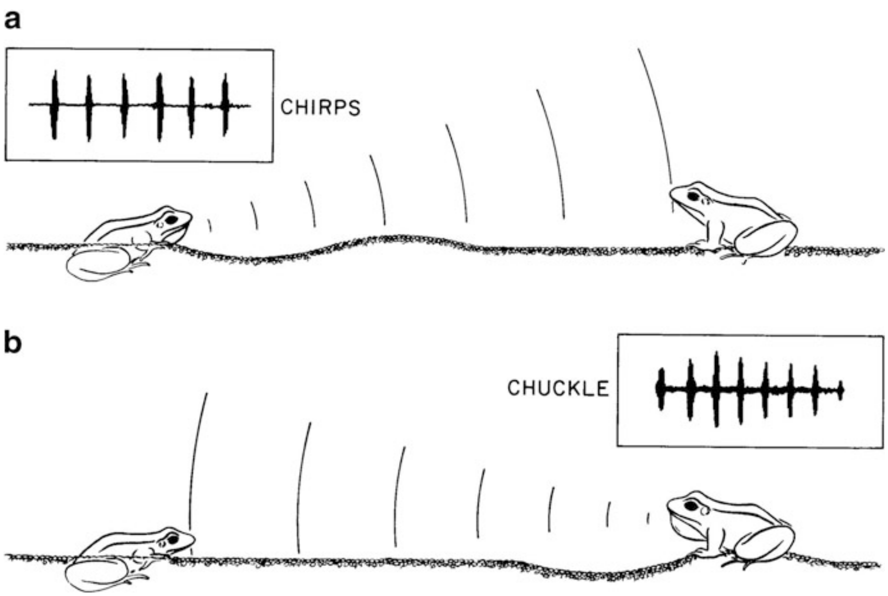

Fig. 14.2 (**a**) A male Caribbean white-lipped frog is shown emitting its species-specific advertisement call (chirps) while partially embedded in the muddy substrate. Each chirp is accompanied by a vocal sac expansion, and a concomitant "thump" as the vocal sac strikes the substrate. This percussive strike generates a vertically polarized surface (Rayleigh) wave that propagates outward from the frog. (**b**) A conspecific male is seen producing the species aggressive call (chuckle) from the surface, resulting in only an airborne call component. Males are only able to entrench themselves in the substrate after a rain; during dry spells, no thumps were detected. Modified from Narins (1995), with permission from Elsevier Science Ltd., Oxford, UK

Concomitantly with these two conspicuous, pulsatile, airborne calls, males produce impulsive, low-frequency seismic vibrations or "thumps" (peak energy <50 Hz) as the vocal sac strikes the moist substrate (Lewis and Narins 1985; Fig. 14.2). Although it has been suggested that thump vibrations may subserve the regulation of spacing between signaling males, this has yet to be experimentally demonstrated.

The Caribbean white-lipped frog of Puerto Rico produces seismic signals when it calls. Such substrate-borne vibrations could simply be a natural consequence of the sound production mechanism in this species, but in fact this animal was the first vertebrate for which morphological, neurophysiological, and behavioral evidence exists to support the use of seismic signals for communication (Narins and Lewis 1984; Lewis and Narins 1985; Lewis et al. 2001).

Bimodal playback experiments reveal that males use these seismic thumps to adjust call timing, ensuring that their calls do not overlap temporally with those of neighboring frogs (Lewis et al. 2001). In these field playback experiments, an individual frog was presented with seismic stimuli generated by an artificial "thumper" placed on the substrate at a known distance from the focal male (typically 1 m). To produce a "pure" seismic signal, the airborne component of the thumper's

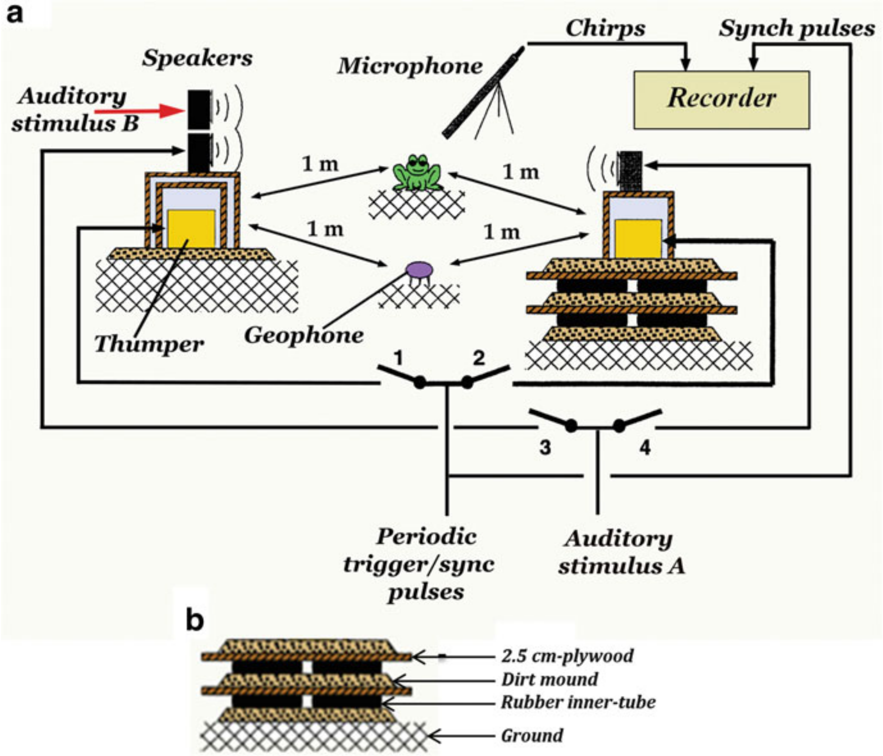

Fig. 14.3 (**a**) Generalized diagram of the field setup for investigating the sensitivity of frogs to substrate vibrations. Prerecorded stimulus patterns comprising periodic trigger/sync pulses and synchronized auditory stimuli (e.g., thump sounds, recorded calls, artificial calls, noise bursts) were played to the vibration transducers (thumpers) and loudspeakers, respectively. Continuous, broadband noise could also be played through the loudspeakers. The frog's vocalizations and the trigger/sync pulses are registered on separate channels of the recorder. (**b**) Construction details of the vibration isolation platform re-assembled in the field for each frog tested. This platform was used in control experiments to ensure that although the thumper in its housing was being electrically activated, any vibrational stimuli being transmitted to the ground, as verified with the geophone, was below the detection threshold of a frog under test. Modified from Lewis et al. (2001), with permission from Oxford

action was attenuated by placing it inside a set of nested plywood boxes (Fig. 14.3a). In some experiments, high levels of broadband noise (20 Hz–16 kHz) were broadcast as a control to further mask the thumper sounds (Lewis and Narins 1985). As an additional control, the seismic "thumper" was placed on top of a vibration-isolation platform constructed in the field and consisting of multiple layers of plywood, soil, and four rubber inner tubes (Fig. 14.3b). This arrangement would ensure that, for this control, the electrical field surrounding the thumper and the thumper's inevitable airborne sounds would be identical to those during an experimental trial, but with greatly attenuated substrate vibrations.

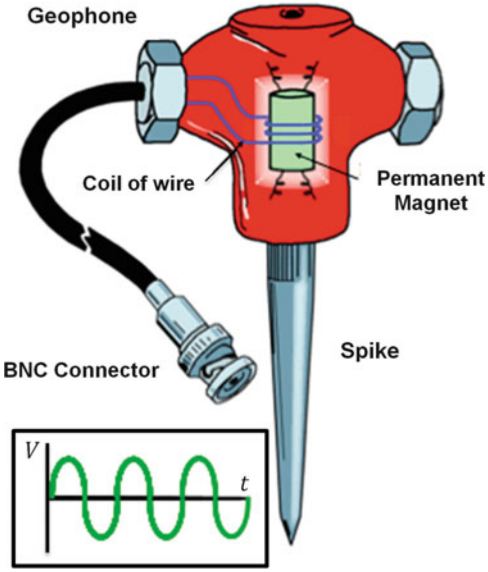

Fig. 14.4 Cut-away diagram of a vertically polarized geophone used for the seismic measurements of terrestrial animals. The spike is inserted firmly into the soil, tightly coupling the geophone housing to the substrate. Any vertical substrate motion thus causes the permanent magnet to oscillate on its four support springs. When the resulting moving lines of magnetic flux cut the coil of wire, the result is an AC voltage available at the BNC connector, with amplitude proportional to the substrate velocity (inset). Drawing kindly supplied by Margaret Kowalczyk

Seismic responses were monitored using a geophone (Fig. 14.4) placed in the substrate 1 m from the focal male. In response to either audio playback of the conspecific call or seismic playback of the vibrational call components, males of *L. albilabris* reliably modify the timing of their own vocalizations (Lewis et al. 2001; Fig. 14.5). Taken as a whole, these results show that males of *L. albilabris* produce seismic signals that propagate in the substrate and elicit changes in the calling behavior of conspecifics; hence, we have the first demonstration of seismic communication in an anuran amphibian.

Electrophysiological studies of the inner ear of this frog have demonstrated that the frequency corresponding to the maximum saccular sensitivity in *L. albilabris* and the peak energy in the seismic component of its vocalization match closely, suggesting that the thumps may be important for communication (Lewis and Narins 1985; Narins et al. 2009).

Single-unit recordings from auditory nerve fibers of males of the Caribbean white-lipped frog revealed clear modulations of their resting discharge rates in response to sinusoidal seismic stimuli with peak accelerations less than 0.001 cm/s^2 (10^{-6} g). Thus, this animal exhibits the greatest sensitivity to substrate-borne vibrations for any known terrestrial vertebrate (Narins and Lewis 1984). Moreover, the vibration-sensitive auditory-nerve fibers in this frog may be grouped into two classes: the first class consists of extremely sensitive fibers with best seismic frequencies (BSFs) between 20 and 160 Hz; the second class is made up of less sensitive fibers with BSFs between 220 and 300 Hz (Lewis and Narins 1985). The peak energy (<50 Hz) in the seismic “thump” signal generated during male calling falls within the low-frequency range of its most sensitive seismic fibers. This “matched filter” between an animal’s *seismic signal frequency* and its *best*

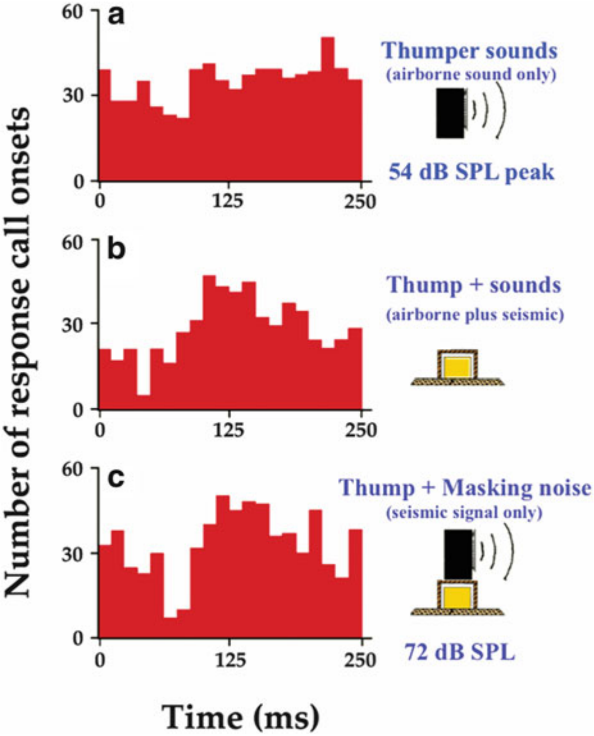

Fig. 14.5 Post-stimulus-time histograms (PSTHs) of the vocal responses of calling males of the Caribbean white-lipped frog to airborne and substrate-borne stimuli delivered with the apparatus shown in Fig. 14.3. Call pattern responses to playback of (**a**) thumper sounds at a peak level of 54 dB SPL measured at the position of the frog; (**b**) seismic thumps with their accompanying sounds played at 1 m from the focal male; and (**c**) seismic thumps with masking noise added at a level of 72 dB SPL (see text for details). All stimuli are chirp notes presented at a rate of 4 chirps/s. The calling patterns of the males under test are stimulus dependent, suggesting that males are capable of altering their vocalization behavior in response to seismic stimuli (**b** and **c**). Modified from Lewis et al. (2001), with permission from Oxford

seismic sensitivity is thought to be one way in which animals improve the likelihood of successful communication in a noisy environment (Capranica and Moffat 1983; Wehner 1987; Smotherman and Narins 2004; Narins and Clark 2016).

14.2.2 American Bullfrog [Rana (Lithobates) catesbeiana]

Recordings from single axons in the VIIIth cranial nerve of the American bullfrog [*Rana* (*Lithobates*) *catesbeiana*] revealed the extraordinary sensitivity of this animal to substrate-borne vibrations (Koyama et al. 1982; Yu et al. 1991). The fibers with the lowest thresholds in this animal (in the frequency range from 15 to 200 Hz) exhibited clear responses to peak accelerations as low as 0.001 cm/s^2, making this the most sensitive quadruped vertebrate to substrate vibrations known at that time. Subsequently, other ranid species have been shown to exhibit remarkable seismic sensitivity: the common frog (*Rana temporaria*; Christensen-Dalsgaard and Jørgensen 1988, 1996; Christensen-Dalsgaard and Walkowiak 1999) and the northern leopard frog (*Rana pipiens*; Christensen-Dalsgaard and Narins 1993); see Sect. 14.2.1.

14.2.3 Common Malaysian Tree Frog (Polypedates leucomystax)

Frogs in the family Rhacophoridae, the Old World tree frogs, comprise 389 species in 18 genera (http://amphibiaweb.org/). One of these genera, *Polypedates*, contains 26 species found in Japan, eastern China, and throughout tropical Southeast Asia (Narins 2001). Acoustic playback studies of the common Malaysian tree frog [*Polypedates leucomystax*; Narins et al. 1998 (non-striped morph raised to species status *P. discantus sp. nov.*; Rujirawan et al. 2013); Christensen-Dalsgaard et al. 2002] revealed that females initiate mating by producing a vibratory signal within the vegetation at night, by tapping their rear toes. The toe tapping lasts for several minutes, only occasionally accompanied by vocalizations. Nearby males were observed to jump toward the toe-tapping female; amplexus ensued. Tapping may function as a vibrational signal advertising the female's presence to neighboring males, but experimental confirmation of this hypothesis remains lacking.

14.2.4 Red-Eyed Tree Frog (Agalychnis callidryas)

In a study of the use of vibrational signals in agonistic interactions, experiments with red-eyed tree frogs (*Agalychnis callidryas*), Caldwell et al. (2010a, b) demonstrated that competing males produce chuckle calls and perform a tremulation display in which one male raises his body off of the substrate, rapidly contracts and extends his hind limbs, and shakes his hind end. The resulting vibrations are transmitted via the animal's legs to the substrate, such as a tree branch or a sapling. A second male, often close by and on the same plant, can detect the substrate-borne vibrations from the first male and often responds to them by exhibiting submissive behavior—either fleeing or by remaining motionless. This is one of the few clear vertebrate examples of aggressive interactions mediated by vibrational signals.

In another series of experiments, Warkentin and her colleagues demonstrated that vibrational cues can trigger a predation response in red-eyed tree frog larvae. Tadpoles of red-eyed tree frogs respond to the vibrations produced during a predator (snake) attack by dropping out of their gelatinous egg mass into the stream below (Warkentin 2005; Warkentin et al. 2006, 2007; Warkentin and Caldwell 2009). Moreover, the vibrations caused by falling raindrops on the egg clutches do not have the same effect on the egg clutch. Thus, the embryos are capable not only of detecting vibrations but also of distinguishing between those produced by a benign stimulus (raindrops) and a potentially lethal source (snake).

14.2.5 Iberian Spadefoot Toad (Pelobates cultripes) and the Natterjack Toad (Bufo calamita)

Toads often occupy underground refugia during periods of daily or seasonal inactivity. Synchrony between rainfall periods and toad activity may be crucial for feeding and reproduction. Yet the sensory cues matching emergence behavior with rainfall periods are poorly understood. It was hypothesized that rainfall-induced soil vibrations are the cues used to trigger the emergence of toads from underground refugia. Using playback experiments in the absence of natural rainfall conditions in the toads' native habitats, Márquez et al. (2016) observed emergence of two toad species (*Pelobates cultripes* and *Bufo calamita*) significantly earlier relative to controls, in response to low-frequency soil vibrations that closely mimic those of rainfall (Fig. 14.6). These results suggest that detection of abiotic seismic events can be biologically relevant and widespread in arid-zone anurans. Moreover, these findings provide new insights into the evolutionary role played by the two low-frequency-tuned inner ear organs in anuran amphibians, amphibian papilla and sacculus, both detectors of extremely weak environmental vibrational cues (Koyama et al. 1982; Yu et al. 1991; Christensen-Dalsgaard and Narins 1993).

14.2.6 Caudate Amphibians: Salamanders and Newts

Only a small fraction of the 708 species of salamanders and newts have been tested for their seismic sensitivity and none have been shown to use vibrations for communication. Acute seismic sensitivities (−90 to −130 dB re rms re 1 g) have been reported in the salamanders: eastern newt (*Notophthalmus viridescens*), eastern red-backed salamander (*Plethodon cinereus*) (adults), and spotted salamander (*Ambystoma maculatum*) (larvae). Whereas such sensitivity measurements bypassed the natural coupling of the inner ears to the substrate (Ross and Smith 1979, 1980; Gridi-Papp and Narins 2010), terrestrial vertebrates exhibit a number of specializations for conducting vibrations from the substrate to the head and inner ear. Anatomical adaptations rely on the skeleton, as the rigid structure of bones makes them suitable for faithfully transmitting vibrations with minimal loss. Amphibians possess an elaborate coupling solution, in which the *opercularis* muscle

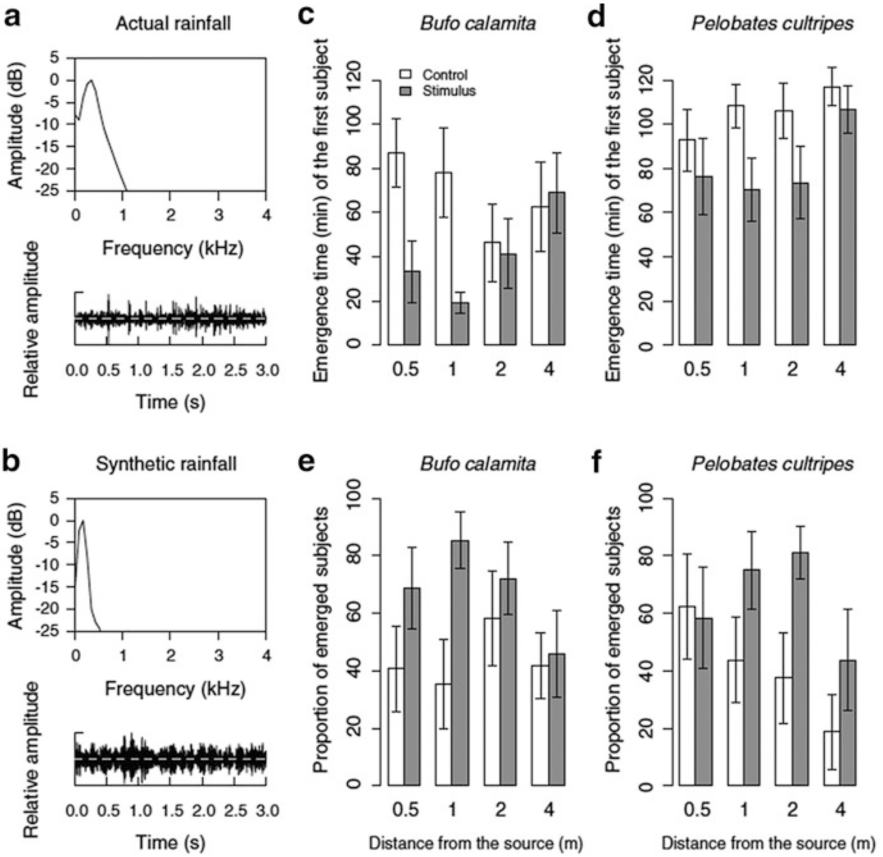

Fig. 14.6 Rainfall vibrations, synthetic stimulus, and emergence of buried toads. (**a**) Spectrum and oscillogram of vibrations produced by natural rain. (**b**) Spectrum and oscillogram of an actual recording of the synthetic vibration. All recordings in the field were made with a geophone, amplified by a custom-made amplifier connected to a portable digital recorder. Mean time (min) between the onset of the playback test and the emergence of the first individual of (**c**) *Bufo calamita* and (**d**) *Pelobates cultripes*. Individuals of both species were buried in the substrate within enclosures exposed to vibration stimuli (gray bars) and in control enclosures (white bars) located at four distances from the vibration source (0.5, 1, 2, and 4 m). Whiskers indicate standard errors of the means. Maximum time (120 min) was assigned to enclosures in which no individuals emerged during the playback test. (**e**) Mean proportion of emerged individuals of *Bufo calamita* at the end of the playback experiments. (**f**) Mean proportion of emerged individuals of *Pelobates cultripes* at the end of the playback experiments. Vertical bars are the proportion of individuals of both species that emerged during the 2-h playback test in enclosures exposed to vibration stimulus (gray bars) and in control enclosures (white bars) located at four distances from the vibration source (0.5, 1, 2, and 4 m). Whiskers indicate standard errors of the means. From Márquez et al. (2016), with permission from Elsevier

connects the scapula to the oval window (Wever 1973; Mason and Narins 2002). Seismic vibrations that reach the shoulders through the forelimbs are, in this way, transmitted directly into the inner ear (Mason 2007; Gridi-Papp and Narins 2010). This system appears to function quite efficiently, as the seismic sensitivity thresholds in *Notophthalmus viridescens* in the range from 100 to 300 Hz are the most sensitive of any vertebrate tested thus far (Gridi-Papp and Narins 2010). Whether salamanders are able to use low-level substrate vibrations as a source of information about their environment remains an open question (Hill 2009).

14.3 Conclusion

In his beautiful and comprehensive review of vibration communication in the invertebrates, Markl (1983) states:

> Behavioral biologists, like many other people are most attracted by the extraordinary, assuming that if something is spectacular it must be important. Therefore we know most about animal communication whenever the performing animals are in the advertisement business: the extravagant display, the resounding song, the far-reaching rhythmic light-flash, the sex-pheromone that attracts males over miles—whatever Natural Selection has perfectly shaped for sales appeal.
>
> All this could not but put vibrational signals in animal communication into the second line of interest. If a signal can hardly be perceived by ourselves, if it can be measured only with considerable difficulty even with sensitive instruments, and if it finally, as a rule, works only over a few centimeters if not only on direct contact, it must be of minor significance. Fortunately, the unobtrusive charm of vibrations has in recent years attracted enough interest from behavioral biologists to reveal the special capacities of this communication channel which only become understandable in the proper ecological perspective to which they have been adapted.

Although these words were written with a focus specifically on the invertebrates, in these few sentences, Markl has captured, without using the term, the essence of the *neuroethology* of seismic communication in all animals, including the terrestrial vertebrates. The “unobtrusive charm” of the vibration communication system of the anuran amphibians has just begun to divulge itself in the relatively few species in which it has been studied. No doubt that future studies, in which seismic signals are recorded, modified and re-broadcast, especially to frogs calling from the substrate or from within dense mats of vegetation, will surely reveal a wide range of interesting phenomena that will shed light on our understanding of this heretofore largely cryptic communication modality among the vertebrates.

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Chapter 15
Vibrational Communication in Heelwalkers (Mantophasmatodea)

Monika J. B. Eberhard and Mike D. Picker

Abstract Mantophasmatodea (Heelwalkers), described in 2002, is the most recently discovered insect order. Additionally, with only 21 species described to date, it is also among the smallest insect orders known. Mantophasmatodea are 1–4 cm long, secondarily wingless predators. They inhabit bushes, herbs, shrubs, or hide within grass tussocks in open semi-arid landscapes of sub-Saharan Africa. Adult males and females use percussive signals to communicate with one another, mainly for mate localization, recognition of male vs female, and potentially also for species recognition. Females drum their entire abdomen onto the substrate, producing single pulses spaced at regular intervals. Males use a special drumming organ located on their subgenital plate to generate groups of pulses (pulse trains), also repeated at regular intervals. Although most of the species investigated thus far occur in allopatry and have limited dispersal abilities, male vibrational signals are still surprisingly distinct from each other at an interspecific level, and most species can be distinguished by the structure of the male signal. Behavioral experiments additionally suggest that some information about species identity is encoded in male and female vibratory signals. However, the signals are probably mainly used for the localization of a potential mate within the structurally complex vegetation that the heelwalkers inhabit. Moreover, Mantophasmatodea possess very sensitive scolopidial organs to detect substrate vibrations—the well-developed subgenual organ complex within the tibia of all legs is probably most sensitive to the species-specific communication signals. Despite their recent discovery, comparatively little is known about their biology, behavior, and diversity.

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15.1 Introduction

Mantophasmatodea (Heelwalkers; Fig. 15.1) is the most recently described insect order; it was discovered in 2001 and formally described in 2002 (Klass et al. 2002). The description was based on two preserved museum specimens, collected in Namibia in 1909 and Tanzania in 1950. This discovery elicited a lot of scientific as well as public interest, since it was not expected that a new insect order comprising comparatively large species would have slipped the taxonomists' attention. The first extant specimens of Mantophasmatodea were found in 2002 in Namibia (Picker et al. 2002; Klass et al. 2003). Some autapomorphies of the order are the antennae that exhibit a well-separated basi- and distiflagellum and unusual antennomere structure (Drilling and Klass 2010), a median process on the subgenital plate of males (used for drumming), a triangular process on the third tarsomere (Buder and Klass 2013), and various details of the tentorium and female ovipositor. Unique characteristics are also found in the behavior of Mantophasmatodea, which keep their large arolia and last (fifth) tarsal segments of all legs lifted up and off the substrate. Only when walking on smooth surfaces, during copulation attempts, or when handling large prey, the arolia are lowered and used for firm attachment to the substrate (Eberhard et al. 2009). This unique habit gave rise to the vernacular name "Heelwalker" for the order. Another distinctive feature of Mantophasmatodea is their communication system, where both males and females drum their abdomens on the substrate to generate vibrational signals. The order is one of the smallest, with currently only 21 extant species described (Zompro 2001, 2005, 2008; Klass et al. 2002, 2003; Zompro et al. 2002, 2003; Engel and Grimaldi 2004; Arillo and Engel 2006; Zompro and Adis 2006; Huang et al. 2008; Eberhard et al. 2011; Wipfler et al. 2012, 2018). However, it is restricted to relatively poorly explored and inventoried southern African countries (South Africa, Namibia, Tanzania, Malawi, and likely Angola) (Roth et al. 2014; Dool et al. 2017) and the number of species is likely to increase with more intensive study in these areas. Additionally, fossil Mantophasmatodea have been found in Baltic amber from the Eocene (Arillo and Engel 2006; Engel and Grimaldi 2004; Zompro 2001, 2005, 2008) and in China from the Middle Jurassic (165 Mya) (Huang et al. 2008), indicating that the extant species are a relictual fauna. Extant Mantophasmatodea are known from sub-Saharan Africa, namely Namibia, South Africa, Malawi, Angola, and Tanzania. Adult individuals are ca. 1–4 cm in body length, and females are usually larger than males (Hockman et al. 2009; Roth et al. 2014). Their body has a brown, gray, green, or yellow basic color, often overlain by a mottled pattern. Dorsal, longitudinal striping patterns are common in many of the species. These secondarily wingless insects inhabit bushes (Fig. 15.2c, d), small trees, herbs, and grass in various semi-arid landscapes where they prey on other arthropods, catching them with their spinose fore- and midlegs (Fig. 15.1g). Their superficial resemblance to juvenile mantids (order Mantodea) likely contributed to their being overlooked for such a long time.

As is known thus far, Mantophasmatodea are annual, univoltine species (Tojo et al. 2004; Roth et al. 2014), appearing in the rainy season. Females oviposit in the

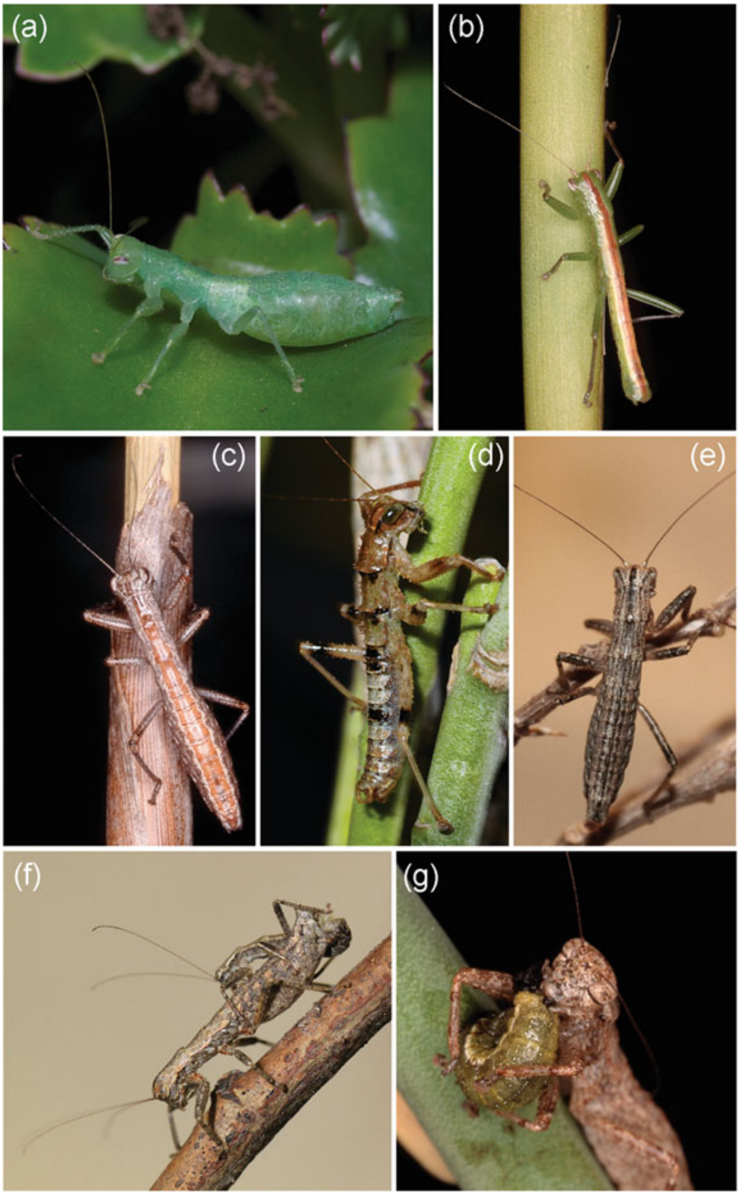


Fig. 15.1 Habitus of adult Mantophasmatodea: (**a**) Female *Viridiphasma clanwilliamense*, (**b**) male *Austrophasma caledonense*, (**c**) female *Lobatophasma redelinghuysense*, (**d**) male *Tyrannophasma gladiator*, (**e**) female *Karoophasma biedouwense*, (**f**) mating pair (male on top of female)—*K. biedouwense*, (**g**) female *Namaquaphasma ookiepense* eating a caterpillar. Photos by M. Eberhard (**e**), A. Lamboj (**a**), G. Nigro (**f**), M. Picker (**b**–**d**, **g**) (**a** and **f** are reprinted from Eberhard et al. 2018, with permission from John Wiley & Sons)

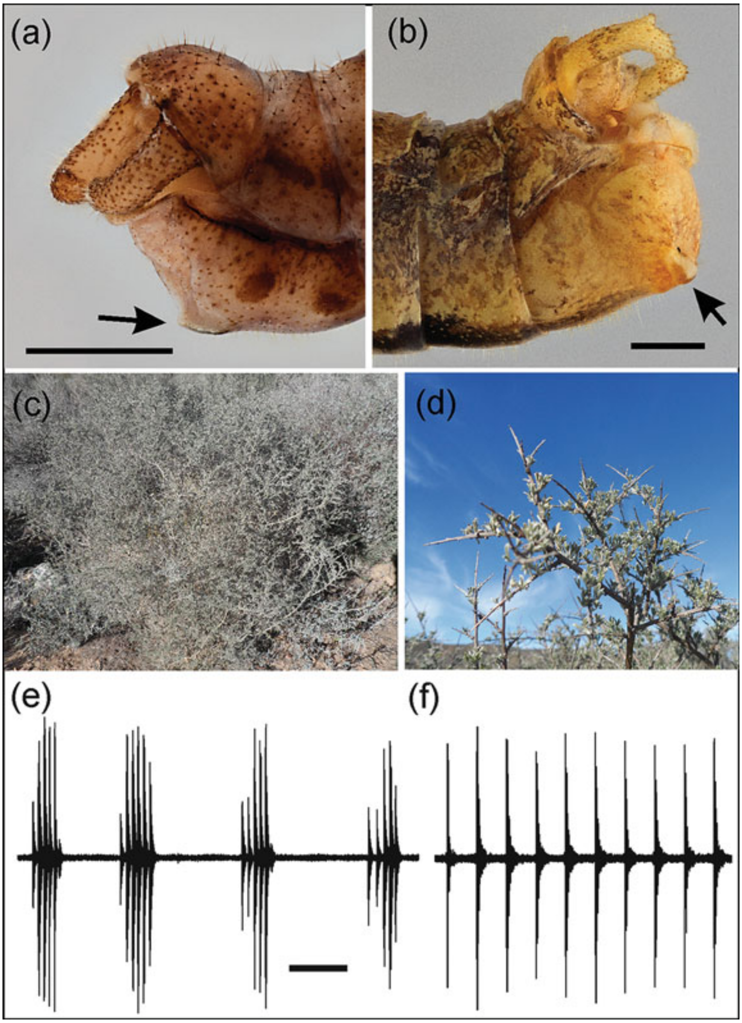


Fig. 15.2 Vibrational communication in Mantophasmatodea: (**a**) Postabdomen of a male *K. biedouwense* (Austrophasmatidae) and (**b**) *Tyrannophasma gladiator* (fam.n.) showing the drumming organ on the subgenital plate (arrows; photos by T.M. Dederichs, bars = 1 mm). (**c**, **d**) host plant (*Wiborgia* sp., Fabaceae) of *K. biedouwense* consisting of thin, woody branches (photos by S. Dool). (**e**, **f**) vibrational signals of Mantophasmatodea: the male signal (**e**) consists of regularly repeated pulse trains, whereas the female signal (**f**) comprises repeated single pulses (both signals from *Austrophasma gansbaaiense*). Bar = 1 s

ground, usually at the base of a shrub. By mixing eggs with a secretion and sand, they produce hard, water-resistant egg pods containing 10–12 (Tojo et al. 2004) or 20–30 eggs (Roth et al. 2014). A recent study showed that the number of eggs within an egg pod corresponds to the number of ovarioles in the paired ovaries of the females (Küpper et al. 2019). The hard, resistant egg pods are adapted to endure the hot and dry seasons; diapause lasts at least 8 months (Tojo et al. 2004; Roth et al. 2014), and egg pods maintained in the laboratory can undergo diapause for a number of years. Egg hatching is initiated by the first heavy rains of the rainy period; nymphs subsequently disperse on the nearest bushes and/or grass tussocks. Nymphs molt five times, each instar can be identified by the number of annuli within the basiflagellum of the antenna: Two annuli are added at each molt, deriving from the most basal annulus (meriston) in each instar, until the final (fifth) adult instar, which possesses 14 annuli in the basiflagellum (Hockman et al. 2009). The time between hatching of nymphs and reaching adulthood is between 2 and 4 months (Zompro et al. 2003; Hockman et al. 2009), depending on habitat and weather conditions (Tojo et al. 2004).

First observations on biotremology in heelwalkers were reported by Zompro et al. (2003) and Tojo et al. (2004), who referred to a "drumming" behavior of both males and females prior to mating. Since their discovery, Mantophasmatodea have been investigated in many different contexts, including taxonomy and phylogeny (e.g., Klass et al. 2003; Terry and Whiting 2005; Damgaard et al. 2008), morphology (e.g., Baum et al. 2007; Eberhard et al. 2009; Drilling and Klass 2010; Wipfler et al. 2015), fossil record (e.g., Zompro 2001; Arillo and Engel 2006; Huang et al. 2008), etc. Still many aspects concerning their ecology and behavior remain unknown. This chapter aims to outline the current knowledge of vibratory communication in Mantophasmatodea, the production and function of substrate-borne vibrational signals, as well as the detection of such signals by extremely sensitive leg scolopidial organs.

15.2 Production and Characteristics of Vibrational Signals

In Mantophasmatodea, individuals communicate via percussive signals generated by both sexes. Males use the median process on their subgenital plate (also called drumming organ) to tap on the substrate (Fig. 15.2a, b), while females drum the entire abdomen against the ground (Eberhard and Picker 2008). Through this behavior, heelwalkers produce substrate vibrations of a defined temporal pattern, transmitted through the branches of bushes or blades of grass on which they reside.

Male vibratory signals consist of repeated groups of pulses (pulse trains, Fig. 15.2e), and the simpler female signals comprise repeated single pulses (Fig. 15.2f, pulse = one tap with the abdomen on the ground). Analysis of the vibrational signals of 13 species of heelwalkers revealed that signals of the different species are of similar overall structure but differ in temporal characteristics such as pulse rate or pulse train duration (Fig. 15.3). Male signals particularly exhibit great interspecific differences concerning their temporal patterns. A principal component analysis (PCA, Fig. 15.4) of all measured parameters revealed that most of the species could be identified by the structure of the male calls alone (Eberhard and Eberhard 2013). This is rather surprising given that most of the extant species do not

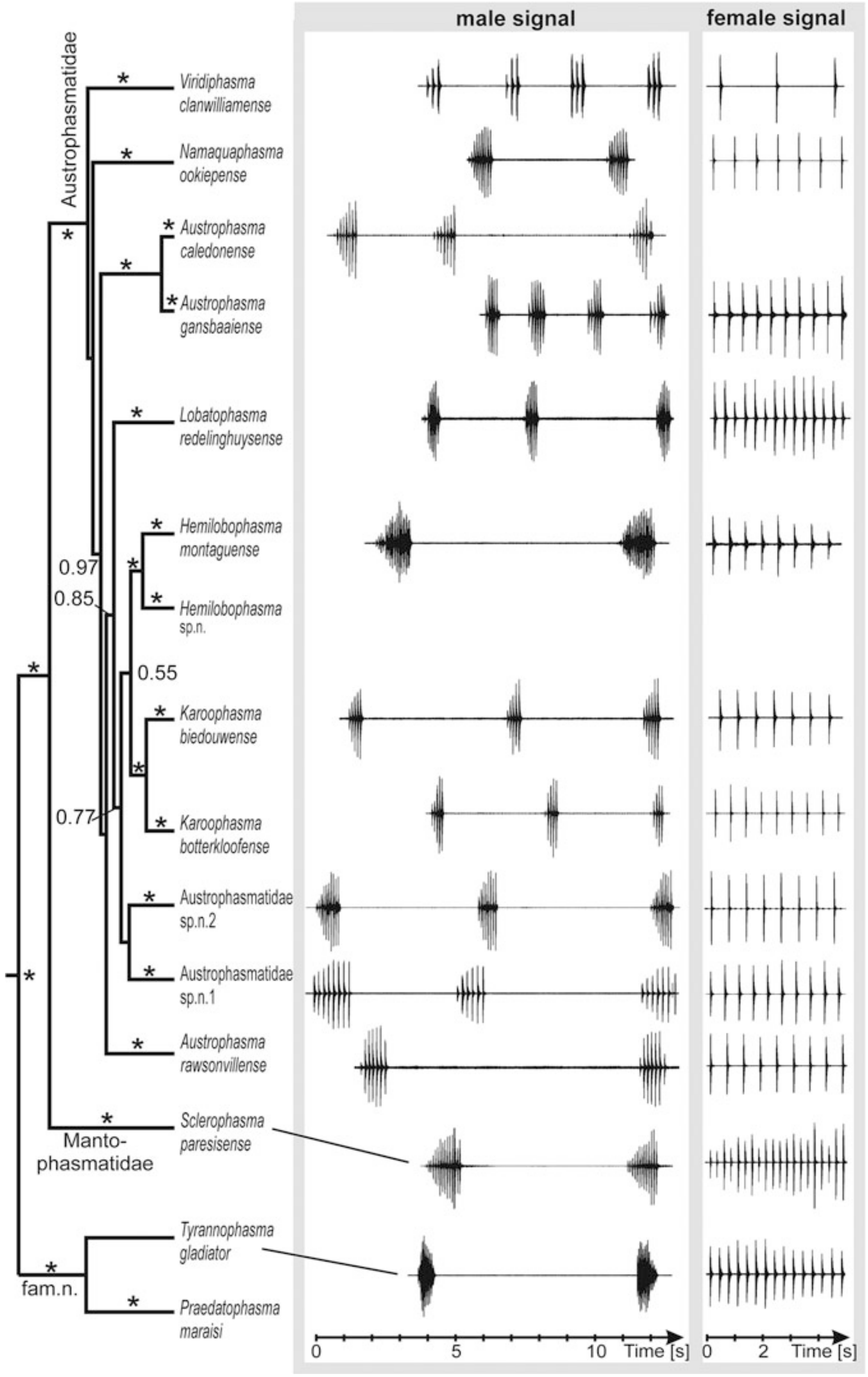
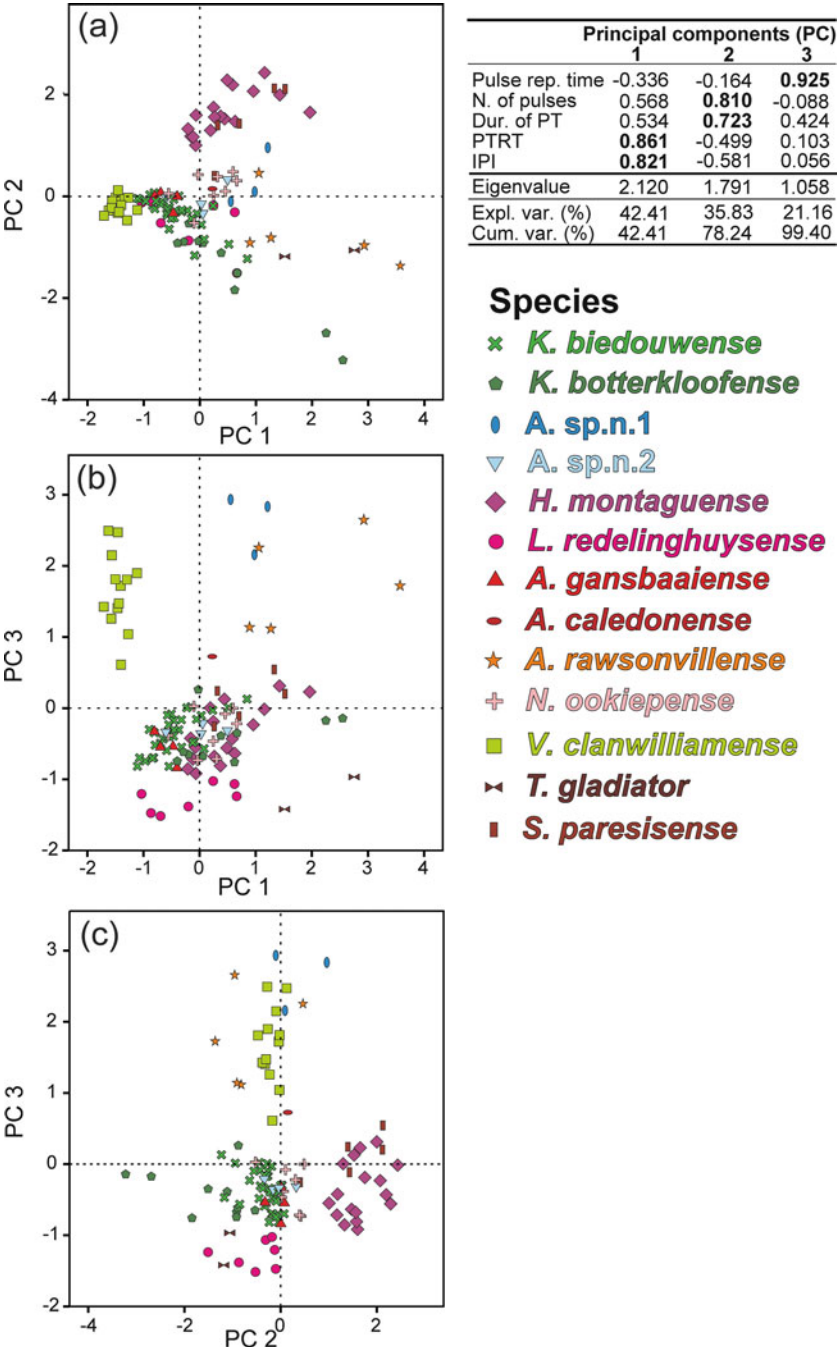


Fig. 15.3 Bayesian COI topology (810 bp) for the order Mantophasmatodea, together with vibrograms of male and female vibrational signals, recorded at ca. 20 °C. Bayesian posterior probabilities are indicated on the branches when ≥0.75 (asterisk indicates 0.99 or 1), outgroups not shown. Sequence data taken from Damgaard et al. (2008), processed by Serena Dool



	Principal components (PC) 1	2	3
Pulse rep. time	-0.336	-0.164	**0.925**
N. of pulses	0.568	**0.810**	-0.088
Dur. of PT	0.534	**0.723**	0.424
PTRT	**0.861**	-0.499	0.103
IPI	**0.821**	-0.581	0.056
Eigenvalue	2.120	1.791	1.058
Expl. var. (%)	42.41	35.83	21.16
Cum. var. (%)	42.41	78.24	99.40

Fig. 15.4 Scatter plots of principal components resulting from PCA of male call parameters of 13 Mantophasmatodea species—slightly modified after Eberhard and Eberhard (2013). (**a**) PC1 vs. PC2, (**b**) PC1 vs. PC3, (**c**) PC2 vs. PC3. Three PCs with eigenvalues >1 were extracted; parameters most strongly associated with a PC depicted in bold in the table. Most species cluster in groups and are separated from each other by at least one PC; however, there is also some overlap. *Dur* duration, *IPI* inter-pulse train interval, *N* number, *PT* pulse train, *PTRT* pulse train repetition time, *rep* repetition

occur in sympatry but are strictly allopatric with little overlap in distribution ranges. Investigation of male vibratory signals recorded from *Striatophasma naukluftense* [which exhibits an unusually long pulse train of 5–6 s duration, see Roth et al. (2014)] and from individuals belonging to the Sclerophasma/Mantophasma clade collected at different localities in Namibia suggests some intraspecific variation in vibratory signals at the population level (Roth et al. 2014). However, this variability might relate to species complexes. Due to the lack of behavioral (mate choice) experiments and detailed taxonomic investigations on these specimens, these questions remain to be solved. Typically, variability of vibrational signal traits within a species is rather low, with mean intra- and interindividual coefficients of variation (CV) below 20% (Eberhard and Eberhard 2013; Roth et al. 2014). This is in accordance with the mean CVs found for acoustic communication signals in insects and amphibians (23.6 and 20.7, respectively; see Reinhold 2009), and substrate vibrational signals in arthropods (26; see Eberhard and Treschnak 2018). Additionally, a positive correlation of the CV with duration of the respective signal trait, as found by Reinhold (2009) for acoustic signals of various insect and amphibian species, is also apparent in heelwalkers (Eberhard and Treschnak 2018).

Eberhard and Eberhard (2013) defined repeated pulse trains as male calls and repeated pulses as female calls, while Roth et al. (2014) argued that each pulse train might be termed a “call”. We suggest using the term “vibratory signal” instead of “call” to avoid such problems of definition. Irrespective of definition of terms, the repetition times of pulse trains within male signals seems to play a role in species recognition (M. Eberhard, personal observation).

Since vibratory signals in heelwalkers are produced by tapping the abdomen (in case of females) or the drumming organ (in case of males) onto the substrate, the spectral properties of the resulting signals mainly depend on the resonant characteristics of the substrate. A single tap on a solid surface produces a complex wave pattern that varies according to the nature of the substrate (Markl 1983; Henry 2006; Eberhard and Picker 2008; Eberhard et al. 2010; Chapman 2013; Mortimer 2017). Dominant frequency patterns elicited by a male heelwalker tapping on different substrates, measured with an accelerometer, changed with the substrate and distance between the accelerometer and the drumming insect; however, frequencies of the signals were similarly low, ranging between 50 and 1000 Hz (Eberhard et al. 2010). More recent investigations using a laser Doppler vibrometer revealed similar results (S. Küpper and M. Eberhard, unpublished data). Due to the complications resulting from the excitation by drumming on nonhomogeneous substrates with frequency-dependent attenuation during transmission of the signals (Mortimer 2017), information is rather coded in the time pattern of vibration pulse series (which remain constant across a range of excitatory substrates) and not in the spectral fine structure of the signals (Markl 1983). Accordingly, the temporal pattern of the vibrational signals is not affected during transmission through the heelwalker’s host plants (which mainly consist of thin stiff woody branches or more flexible grass culms, Fig. 15.2c, d). Recordings of male vibrational signals played back at the bottom of a bush in the natural habitat of *Karoophasma biedouwense* revealed that pulse repetition times, pulse train repetition times, and durations remained unchanged throughout the whole plant—even after several bifurcations and up to a distance of 70 cm. The vibration amplitude, measured as velocity with a laser Doppler vibrometer, even slightly increased (by +1.5 dB) at distances of 39 and 46 cm, but was attenuated by ca. –16 dB (but still detectable over background noise) after several bifurcations at a measuring distance of 70 cm from the source of vibration (D. Metze and M. Eberhard, unpublished data).

15.3 Function of Vibrational Signals

The only detailed behavioral study on heelwalker vibrational communication to date used two Austrophasmatid species, which occur in sympatry at Clanwilliam Dam, South Africa (Eberhard and Picker 2008). Here, both male and female vibrational signals differed significantly in all measured parameters between the two species. Male and female *K. biedouwense* did not react to heterospecific vibratory signals of *Viridiphasma clanwilliamense*. In contrast, when presented with vibrational signals of conspecific mates, female *K. biedouwense* ceased locomotion and started tapping continuously. Additionally, opening of the ovipositor valves was observed. None of the tested females reacted with continuous tapping to the playback of *V. clanwilliamense* males. In contrast, they increased locomotor activity. When subject to the playback of a conspecific female, *K. biedouwense* males exhibited enhanced locomotion, antennation, drumming, and searching behavior (Eberhard and Picker 2008). Before drumming, many males rubbed their abdomens against the substrate; the function of this unusual behavior is unknown. The searching behavior of males at bifurcations is noteworthy: when arriving at a furcation, excited males stopped and placed their forelegs on the branches of the fork, while keeping their mid- and hind legs on the original stem. After having received some signals from the continuously calling female, the male moved forward, placing its fore- and middle legs first onto both branches and finally onto the one branch that they had selected as being associated with the drumming female. Eberhard and Picker (2008) suggested that males might be able to detect minute differences in reception time of the female signal between their stretched legs and use this to localize the female, similar to the situation in chelicerates (Brownell and Farley 1979; Hergenröder and Barth 1983), stink bugs (Čokl and Virant-Doberlet 2003), and termites (Hager and Kirchner 2014). Males significantly decreased their reaction when presented with the playback of the sympatric, heterospecific female signal. However, they sometimes emitted a few vibratory signals in the absence of any playback stimulus. This suggests that adult males emit signals at random to test their environment for nearby, receptive females (Eberhard and Picker 2008).

As mating occurs in the absence of vibrational communication when males and females are in very close proximity (8–10 cm) (Eberhard and Picker 2008; Roth et al. 2014), vibratory signals are thought to serve for mate localization at the mid-range, mainly to bring the sexes together in the structurally complex bushes in which they reside. However, the playback experiments conducted by Eberhard and

Picker (2008) suggest that at least some information about species identity and sex is encoded in the vibratory signals, since male and female *K. biedouwense* did not react (or had a significantly lower reaction) to signals of the heterospecific, sympatric *V. clanwilliamense*.

When the male arrives at the female's position, he slowly approaches her and then quickly leaps onto her back, grabbing her with his legs. Both male and female do not display any vibratory signaling at this stage of mating (Eberhard and Picker 2008). The male bends his abdomen down in an S-shape around the right side of the female, who lifts up her abdomen. The male's large cerci facilitate the coupling, when the membranous phallus is expanded and inserted into the female vagina (Tojo et al. 2004; Eberhard and Picker 2008; Roth et al. 2014). Copulation lasts up to 3 days, during which the male does not feed, while the female still continues to capture prey and feeds (Zompro et al. 2003; Tojo et al. 2004; Klass 2009; Roth et al. 2014). Multiple matings have been observed, but no critical experiment has been conducted yet to investigate this in detail.

15.4 Detection of Vibrational Signals

Sensory organs (leg chordotonal organs) within all six legs detect substrate vibrations (Eberhard et al. 2010). These sensory organs consist of groups of scolopidia—details on the fine structure of such sensilla can be found in the extensive review by Field and Matheson (1998).

Eberhard et al. (2010) studied the anatomy and sensitivity of the leg scolopidial organs in *K. biedouwense* and *V. clanwilliamense* using serial semithin sections (light microscopy), SEM, micro-CT, and electrophysiology. They found five different scolopidial organs within each leg: a femoral chordotonal organ (FCO) spanning the femur, a subgenual organ (SGO), distal organ (DO), tibiotarsal scolopidial organ (TTO) within the tibia, and a tarso-pretarsal scolopidial organ (TPO) in the tarsus (Fig. 15.5). Additionally, groups of campaniform sensilla are located at the proximal tibia, in close proximity to the SGO inside. The number and location of scolopidial organs within the legs of the two heelwalker species corresponds well with that found in most other insect orders (Debaisieux 1938; Field and Matheson 1998; Lakes-Harlan and Strauß 2014).

The FCO consists of two separate scoloparia: the proximal scoloparium contains at least 20 scolopidia, located close to its proximal attachment site, whereas the distal scoloparium contains scolopidia and connective tissue dispersed along the whole length of the scoloparium. Such a separation of the FCO into two distinct scoloparia has also been described for orthopterans, stick insects, and stoneflies (Debaisieux 1938; Field and Matheson 1998). In locusts, the proximal scoloparium of the FCO was suggested to be a functional low-frequency receiver (Field and Pflüger 1989). This is probably also the case in Mantophasmatodea, since summed recordings from the leg nerve showed a response to vibrational stimuli of 5–80 Hz, even after destruction of all scolopidial organs distal to the FCO, whereas additional

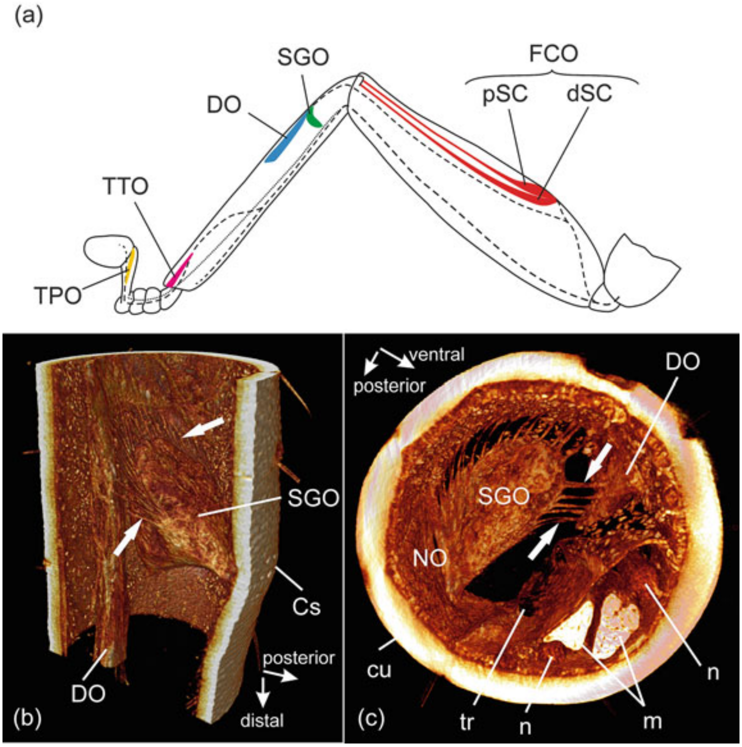


Fig. 15.5 (**a**) Schematic drawing of the leg scolopidial organs found in all six legs of Mantophasmatodea (slightly modified and reprinted from Eberhard et al. 2010, with permission from Elsevier; leg nerves shown as dashed black lines). The femoral chordotonal organ (FCO) consists of a proximal and distal scoloparium (pSC, dSC). The subgenual organ complex, which is probably most sensitive to substrate vibrations, consists of subgenual organ (SGO), Nebenorgan (not shown), and distal organ (DO), whereas the tibiotarsal scolopidial organ (TTO) and tarso-pretarsal scolopidial organ (TPO) are most probably proprioceptors. (**b**) Volume-rendered micro-CT image of an SGO within the hind leg of a *V. clanwilliamense* male in lateral view. (**c**) SGO within the front leg of a female *K. biedouwense* in transverse view. Arrows show scolopidia spanning from their posterior attachment site to the anterior border of the tibial cuticle. *cu* cuticle, *Cs* campaniform sensilla, *m* muscle, *n* nerve, *NO* Nebenorgan, *tr* trachea

ablation of the FCO dramatically decreased all responses to vibrational stimuli (Eberhard et al. 2010). These ablation experiments additionally showed that the TTO and TPO probably serve for proprioception (as joint chordotonal organs) rather than for vibration detection (Eberhard et al. 2010).

Most insect taxa studied so far have scolopidial organs within the proximal tibia, with the exception of Archaeognatha, Coleoptera, and Diptera (Debaisieux 1938; McIver 1985; Field and Matheson 1998; Lakes-Harlan and Strauß 2014). The subgenual organ complex of Mantophasmatodea consists of an SGO, a Nebenorgan [considered as part of the SGO, but see Strauß (2017)], and a DO. The SGO, which consists of 15–30 scolopidia, has a sail-like structure and spans the hemolymph space, approximately perpendicular to the longitudinal axis of the tibia (Fig. 15.5b, c). This organization is similar to other polyneopteran insects such as cockroaches, locusts, bush crickets, stick insects, and praying mantises (Lakes-Harlan and Strauß 2014). As in other insects, the SGO is considered to be most sensitive to substrate vibrations (Čokl and Virant-Doberlet 2003; Lakes-Harlan and Strauß 2014). Mantophasmatodea have one of the most sensitive receptor systems among insects, and are capable of perceiving vibrational stimuli with a threshold of less than 0.001 m/s^2 at a stimulus frequency of 600 Hz (Eberhard et al. 2010).

15.5 Conclusions and Outlook

Given the recent discovery of the order, it is not unexpected that many details on biotremology and mating behavior, as well as the ecology, diversity, phylogeny, and other aspects of mantophasmatodean biology are not, or only superficially, investigated so far—leaving huge research lacunae. Since Mantophasmatodea use a rather simple mode of vibrational communication (percussive signals), this fascinating insect order is perfectly suited to investigate the selective forces at work that produced and maintained the surprisingly high interspecific variability of advertisement signals, despite its low dispersal abilities.

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Chapter 16
Vibrational Behavior in Termites (Isoptera)

Felix A. Hager, Kathrin Krausa, and Wolfgang H. Kirchner

Abstract Communication with nestmates is among the characteristic features of termites and relies, as in other highly social taxa, on a complex network of chemical and mechanical signals. In contrast to other social insect taxa, the role of visual cues is negligible. Termites make use of substrate-borne vibrations as alarm signals to communicate with nestmates. Furthermore, vibrational cues, such as the resonance vibrations induced by gnawing, are of major importance for nesting and foraging decisions. In this chapter, we review the literature on vibrational communication in termites. First, we will focus on the production of vibrational signals by drumming and tremulation. Second, the current knowledge on vibrational perception in termites is summarized. Further, the context of signaling, the reaction of signal receivers, and the intra- and interspecific use of vibrational cues produced by termites are reviewed. The physical properties of the substrate, through which vibrational signals travel, are crucial for successful communication. In this context, we discuss the outstanding fact that termites construct the substrate, i.e., the nest, mound, and galleries they live in and communicate through, by themselves.

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16.1 Introduction

> Mich deucht, diese Thiere verdienen Convulsionarii genannt zu werden. (König 1779, p. 25)

Termites are eusocial insects that comprise approximately 2600 species (Kambhampati and Eggelton 2000). Termites are subdivided into seven families (Inward et al. 2007a; Cameron et al. 2012). They have recently been placed in the order Blattodea within the suborder Dictyoptera (Inward et al. 2007b), and it is now clearly established that termites are a fully social form of cockroaches (Eggleton 2011).

Termites live in colonies comprising typically immatures and three main adult castes that form the animated part: reproductives (queen, king, and alates), workers, and soldiers. The inanimate part of the colony consists of the structures (mound, nest, galleries) built by the termites. Workers forage for food and water, build and repair colony structures, and tend the king and the queen. The only task of the soldier caste is to defend the colony (Eggleton 2011). Levels of social organization differ distinctly across termite taxa, corresponding tightly to nest and foraging habits. Social organization ranges from simple organization with small colonies, to some of the largest and most complex societies among animals. Termites fall into two fundamental groups, with just a few species showing intermediate characteristics: one-piece-life-type termites, thought to reflect ancestral life history patterns, and separate-life-type termites (Korb and Thorne 2017). One-piece-life-type individuals spend their entire lives nesting and feeding within the same piece of wood (i.e., tree, log) where their founding queen and king initiated the colony. They are restricted to that one resource and do not search for or exploit nearby pieces of wood (Korb and Thorne 2017). Separate-life-type termites have a nest that is separate from their food site. Termites forage to one or more resources spatially separated from the nest (Korb and Thorne 2017). There is little doubt that termite evolution proceeded from small wood-dwelling colonies toward larger colonies that forage outside of the wood (Roisin and Korb 2011). This also has consequences for the communication mode. In termite species that have large colonies, more and more sophisticated solutions for social organization, caste differentiation, and communication have evolved.

Predation plays a key role in termite caste evolution, and various morphological adaptations, especially in the soldier caste, have evolved. Termite colonies lack a centralized control, but function as a coherent unit that can adjust its actions in response to internal and external environmental changes. Communication in termites relies on a complex network of chemical and mechanical, i.e., vibrational, cues and signals. In contrast to the other social insect taxa, visual cues are insignificant, as most castes of most termite species are blind. Vibrational cues and signals are used in a broad range of behavioral contexts and are present in all termite species studied so far. Vibrational communication is likely to be ancestral to termites, as it is also observed in *Cryptocercus* woodroaches (Bell et al. 2007), the sister group of termites (Lo et al. 2000; Cameron et al. 2012). Striking ethological similarities in cockroaches and termites have been recognized since the early nineteenth century (for review, see Bell et al. 2007). Adults and nymphs of *Cryptocercus* transmit alarm to family members via oscillatory movements nearly identical to those of termites (Cleveland et al. 1934; Seelinger and Seelinger 1983).

There are reviews available about communication and social regulation in termites (Bagnères and Hanus 2015), pheromones and chemical ecology of dispersal and foraging (Bordereau and Pasteels 2011), chemical warfare in termites (Šobotník et al. 2010), and intracolony chemical communication in social insects (Richard and Hunt 2013). These reviews focus on the chemical mode; the mechanical mode is, if at all, only briefly examined. The available reviews dealing with vibrational communication with a broader approach focus on social insects, but not specifically on termites (Kirchner 1997; Hunt and Richard 2013). Here, we review specifically the literature on vibrational communication in termites for the first time.

16.2 Production of Vibrational Signals in Termites

There has been some confusion about the terminology of different vibrational behaviors in termites. For a more cohesive language in the field of biotremology, we use the terminology suggested by Hill (2014).

16.2.1 Drumming

Drumming is the term used more frequently than others to describe the production of substrate-borne vibrations using some body part to strike the substrate in a percussive event (Hill 2014). Termites drum by hitting the head or abdomen on the substrate (Fig. 16.1a). This behavior has been referred to as vertical oscillatory movements (VOM) in termites by Howse (1965a) and following authors (Leis et al. 1994; Connétable et al. 1999; Delattre et al. 2015). VOMs are performed by workers and soldiers in many termite species and often result in drumming the head against the substrate. Every hit of the termite's head on the substrate induces a vibratory pulse that is transmitted through the substrate. Usually termites produce drumming signals composed of several consecutive pulses, termed pulse groups (Fig. 16.2). Pulse groups are also referred to as bursts (Connétable et al. 1999; Delattre et al. 2015; Hertel et al. 2011; Christaldo et al. 2015) and sound groups (Howse 1964b). In some species only soldiers show drumming behavior (Connétable et al. 1999; Hertel et al. 2011), and in other species workers also drum (Kirchner et al. 1994; personal observation).

The first termite species in which the production of vibrational signals has been studied in some detail are the New World damp-wood termites of the genus *Zootermopsis*, which inhabit rotten wood in temperate climates (Stuart 1963, 1988; Howse 1964b, 1965a; Kirchner et al. 1994). The drumming signals of *Z. nevadensis* are composed of several pulse groups formed by several consecutive pulses with a

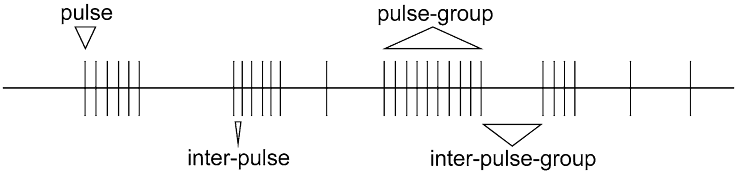


Fig. 16.1 Schematic oscillogram of a drumming signal's temporal pattern

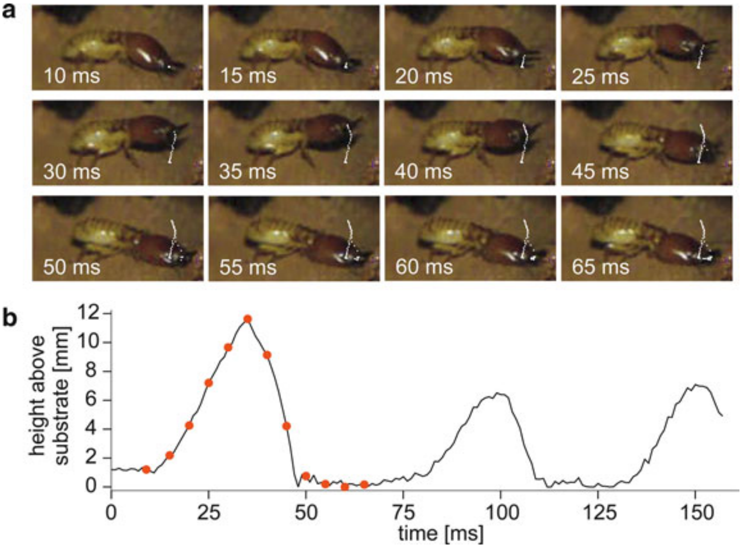
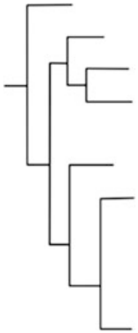


Fig. 16.2 Kinematic of a drumming termite soldier (**a**) Single frames from a high-speed video recording (1000 frames s^{-1}) of a drumming major soldier of *M. natalensis*. Every fifth frame is shown. The position of the head is marked white dots in each frame. (**b**) Height of the termite's head above the nest substrate while performing three drum beats. The single frames shown in (**a**) are marked as red dots (adapted from Hager and Kirchner 2013)

pulse repetition rate of about 20 Hz (Table 16.1). The carrier frequency depends on the mechanical properties of the substrate on which the termite drums. The highest vibrational amplitudes measured close to the signaling termite are in the range of 10 ms^{-2} RMS (Kirchner et al. 1994).

Relatively well studied in terms of vibrational communication are termites of the genus *Macrotermes*. Major soldiers of *M. natalensis* produce a vibrational signal with a pulse repetition rate of about 11 Hz (Fig. 16.3, Hager and Kirchner 2013). High-speed video recordings of some species have been made to reveal the equations of motion (Howse 1965a; Connétable et al. 1999; Hager and Kirchner 2013). Drumming major soldiers of *Macrotermes natalensis* raise their heads around 1 cm vertically in the air before accelerating it down to the ground (Fig. 16.1). The postmentum of their heads hits the ground with a velocity of up to 1.5 ms^{-1}; thereby the head is accelerated at about 0.1 ms^{-2} (Hager and Kirchner 2013).

Table 16.1 Synthesis of some characteristics of termite drumming

Phylogenetic relationship[a]	Family	Species	Caste	PRR	Social ampl.	Eliciting stimuli	Life type[b]
	Mastotermitidae	*Mastotermes darwiniensis*[c]		21 Hz	Yes?	A, C, V	ST
	Stolotermitidae						
	Hodotermitidae						
	Archotermopsidae	*Zootermopsis angusticollis*[d]		24 Hz	No	A, L, V	OPT
		Zootermopsis nevadensis[e]	S, W	20 Hz	No	A, L	OPT
	Kalotermitidae	*Kalotermes flavicollis*[f]	N		No	C, L, HS, V	OPT
	Rhinotermitidae	*Reticulitermes flavipes*[g]		25 Hz			ST
		Coptotermes acinaciformis[h]		13 Hz			ST
		Coptotermes formosanus[g]		14 Hz			ST
		Coptotermes gestroi[i]	S	16 Hz		A, L, V	ST
	Termitidae	*Odontotermes* sp.[j]	S	19 Hz	2.1 ms^{-1}	A, L, V	ST
		Pseudacanthotermes militaris[k]	S	19 Hz	Yes	A, L, HS, V	ST
		Pseudacanthotermes spiniger[k]	S	14 Hz	Yes	A, L, HS, V	ST
		Constrictotermes cyphergaster[l]	SW	19 Hz15 Hz		C	ST
		Macrotermes bellicosus[m]	S	26 Hz	1.7 ms^{-1}	A, V	ST
		Macrotermes natalensis[j]	S	11 Hz	1.3 ms^{-1}	A, L, V	ST
		Macrotermes subhyalinus[m]	S	13 Hz	0.3 ms^{-1}	A, V	ST

PRR pulse repetition rate, *OPT* one piece life type, *ST* separate life type *S* soldier, *W* worker, *N* nymph, *A* air current, *C* chemical, *HS* heterospecific, *L* light, *V* vibration

[a] Cameron et al. (2012), [b] Korb and Thorne (2017), [c] Delattre et al. (2015), [d] Howse (1964b), [e] Kirchner et al. (1994), [f] Leis et al. (1994), [g] Fink et al. (2006), [h] Inta et al. (2009), [i] Hertel et al. (2011), [j] Hager and Kirchner (2013), [k] Connétable et al. (1999), [l] Christaldo et al. (2015), [m] Röhrig et al. (1999)

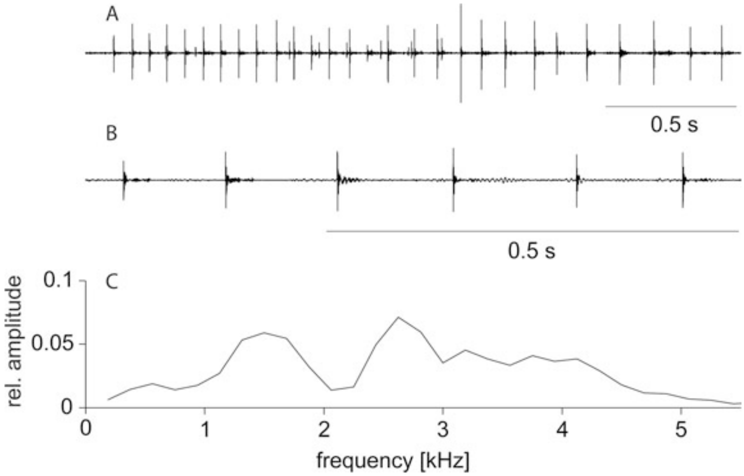


Fig. 16.3 Typical drumming signals of *Macrotermes natalensis*. (**a**) Oscillogram of several pulse groups produced by several termites. (**b**) Oscillogram of a pulse group produced by a single termite. The pulse repetition rate is 11 Hz. (**c**) Frequency spectrogram of the pulse group shown in (**b**). Most energy is found between 1 and 5 kHz (band-pass filter 10 Hz to 10 kHz) (adapted from Hager and Kirchner 2013)

Vibrational signals have been investigated by many authors to reveal whether information is encoded in their temporal structure. Drumming on a substrate produces broadband 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 receiver's site are due to filtering by the substrate through which the signal is propagated. The temporal patterns are thus more likely to encode information than spectral properties (Hill 2014).

Howse (1964b) measured the pulse repetition rate of drumming *Z. angusticollis* and found that it varies with temperature. At 17.5 °C the pulse repetition rate is about 18 Hz and increases linearly up to 36 Hz at a temperature of 23 °C. At temperatures above 23 °C the pulse repetition rate decreases. At a given temperature the pulse repetition rate is in many termite species nearly constant (Howse 1964b; Röhrig et al. 1999; Hertel et al. 2011; Hager and Kirchner 2013) and appears to be species-specific (Table 16.1). Because termites do not modulate the pulse repetition rate, it is unlikely that specific information is encoded. Therefore, it was pointed out that information may be encoded in other temporal patterns than pulse repetition rate (Howse 1964b; Hertel et al. 2011). Further temporal patterns that have been investigated are the pulse group repetition rate (repetition period, Howse 1964b), the number of pulses per pulse group and the ratio of two to three pulse groups (two sound groups, Howse 1964b), and pulse group duration (time between the first and the last sound of sound groups, Howse 1964b). Howse (1964b) could not find any clearly defined variation in the temporal patterns apart from the variation with temperature, which is unlikely to have any significance from an evolutionary point of view. To our knowledge no study demonstrates modulation of drumming signals in termites. However, the temporal patterns of vibrational signals are relevant. Delattre et al. (2015) demonstrated the significance of the temporal patterns for *Mastotermes darwiniensis*. The termites respond to a playback of natural signals with positive feedback, but not to computer-made signals of the same overall energy and technical characteristics (intensity and frequency content). To reveal whether drumming signals can be modulated to inform nestmates about specific threats or different levels of alarm, detailed studies controlling the level of threat, the former experience of the drummers, and the reaction of the receivers are required.

16.2.2 Tremulation

The term "tremulation" describes body motions without any percussive impact with the substrate. Typically, the vibrations pass to the substrate via body parts that couple with the surface like legs, tarsi, or the thorax. Howse (1965a) referred to tremulations as longitudinal oscillatory movements (LOM). In the LOM the termite jerks backward by extension of the forelegs and then jerks more slowly forward, sometimes repeating this maneuver several times in rapid succession. A clear vertical component is lacking (Howse 1965a). LOM is also referred to as jittering, jerking (Emerson 1929), and horizontal reciprocating movement, nudging, bumping, or quivering (Stuart 1963). Vibrational signals produced by tremulation might be transmitted by direct contact between nestmates (Kettler and Leuthold 1995; Reinhard and Clément 2002; Šobotník et al. 2008) or possibly up to a certain distance via substrate-borne vibrations. Unlike drumming, tremulatory movements produce substrate-borne vibrations in frequencies that are low and narrowbanded, more like a pure tone (Hill 2014). However, studies of the substrate-borne vibrations induced by tremulation in termites are scarce. Insights from Hymenoptera might be adduced instead. In the context of recruitment, honey bees and stingless bees produce tremulatory signals by rhythmic thoracic oscillations that are transmitted to the substrate. The substrate vibrations are narrowbanded with a frequency range of 200–600 Hz (Hrncir et al. 2006). To our knowledge no study has measured the substrate-borne component of tremulating termites in their natural substrate. However, Delattre et al. (2015) observed *M. darwiniensis* in Petri dishes and found that the frequency band of 10–200 Hz was excited by the vibratory movements of termites and not by other behaviors like walking or chewing.

Another term introduced by Howse (1965a) is the complex oscillatory movement (COM), which comprises a combination of horizontal and vertical movements and often involves bumping into nestmates. Emerson (1929) suggested that during COM an odor might be released. Stuart (1963) was unable to find any evidence for the release of an odor. Some authors, however, consider that the oscillatory movements are one and the same but indicate varying degrees of alarm (Grabensberger 1933; Stuart 1963; Howse 1965a). A hint to a common evolutionary basis for VOMs and LOMs is the almost identical frequency of tremulation and drumming in termites.

The monotony of both rhythmic movements suggests the possibility that an external interference may change an intrinsic threshold for coupling both motor systems to a central pattern generator (Hertel et al. 2011).

16.3 Perception of Vibration in Termites

Drumming termites produce substrate-borne vibrations that travel through the substrate and are perceived by other individuals standing nearby. The perceptual threshold, defined by the lowest displacement or acceleration stimulus that elicits a response, has been studied using electrophysiological and behavioral approaches.

16.3.1 Electrophysiological Studies

Subgenual organs (SGO) react to substrate vibrations and have been found in several termite species. A detailed description of the SGO of *Kalotermes flavicollis* is given by Richard (1950). The SGO is considered to be the most sensitive vibration receptor in insects (Čokl and Virant-Doberlet 2003). In termites the subgenual organ is club shaped (Howse 1965b). The function of the SGO in *Zootermopsis angusticollis* and the perception of vibration have been described by Howse (1962, 1964a, 1965b). For physiological characterization of the SGO, an important parameter is the perceptual threshold: the lowest displacement or acceleration stimulus that elicits a neuronal response. In a physiological study of the sense of vibrations of *Zootermopsis angusticollis*, Howse (1964a) reported thresholds that were in the range of 1 ms^{-2} RMS between 50 Hz and 1 kHz (Fig. 16.4). Nervous responses to vibratory stimuli were measured at the central nerve cord between the first and second thoracic ganglia. As in electrophysiological studies where recording techniques and stimulus calibration influence the recorded sensitivity (see Chap. 12, this volume), comparisons with other species and studies are difficult.

16.3.2 Behavioral Studies

Compared to the number of neuronal approaches, more studies have been conducted that investigate the perceptual threshold of vibrations by behavioral means. The perceptual threshold was either defined by the lowest acceleration amplitude that elicits a behavioral response in a certain proportion of termites (Howse 1964a; Kirchner et al. 1994; Röhrig et al. 1999) or as the lowest acceleration amplitude that elicits a significant behavioral response in comparison with control experiments with sham stimuli (Hager and Kirchner 2013). In these studies, substrate-borne

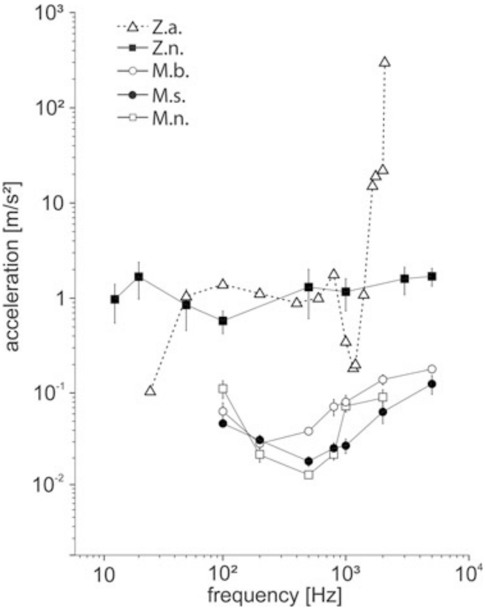


Fig. 16.4 Threshold amplitudes of vibratory stimuli eliciting a behavioral response (solid lines) and by electrophysiological means (broken line) in termites. The threshold is expressed as an acceleration amplitude (RMS, mean ± SE). *Open triangle Zootermopsis angusticollis* adapted from Howse (1964b); *solid squares Zootermopsis nevadensis* adapted from Kirchner et al. (1994); *open dots Macrotermes bellicosus and solid dots Macrotermes subhyalinus* adapted from Röhrig et al. (1999); *open squares Macrotermes natalensis* (adapted from Hager and Kirchner 2013)

vibrations elicited responses in the entire range of tested frequencies from 100 to 5000 Hz (Fig. 16.4). *Macrotermes natalensis* soldiers are most sensitive to frequencies around 500 Hz. They are sensitive to amplitudes of about 12 mms^{-2}, which correspond to a displacement of the substrate of 1–2 nm. In *Zootermopsis nevadensis* the perceptual threshold is nearly identical for all tested frequencies, with a threshold amplitude of about 1 ms^{-2} RMS (Kirchner et al. 1994). This is in the range from 50 Hz to 1 kHz that is nearly identical to the thresholds found in the physiological assay previously reported (Howse 1964a). The striking differences in the amplitude above 1 kHz may be due to the experimental calibration (for a detailed review, see Chap. 12, this volume). There is no evidence that termites perceive drumming signals via airborne sound (Kirchner et al. 1994; Connétable et al. 1999; Röhrig et al. 1999).

16.4 Vibrational Signaling

In studies of animal communication, a fundamental distinction is made between signals, which have evolved specifically to alter a receiver's behavior, and cues, which are incidental sources of information detected by unintended receivers (Maynard Smith and Harper 2003; Scott-Phillips 2008). Many animals respond to a threat of predation by producing alarm signals that warn other individuals of the presence of danger.

16.4.1 Alarm Behavior in Non-Termitidae

As early as in the eighteenth century, Smeathman (1781) supposed that termite drumming serves as an alarm signal, and Grassi and Sandias (1897) stated that these convulsions (drumming signals) serve as a cry to summon help or give alarm. Since then some efforts have been undertaken to reveal the message and meaning of alarm signals by describing the releasing stimuli, analyzing the temporal pattern and frequency structure of the signals and observing the reaction of nestmates (Table 16.1). Stimuli that elicited drumming were a sudden bright light, water sprayed into the nest, and air currents (Howse 1964b; Leis et al. 1994; Kirchner et al. 1994). The drumming signals are transmitted through the wooden nesting material and thereby alert nestmates, which are not exposed to the source of disturbance. However, only those nestmates that are close enough to the site of disturbance will perceive the drumming signals. This might be sufficient in the relatively small colonies of *Zootermopsis*, i.e. in termites that display the one-piece-life-type but it would be of very limited value in separate-life-type termites (Kirchner et al. 1994).

The dampwood termite *Zootermopsis angusticollis* shows an alarm response after detecting spores of a pathogenic fungi (Rosengaus et al. 1999). Termites in direct contact with a high concentration of spores show a striking vibratory display which appears to convey information about the presence of pathogens to nearby unexposed nestmates through substrate vibration. Nestmates not directly in contact with spores that perceive the vibrational signal increase significantly their distance from the spore-exposed vibrating termites, apparently to escape from the source of infection. The fleeing response is not induced by the presence of the spores alone or by pheromones, but requires the perception of the vibrations propagated through the substrate (Rosengaus et al. 1999). The question whether this behavior displays a specific pathogen alarm or an unspecific alarm remains open, because alarm signals in a predation context in other termite species also lead to a fleeing response (Connétable et al. 1999; Röhrig et al. 1999; Hager and Kirchner 2013).

Drumming is not the only behavior displayed by termites after a disturbance. Howse (1965a) found that tremulation occurred after the termites were disturbed and that it appeared to be a response to a relatively low-intensity stimulus to antennal sensilla. Tremulation can also be observed in undisturbed groups in many species (Sbrenna et al. 1992; Maistrello and Sbrenna 1996; Hertel et al. 2011). Both workers and soldiers of *M. darwiniensis* respond to disturbance with tremulation and drumming. These two alarm modes are clearly not exclusive. It is thought that tremulation increases the efficiency of alarm propagation by alerting nearby calm individuals, while drumming is used to inform nestmates at some distance from the source of disturbance (Delattre et al. 2015).

16.4.2 *Alarm Behavior in Termitidae: Long-Distance Communication via Social Amplification*

Termitidae display the separate life type and many species cultivate fungi. To supply the fungus with dead dry plant material, they forage in a large territory around the nest. They build long subterranean galleries that lead outward from the nest to their foraging sites. These gallery systems can spread over an area of up to 2000 m^2 (Lys and Leuthold 1991; Jmhasly and Leuthold 1999).

During foraging, termites are exposed to high predation risk. A variety of predators specialize on termites (Wilson and Clark 1977; Kok and Hewitt 1990; Buczkowski and Bennett 2007). Collective handling of a threat requires effective communication that allows the escape of vulnerable individuals and the recruitment of defenders. Alarm communication in termites appears to be multimodal, combining chemical and mechanical cues and signals (Šobotník et al. 2010). Studies have shown that in *Pseudacanthotermes spiniger*, *P. militaris* (Connétable et al. 1999), *Macrotermes subhyalinus, M. bellicosus* (Röhrig et al. 1999), *M. natalensis*, and *Odontotermes* sp. (Hager and Kirchner 2013) neither tactile contacts nor pheromones are necessary to propagate the alarm. Pheromones are unlikely to play a dominant role in fast alarm transmission. Under conditions where a fast alarm transmission along the gallery is advantageous, vibrational signals are more efficient.

Vibrational long-distance communication is composed of the physical propagation of the vibrational wave in the substrate (Fig. 16.5, solid gray line), as well as

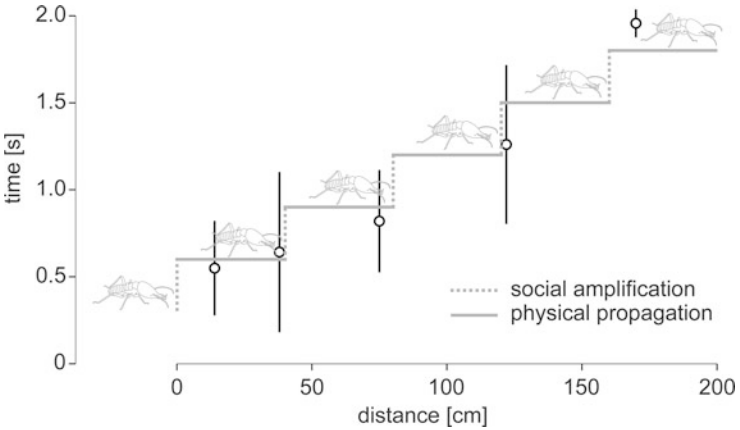


Fig. 16.5 Vibrational long-distance communication in *M. natalensis*. The time delay within chains of drumming termite soldiers is plotted as a function of spatial distance between the drummers (*dots* means, *bares* SD). The alarm transmission velocity is 1.3 ms^{-1}. The model view of social long-distance communication is shown in gray. *Solid gray line* physical propagation of the vibrational wave in the substrate. *Broken gray line* social amplification through positive feedback (adapted from Hager and Kirchner 2013)

the social amplification and transmission of the signal through positive feedback mechanisms by the termites (Fig. 16.5, broken gray line). Both processes are characterized by specific and very different velocities of propagation and attenuation with distance. The velocity of propagation of vibrational signals in the nest substrate is in the range of 100–130 ms^{-1} (Röhrig et al. 1999; Hager and Kirchner 2013). The range of the signal depends on the amplitude at the signal's source, attenuation on the way to the receiver, and the perceptual threshold of the receiver. The highest recorded amplitude in *M. natalensis* is about 0.7 ms^{-2}. Based on a signal attenuation of 0.4 $dBcm^{-1}$ in the nest substrate and a perceptual threshold of 0.012 ms^{-2}, the range of this signal is about 0.4 m (Hager and Kirchner 2013). This means that initial drumming can alert nestmates in the vicinity but would not reach nestmates in meter-long galleries. Soldiers of many termitids respond to drumming nestmates in the vicinity by drumming themselves (Connétable et al. 1999; Röhrig et al. 1999; Hager and Kirchner 2013). This leads to significant changes in both attenuation of the signal amplitude with distance and velocity of propagation. The velocity of long-distance vibrational communication due to social amplification is in the range of 1–2 ms^{-1}. Given that the distances from the nest to the foraging sites range from a few to some tens of meters, this velocity leads to colony responses within seconds. Signal attenuation with distance is reduced to zero by this mechanism of social reamplification. Such a signal transmission without decrement seems to be rare in animal communication (Hager and Kirchner 2013).

For a long time it was thought that positive feedback to vibrational alarm signals is unique to Termitidae. However, recently it was shown that *Mastotermes darwiniensis*, perhaps the oldest extant eusocial termite, displays positive feedback to vibrational signals. The energy ratio resulting from vibratory behavior in *M. darwiniensis* is significantly higher after exposure to a playback of natural alarm signals than before (Delattre et al. 2015). One of the limitations of this report is that it does not specify whether the vibratory feedback is composed of drumming or tremulatory signals. As the amplitude of vibrational signals produced by tremulation is thought to be very small, it is unlikely that an alarm would spread over long distances. In chains of reamplifying termites, they would have to stand very close to each other to be able to perceive the tremulatory signals. *M. darwiniensis* lives in populous colonies monopolizing large foraging territories and display a multitude of other advanced characters of Termitidae (Delattre et al. 2015). *M. darwiniensis* belongs to the separate-life-type species (Table 16.1), and individuals do not feed only on the wood in which they nest, but also forage in the soil or on the ground. Therefore, it would not surprise if they have evolved a vibratory long-distance alarm system through chains of drumming termites like *Macrotermes*. Further studies should clarify whether the positive feedback of *M. darwiniensis* contains drumming signals and should measure the relevant physical properties of the natural nest substrate.

As shown before, soldiers react to drumming signals with positive feedback and thereby transmit the alarm. Furthermore, in *Macrotermes* and *Pseudacanthotermes* soldiers stay close to the site of disturbance, probably to defend the nest. Vulnerable workers in contrast respond to drumming signals by tremulation (jittering) and often flee from attacked sites (Connétable et al. 1999; Röhrig et al. 1999; Hager and Kirchner 2013). Thus, a termite somewhere in the vast gallery system that detects alarm signals has to make a decision to walk either in one direction or the other. In this context it would be advantageous for the termites to extract information about the direction of the source of vibration from the vibrational signals. And indeed, *M. natalensis* makes use of a directional vibration sensing in the context of colony defense. In the field, soldiers are recruited toward the source of the signal. In arena experiments on natural nest material, soldiers can localize the source of vibration. Using two movable platforms through which vibrations were introduced to the legs of the left and right sides of the body with a time delay, it was shown that the difference in time of arrival is the directional cue used for orientation. Delays as short as 0.2 ms are sufficient to be detected. Soldiers show a significant positive tropotaxis to the platform stimulated earlier, demonstrating for the first time perception of time-of-arrival delays and vibrotropotaxis on solid substrates in insects (Hager and Kirchner 2014).

The vibrational signals, particularly drumming signals, could additionally be addressed to predators. It was speculated that the synchronized drumming of termites serves as a signal to warn or deter predators (Howse 1984; Connétable et al. 1999; Röhrig et al. 1999). Until now no experiments have been carried out to investigate whether drumming warns predators away from termites. Drumming may also act as a territorial signal directed to neighboring termite colony members. The galleries of neighboring *Macrotermes* colonies can overlap, and *Macrotermes* displays a strong aggressive reaction toward non-nestmates (Jmhasly and Leuthold 1999). Hence, drumming signals could be used for communication with neighbors to prevent expensive aggressive interactions at the territorial boundaries. This would require that termites discriminate conspecific from heterospecific drumming signals. However, studies on *P. spiniger*, *P. militaris* (Connétable et al. 1999), *M. subhyalinus*, *M. bellicosus* (Röhrig et al. 1999), *M. natalensis*, and *Odontotermes* sp. (Hager and Kirchner 2013) could not find discriminative behavior in the relevant pulse repetition range.

Christaldo et al. (2015) integrated chemical and vibroacoustic signals, revealing the existence of different alarm levels in *Constrictotermes cyphergaster*. Lower levels are communicated through vibrational signals, and higher levels causing general alarm or retreat are communicated through alarm pheromone. Lower doses of the pheromone provoked higher numbers of vibrational signals compared to higher doses. Higher doses induced long-term running of all termites without the stopping necessary to perform vibratory behavior. This shows that vibrational alarm signals are closely intertwined with chemical alarm signals. The reactions of many termite species to chemical alarm signals are caste-specific. Soldiers tend to reach its source, while other castes hide away or stay unalarmed; the alerted soldiers then propagate the alarm by active running and physical contacts with nestmates or through the release of further frontal gland secretion (for review, see Šobotník et al. 2010).

16.5 Vibrational Cues

Vibrations produced by walking, foraging, and chewing termites can be exploited by conspecific and heterospecific termites, as well as competitors, predators, and pest controllers. If these vibrations are not produced only in the context of information exchange, but rather during general maintenance activities, they will be considered cues. Vibrational cues emitted by termites, for example, can be used to detect termite infestation, either by heterospecific termites or by pest controllers. In this context, the drywood termites of the genus *Cryptotermes* are relatively well studied. They are distributed worldwide, originally from tropical-subtropical regions, but many species are now known to migrate far out of their native home range, via infested furniture and other wood pieces.

16.5.1 Food Size Assessment

One-piece-life-type termites live and feed in a single piece of wood. They do not forage outside. Therefore, the size of the wood piece chosen for nesting is of major importance. There should be high selective pressure on the evolution of mechanisms that enable termites to gather information about putative nesting, i.e., food sites. Concerning this, some experiments have been conducted to reveal whether the mechanosensory mode is employed. In this respect, important characteristics of a piece of wood are its material characteristics, such as density, mass and internal damping, as well as its geometry and boundary condition (Inta et al. 2007). These characteristics can be very complex and have not been measured in natural termite nests. However, choice experiments offering uniform wood pieces with nearly identical characteristics have been conducted. Vibrational playback experiments with recorded termite gnawing on different sized wood pieces suggest that *Cryptotermes domesticus* and *C. secundus* assess wood, i.e., food, size using the resonant frequency of their own gnawing vibrations (Evans et al. 2005, 2007). However, this is probably not the only information that the termites perceived, because in playback experiments with artificially produced vibrations matching the recorded gnawing vibration in center frequency termites do not show preferences between wood pieces of different sizes (Evans et al. 2005).

Inta et al. (2007) conducted choice experiments that tested the ability of the drywood termite *Cryptotermes secundus* to assess wooden block size, using a solid wooden block paired with a composite block of either wood and aluminum or wood and rubber. Each composite block was constructed to match mass or low-frequency vibrational modes (i.e., fundamental frequency) of the solid wooden block. The termites always chose the blocks with more wood. Termites were not fooled by composite blocks matched for mass or frequency, which implies that they probably employ more than a single simple measure in their food assessment strategy. This implies a degree of sophistication in their ability to assess their environment hitherto unknown (Inta et al. 2007).

16.5.2 Competition and Predator Avoidance

The drywood termite *Cryptotermes secundus* is attracted to playbacks of its own vibrational cues, but is repelled by those of the competing termite *Coptotermes acinaciformis*. This response increases with decreasing wood size, corresponding with both increased risk and strength of the cue. The drywood termites appear to avoid confrontation by using vibrational cues emitted by the heterospecific competitor (Evans et al. 2009). Vibrational cues are also employed in predator avoidance. Comparisons of 16 termite and ant species indicate that vibrations induced by walking ants had larger amplitudes than those of termites (Oberst et al. 2017). Two choice experiments reveal that the termite *Coptotermes acinaciformis* avoids predation using vibrational cues. They detect vibrations caused by walking of their major predator, the ant *Iridomyrmex purpureus*, and not chemical cues (Oberst et al. 2017).

16.5.3 Termites as Pests: Detection of Vibrations Caused by Termites

Several termite species are significant economic pests, mainly in urban areas where they attack human-made structures, but also in agriculture and natural forest habitats. Substrate-borne vibrations caused by termites, either due to feeding, walking, constructing, or vibrational communication, have been used to detect noninvasive termite infestation. Termites can be detected up to 2 meters with accelerometers along the wood grain (Lemaster et al. 1997; Yanase et al. 2000). While feeding, termites stress and snap wood fibers, which cause the wood fibers to spontaneously emit broadband acoustic emissions (Fujii et al. 1990) that can be detected (Mankin et al. 2011). According to Lemaster et al. (1997), the detectability of acoustic emissions from termite infestations depends on the resonant frequencies of the piezoelectric transducers; transducers that have resonant frequencies near 60 kHz provide the best overall performance for ultrasonic signal detection. A number of devices are now available for vibrational termite detection (Mankin et al. 2011).

16.6 Conclusions and Outlook

Contrary to acoustic signals that propagate primarily through air, vibratory signals are transmitted through various mediums with very different physical properties. For efficient communication, a match between the signal and the medium is essential (Hill 2009). Signals could be adapted to match a specific medium or, up to a certain level, vice versa. There have been very few studies analyzing this relationship. Most of them focus on insects communicating on plant stems. In such cases insects could choose a specific plant stem because the physical properties promote vibrational communication in the relevant frequency range, or insects could produce vibratory signals in a frequency range traveling best in a specific medium to achieve a match between the signal and the medium (Hill 2001; Cocroft and Rodriguez 2005; Cocroft et al. 2006). In this context termites are particularly interesting to study, as an exceptional feature of social insects is that most of them live inside self-built nests. The nests are the result of self-organization in interaction with stigmergy and templates (Korb 2011). The nests function primarily as fortresses to protect against enemies and hostile environmental conditions (Noriot and Darlington 2000), but secondly the nest structure should favor communication with nestmates. Up to several thousand individuals are living in these nests. Therefore, communication with nestmates is a basic requirement. The construction of nest structures that allow unimpeded communication with nestmates should be favored by natural selection. There remain many open questions in understanding social nest architecture, especially in a communication context. To resolve them detailed studies are required, both in nature and in the laboratory. Furthermore, carefully conducted experiments measuring substrate-borne vibrations produced by tremulation of termites and linking these signals to releasing stimuli and the reaction of the receivers are lacking.

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Part VI
Applied Biotremology

Chapter 17
Mating Disruption by Vibrational Signals: State of the Field and Perspectives

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Abstract Until a few years ago, the concept of mating disruption had been exclusively associated with the use of pheromones to reduce population density of insect pests. Since the early 2000s, a novel approach has been proposed to the scientific community: vibrational mating disruption (VMD). The novelty is the use of disturbance vibrations to disrupt the mating behavior of insect pests that communicate by means of substrate-borne vibrations. This research falls within the new field of biotremology and it brought the VMD from a theoretical concept to practical open field experimentation: in 2017, VMD was applied in an organic vineyard in Northern Italy to control leafhopper pests' population density. This achievement gave us the opportunity to report the state of the field for the method, to discuss the ongoing research and to make a comparison between pheromone mating disruption (PMD) and VMD. In this chapter, we review the salient moments that led to the field application of VMD. Then, we discuss the VMD characteristics and we provide a benchmark, using as reference the traditional PMD to discuss similarities and differences. Furthermore, we analyze the advantages and disadvantages of applying VMD to commercial crops. We are convinced that the first vibrational vineyard is a starting point and that biotremology will provide many innovative possibilities for farmers to control pests in the future. We also think that the

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introduction of electronic devices in the vineyard could be a trailblazer for the diffusion of smart technology in viticulture, thus improving its general management.

17.1 The Birth of the Concept

In summer 2017, the world's first vineyard managed with vibrational mating disruption (VMD) was activated in San Michele all'Adige, TN, Italy. Special devices, consisting of mini-shakers, were attached to a few trellis poles of each row to transmit disruptive vibrational signals into the grapevine tissues, which were specifically designed to target the mating behavior of a leafhopper pest, *Scaphoideus titanus* (Fig. 17.1a, b). The novelty was not doing mating disruption per se, but rather doing it using vibrations instead of pheromones. Supported by the studies of chemical ecology, the method of pheromone mating disruption (PMD) at the end of the twentieth century was already an established method to control moths, beetles, true bugs, and other insects worldwide (Fig. 17.1c, d). Chemical ecology originated much earlier, at the end of the nineteenth century when Fabre and Lintner first demonstrated that insects communicate using chemical compounds (Lintner 1882; Fabre 1966). Then, field trials in the 1960s (Gaston et al. 1967; Cardé and Minks 1995) paved the way for the application of PMD. It took another 10 years before scientists demonstrated that insects use substrate-borne vibrations as signals for intraspecific communication (Gogala et al. 1974; Ichikawa and Ishii 1974) and other 60 years before biotremology, the science that studies the vibrational communication, was officially primed as a formal discipline (Hill and Wessel 2016). No wonder, then, that applicative studies of biotremology were basically missing up to the first decade of the 2000s.

The key point the VMD came from was the fine-scale comprehension of *S. titanus* mating behavior. As all leafhoppers studied so far, this species also relies almost exclusively on vibrations for mating (Čokl and Virant-Doberlet 2003). Usually, a duet made of male's and female's signals is established and maintained until copula occurs (Mazzoni et al. 2009b). In particular, the emission of a disturbance noise by rival males to interrupt the ongoing mating duet of a pair was crucial in developing the concept of VMD (Mazzoni et al. 2009a). Males of *S. titanus* are normally calm and do not move much around the plant (Mazzoni et al. 2009b). As with females, they spend most of the time feeding, grooming, and producing brochosomes (Rakitov 2002). The latter is a very curious activity: the individual pierces the leaf with the mouth stylets and then lifts up the abdomen and stretches the legs backward, first the posteriors then the medians and finally even the anteriors. Thus, it assumes a vertical position, standing on the mouth stylets. At this point, it emits a droplet of brochosomes that is collected by the rear tarsi directly from the anus. Then, all six legs together start to rub quickly against the droplet for a few seconds before the same droplet is kicked away and the insect resumes the normal position on the leaf. Such amiable males can suddenly change mood and turn aggressive if they detect an ongoing mating duet between another

Fig. 17.1 The two model species of pheromonal mating disruption (PMD) and vibrational mating disruption (VMD), respectively: *Scapoideus titanus* (**a**) and *Lobesia botrana* (**c**). On the right, the instruments used to transmit the disrupting signals: in (**b**), an active and a passive double dispenser of pheromones, and in (**d**), the last version of vibration transducer mounted on a pole of the trellis system

male and a female. As a matter of fact, mating is a priority over anything else in the life of an adult leafhopper and things can become very serious when the only available female is already courted by another male, a rival. Since all is fair in love and war, males tend to adopt two different strategies to delay and then anticipate the rival (Mazzoni et al. 2009b). Option 1 is the so-called satellite behavior or silent approach (Virant-Doberlet et al. 2014). A male listens to the pulses emitted by the female engaged in a duet and does not produce any of his signals. He silently searches for the female by exploiting the rival courtship, trying to be faster than the calling male to get close to the female. If so, once he is less than one body distance from the female he assumes a typical "pre-copula position" behind the female with an angle of 30–45°, and the head near her wingtips. Then, he can either try to mate or wait for the other male until the latter inevitably comes close to the pre-copula position. At this point, the first male will get the chance to throw the rival off the leaf with a powerful body sweep. Option 2 is much more interesting for the purposes of this chapter, in that it is based on the emission of a specific disturbance noise (DN) by males. In fact, males for some reason can decide to not adopting a silent approach, but rather to challenge the rival by emitting DN in exact correspondence with the female pulse emission. Briefly, the rival male overlaps with the female's reply and this causes the immediate interruption of the other male's search (Mazzoni et al. 2009b). Since the *S. titanus* mating strategy is unidirectional (male ⇒ female: males constantly lead the duet and search for stationary females that emit pulses that contain directional cues), the missed reception of female pulses by males makes localization of the female impossible. However, unidirectionality is not a rule in Auchenorrhyncha. There are species (i.e.,the sharpshooter *Homalodisca vitripennis* and the planthopper *Hyalesthes obsoletus*) where either males or females can start the mating communication and females lead the duet at least for part of the mating process (Mazzoni et al. 2010; Nieri et al. 2017). Nevertheless, in all known cases, males search for females and the female reply is the crucial cue that leads to her location (Mazzoni et al. 2009b; Kuhelj et al. 2016; Nieri and Mazzoni 2018). During the whole mating process, the role of *S. titanus* females is to follow a precise temporal pattern that is required for reciprocal identification (Polajnar et al. 2014). Any failure in this could negatively affect the duet, thus preventing mating success. This is also the main reason why it is extremely difficult to simulate a female in playback experiments: the strict synchronization of male–female duetting on the millisecond scale makes manual triggering of replies impossible, requiring technological solutions (Mankin et al. 2013; Korinšek et al. 2016). In nature, the search for the *S. titanus* female is characterized by the so-called location duet, which is the continuous alternation of male–female pulses periodically interrupted by the male's walking bouts (Mazzoni et al. 2009b). Males must constantly elicit the female's response to catch a directional cue. We observed in our lab bioassays that male's search was compromised whenever the female stopped to emit replying signals (Mazzoni et al. 2009b). Males do not stop calling even if females are physically removed from the arena and may go on for many minutes further, but they do not move any longer. Eventually, they jump off the leaf, thus starting the so-called call and fly behavior: they alternate calls (1–3) and short flights to other leaves, trying to establish a new duet with a female. We must consider that the time window of male call and fly activity is rather short, being mostly concentrated between 6 pm and 10 pm.

In essence, all experiments support two important statements: (1) males need to perceive clearly the female signal to identify and then locate them; (2) males do not search when the perception of the female signal is even partially compromised. The question that follows is simple: is it feasible to transmit a disruptive playback into the plant tissues to mask both male and female signals to prevent mating? In other words, would it be feasible to apply a technique of mating disruption based upon vibrations to control insect pests that communicate through vibrational signals? We have been trying to provide an answer to this question in the course of the past decade. First, we started to test the hypothesis in the laboratory, then in controlled conditions (potted plants in semi-field trials) (Mazzoni et al. 2009a). In 2012, we finally demonstrated the proof of concept also in field conditions: disturbance vibrations (i.e., DN playback) transmitted into plant tissues of rooted grapevines in a commercial vineyard can disrupt the mating behavior of a leafhopper species (Eriksson et al. 2012). The next obvious step was to transfer the acquired knowledge into a commercial vineyard and assess whether making the vibrational mating disruption a tool for viticulture was just a dream, or not.

17.2 The Vibrational Vineyard

Once the proof of concept was demonstrated, several practical issues still needed to be solved to develop a tool suitable for field application, in terms of both biological and technical aspects (Polajnar et al. 2016). On the one hand, a more accurate investigation of the biology and physiology of the insect were required to define (1) the time of device functioning in the course of the 24 h and (2) the amplitude threshold of efficacy of the disruptive noise. On the other hand, it was important to take into account several technical aspects to optimize (3) energy consumption/supply and (4) signal transmission through the trellis and from there to the plants to ensure the efficacy of the method.

All these aims go together in that the energy cost reduction passes through a significant decrease of the operational time window during the 24 h. Polajnar et al. (2016) tested the efficacy of the method by setting up an experiment with *S. titanus* pairs included in sleeve nets enclosing grapevine shoots. The DN was released according to many different time windows of the day and the conclusion was that the method still succeeded (not significantly different from the full time—DN control) even when the mini-shakers were inactive during the central hours of the day (10.00–18.00). One reason for it could be that during summer afternoon hours, individuals tend to reduce their activity in the field due to light and/or temperature conditions (Lessio and Alma 2004). However, it cannot be excluded that in the median/long-term insect populations will adjust their behavior in response to high selective pressure. There are several examples of species that switched their temporal calling pattern to overcome predictable periods of wind (McNett et al. 2010; Tishechkin 2013) or to reduce the impact of eavesdropping parasitoids (Vélez and Brockmann 2006). Therefore, a temporal shift of sexual activity cannot be excluded a priori and individuals after some time could use the silent windows even outside the preferred time for mating activity (Polajnar et al. 2016). More promising seems the strategy to find precise thresholds of insect activity based on measurable climatic parameters (e.g., temperature, humidity, wind, and rain) that could be monitored with simple instruments directly in the field. Also, the knowledge of physiological thresholds would be useful in optimizing the system. For example, the minimum effective amplitude of the DN is a prerequisite to design playback that would cover a reasonable active space. In fact, by recording the DN with a laser vibrometer at any point in the vineyard, it will be possible to understand whether it is effectively disruptive or not and to set the number of devices needed per unit of distance along the row. The *S. titanus* pairs ceased completely to communicate when the DN reached 2×10^{-2} mm/s of amplitude (that we can define as the safety threshold), which is approximately in the same amplitude range of the *S. titanus* natural calling signals when the signal is recorded from the same leaf of the calling individual (Eriksson et al. 2011; Polajnar et al. 2016). The same threshold was later confirmed in field trials, with an effective range of mating disruption of 10 m to each side of a prototype shaker that was hung directly on the metal wires of the trellis (Polajnar et al. 2016). However, it is important to emphasize that the natural calling signal amplitude drops of about 5–10 dB if the signal is recorded from outside the leaf (i.e., from the stem or from another leaf) (Polajnar et al. 2014); therefore, the safety threshold can be defined as the DN amplitude needed to interrupt mating communication when males and females occur on the same leaf. This is reflected also in the general species behavior: if a male perceives a female reply over 1×10^{-2} mm/s he starts emitting courtship signals; if the signal is in the range between 1×10^{-2} and 1×10^{-3} mm/s, he establishes a location duet with the female and starts searching for her, assuming that the female is on a separate leaf; finally if the signal is below 1×10^{-3} mm/s, the male–female duet is not established and the male performs the call-fly behavior, probably assuming that the female is very distant (Eriksson et al. 2011; Polajnar et al. 2014). Thus, we can hypothesize that the DN amplitude between 1×10^{-2} and 1×10^{-3} mm/s could be effective to disrupt the communication of males and females occurring on separate leaves (secondary threshold).

Starting from these considerations and assumptions, we tested the system in a large-scale field trial with a naturally occurring insect population. In spring 2017, we selected an organic productive vineyard in S. Michele all'Adige (Italy) in which we installed a total of 110 transducers on an area of 1.5 ha of Cabernet Franc (Fig. 17.2).

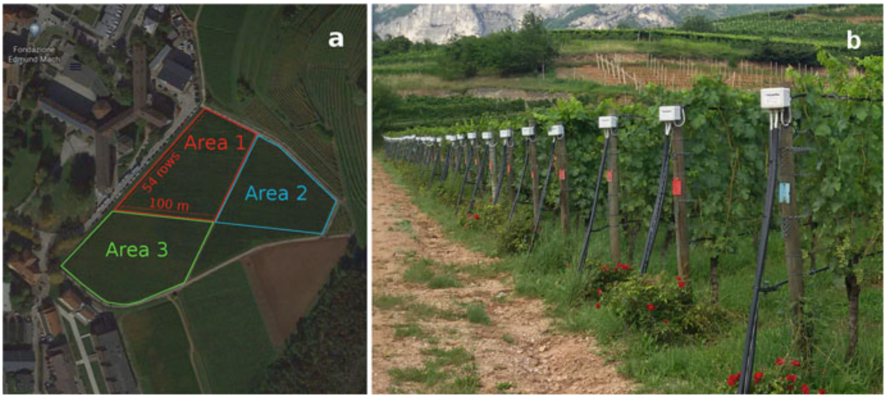

Fig. 17.2 The first vibrational vineyard. On the left, an aerial picture of the selected vineyard in S. Michele all'Adige (Italy): Area 1 is the treated area, Area 2 the negative control, and Area 3 the second control. On the right, the wired rows for the set-up of vibrational transducers

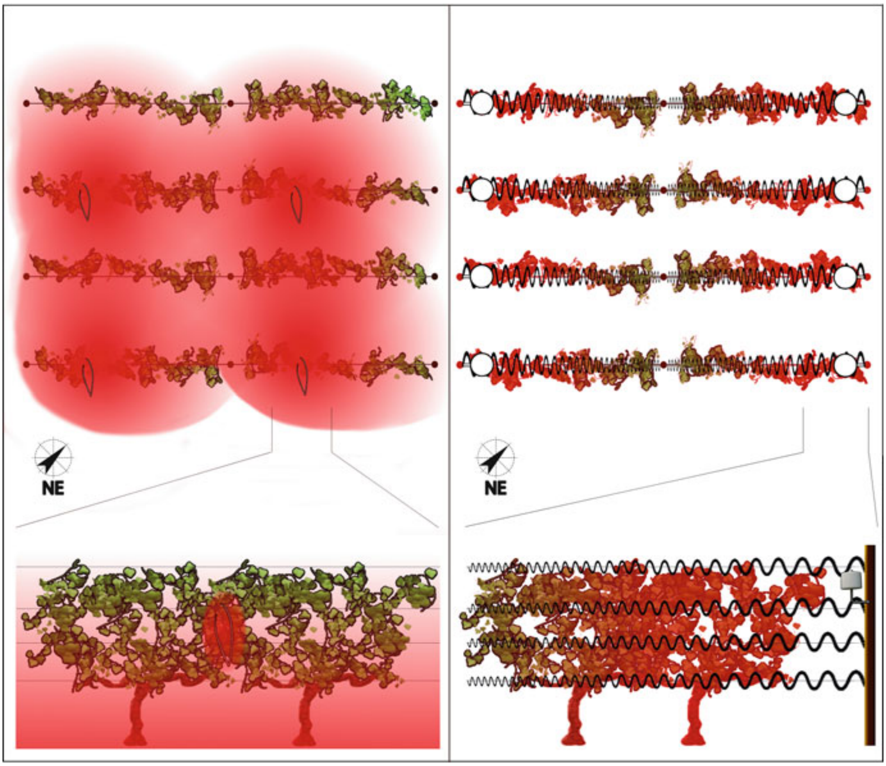

Fig. 17.3 Pattern of signal's dispersion in a vineyard with PMD (left) and VMD (right). The color gradient represents the intensity of the signal from the source. The black wave in the VMD vineyard represents the amplitude of vibrations that is higher in proximity of mini-shakers. The figure is a schematic representation of the signal dispersion; the color gradient does not represent the real concentration/intensity of the signal as measured in the field (i.e., on average in the order of ng/m^3 and μm/s for pheromones and vibrations, respectively). Also the number and location of dispensers and mini-shakers is not real (on average 4–500 dispensers per hectare and one mini-shaker every 50 m)

Preliminary experiments conducted during winter 2016 showed that the application of the shaker to the trellis poles instead of to the metal wires considerably improved the working distance (defined as the maximum distance from the shaker at which the secondary threshold is guaranteed). This is because the pole vibrated by the shaker functioned as an "active pole" vibrating all the wires (4) connected to it (Fig. 17.3). On the basis of this knowledge, we applied the transducers at 50 m intervals (i.e., two per row in the tested vineyard, being the longest rows were 100 m long). Later, from the second half of July until late September, we assessed the working distance through a periodical monitoring (once a month) of the DN transmission in eight randomly chosen rows. We measured the DN amplitude on leaves at different distances from the "active pole" using a portable laser vibrometer (Polytech

PDV-100). The results were satisfying in that they indicated the respect of the secondary threshold (>1 × 10^{-3} mm/s) within 25 m and of the security threshold within 15 m (>1 × 10^{-2} mm/s) from the "active pole," thus covering the whole row.

Technical and biological aspects must go in parallel. To prove the efficacy of the VMD method in the field it was crucial to have a reliable method of assessment. Among the possible options, we focused on two: population density and mating status of females. In the case of *S. titanus*, which is a univoltine species, the population density must be evaluated in the course of several years by monitoring both nymphs and adults. We chose an adjacent vineyard as negative control (same variety, same management, and approximately same size) and the rest of the vineyard as a second control to monitor arthropods' dispersal capability (different variety, same management, and approximately same size) (Fig. 17.2). Because monitoring different developmental stages of leafhoppers requires different surveying practices (Chuche and Thiéry 2014) and also because we aimed at collecting other nontarget arthropods, we used three different methods: (1) counting the number of individuals on leaves, (2) beating (i.e., frappage), and (3) yellow sticky traps. In this way, we monitored also the presence of antagonists of leafhoppers such as generalist predators (i.e., spiders and lacewings) and parasitoids (i.e., Hymenoptera: Mymaridae and Dryinidae and Diptera: Pipunculidae) (Chuche and Thiéry 2014; Liu et al. 2015). To our knowledge, the only method to assess the mating status of *S. titanus* females was validated only for individuals kept in captivity and deprived of oviposition substrate (i.e., a grapevine shoot at least 2 years old) since their eclosion (Eriksson et al. 2012). Therefore, a new protocol was needed to ascertain whether females collected in the field are mated or not.

The field MVD experiments conducted starting from 2017 will require a long observation period, during which we will work on technological and methodological improvements and perform constant monitoring of insects and plants. In this regard, the half century of experience with PMD could be an essential source of information to boost the VMD advancement.

17.3 Vibrations and Pheromones: Similarities and Peculiarities

Nowadays, PMD is an excellent tool in the suppression of insect pests in various agroecosystems; it is safe for most nontarget organisms and compatible with modern IPM programs (Brunner et al. 2002; Sarfraz et al. 2006; Witzgall et al. 2010; Ioriatti and Lucchi 2016; Pertot et al. 2017). PMD has proved to be sufficient to suppress pest reproduction, with reduced egg-laying and crop damage in the treated areas (Howse et al. 1998). Besides disrupting localization of the mating partner, the use of MD can also delay mating, thus significantly reducing the fecundity of females (Torres-Vila et al. 2002). Females have a limited time to mate, develop eggs and find suitable oviposition hosts; a delay in mating could be considered an indirect mechanism by which mating disruption works to control pest populations (Barclay and Judd 1995; Jones and Aihara-Sasaki 2001; Baker and Heath 2005; Jones et al. 2008). In general, PMD has the following four advantages: (a) high specificity to the target pest; (b) safe handling; (c) no interference with biological control agents; and (d) environmental compatibility. The correct and successful application of PMD depends on numerous factors that are worthy to be discussed from the perspective of VMD improvement and application. We analyzed 50 years of experience with PMD to evaluate the general feasibility of VMD in the field, by identifying strengths and weaknesses. Among those, we list below eight factors that must be necessarily taken into account when applying any MD technique. For each of these, we briefly discuss differences and similarities between the PMD and VMD, and hypothesize advantages and disadvantages (Table 17.1) in the use of VMD for viticulture.

17.3.1 Sensorial Unimodality and Signal Specificity

A unimodal mating communication system is prerequisite for successful application of MD methods. The exclusive reliance of moths on sex pheromones facilitated the application of PMD programs by releasing adequate quantities of synthetic copies of these signals in the crops to interfere with mate finding (Miller et al. 2006). Similarly, leafhopper species rely almost exclusively on vibrational signals during the process of pair formation (Čokl and Virant-Doberlet 2003). Vibrational signals guide key steps of pre-mating behavior, such as identification, location, courtship, and acceptance (Virant-Doberlet et al. 2006; Mazzoni et al. 2009b; Polajnar et al. 2014). Therefore, interfering with this communication channel alone should be sufficient to disrupt the mating behavior of leafhoppers. However, the specificity of PMD and VMD is quite different because of the features of chemical and vibrational signals. The PMD strategy is mainly based on the specific chemical structure of the pheromone molecules to such an extent that the insect behavioral response can be affected by isomeric purity of the synthetic blends (Bengtsson et al. 1994; El-Sayed et al. 1998; Cardé 2007). On the contrary, the VMD is based on playback of a low-frequency vibration (i.e., the disturbance noise) (Eriksson et al. 2012). Vibrational mating signals have rather low specificity in the spectral structure (frequency and amplitude), but high specificity in the temporal pattern of signal emission (Čokl and Virant-Doberlet 2003; Derlink et al. 2014). Since the disturbance noise must be transmitted continuously to be effective, only the spectral features are maintained and the noise can be perceived and interfere with the behavior of nontarget species. In fact, there are several arthropod species that rely on low-frequency vibrations to mate or locate their prey, among these there are numerous beneficial arthropods that could be negatively affected by a disturbance noise (Meyhöfer and Casas 1999; Zschokke et al. 2006; Virant-Doberlet et al. 2011; Canale et al. 2013; Wu and Elias 2014; Gemeno et al. 2015).

Table 17.1 Advantages and disadvantages in the use of VMD in viticulture

	PROS	CONS
Signal specificity	Since high specificity is not required in the case of VMD, one device can potentially be used to disrupt multiple target species simultaneously, thus considerably reducing the economic impact of VMD.	Possibility of negative effects on nontarget species. Parasitoids and predators could have difficulty in locating their prey or they may even abandon the area if disturbed by noise.
Searching behavior	Higher susceptibility to disruption in that both male and female are targetable while performing a duet. VMD is most likely to be effective when vibrational signals contain key directional cues.	Suboptimal signals can increase mating motivation, thus reducing the female location time of searching males.
Male rivalry behavior	VMD naturally occurs in species that emit specific rivalry signals, contrary to PMD, which is a human invention. Thus, it has a natural potential to work in the field.	Some insects have developed alternative strategies to overcome naturally occurring disruptive techniques (e.g., call & fly, satellite behavior), which may decrease the efficiency of VMD.
Insect spatial dispersion	Re-infestation from untreated areas is less likely for monophagous species like *S. titanus*, which are also known to have restricted dispersal ability. This implies that the size of the treated area would be a factor of less importance than in PMD. On the other hand, in case of high-density populations, the secondary threshold of signal intensity would not be enough to significantly reduce mating success.	In the absence of AWM programs, polyphagous species (i.e., *E. vitis*) can re-infest grapevines. The presence of wild hosts in the surroundings can negatively affect the efficiency of the method for both monophagous and polyphagous species.
Insect Phenology	VMD can be adapted to the yearly phenology trend of the target species. By means of a monitoring system it is possible to achieve timely intervention by simply switching on the devices that were already installed in the vineyard, thus also allowing energy saving.	Polyvoltine species can infest the crop for long periods. If no duty cycles of operation are adopted, the energy consumption to keep the device active for a long time can be high.

(continued)

Table 17.1 (continued)

	PROS	CONS
Signal active space	VMD application is not affected by the vineyard geographical location, land orography, variety, and specific weather conditions such as winds.	VMD performance can vary according to the trellis system, plant age, and the vegetation growth during the season. Furthermore, at least one transducer per each vineyard row must be used to ensure continuity of the transmission in the substrate, independently of the length of the row.
Mechanism of action	The VMD development process will be facilitated because the use of a disturbance noise instead of a mimicking signal gives us immediate information about the MD mechanisms of action.	There is still lack of knowledge of the mechanism of actions of mimicking signals (e.g., calling and courtship signals) and how they could be employed in practice. More dedicated research on this topic is warranted.
Efficacy assessment	The monitoring of population density and measuring of crop damages are techniques already commonly used to control orchards and identify the action threshold for chemical interventions. They can be easily adapted to assess VMD efficacy.	The small size of leafhoppers makes it difficult to use sentinel females. Moreover, a method to assess the mating status of females still needs to be validated. As a whole, a protocol of efficacy assessment must be developed and tested.

17.3.2 Searching Behavior

Even if the searching behavior of both moths and leafhoppers is similar, in the sense that in both cases the male follows the female signal to locate her, mechanisms driving the male search are different. In Lepidoptera, mate finding is usually mediated by female sex pheromones (Tamaki 1985; Wyatt 2003; Cardé and Haynes 2004; Johansson and Jones 2007). This has led to the evolution of a communication system in which females release tiny amounts of species-specific sex pheromone and males respond via a highly sensitive neurosensory system to locate the pheromone source (Bengtsson and Löfstedt 2007). In leafhoppers, either males or females emit a calling signal (e.g., Nieri et al. 2017) to establish a duet with the potential partner. Therefore, the pair formation process relies upon the continuous exchange of vibrational signals between the partners (Čokl and Virant-Doberlet 2003). Such a duet is characterized by a strict temporal pattern, which means that the signal emission is adjusted according to the perception of the other partner's signal, but males are still the more active partner, searching for the females (Kuhelj et al. 2015). In the case of grapevine moths, the natural air turbulence commonly occurring in the open field transforms the female pheromone plume into countless filaments of pheromone-carrying currents interspersed with pockets of zero to low concentrations (Sanders 1997). Flying upwind, the male is exposed to a series of rapidly changing concentrations, which requires both the interpretation of the odor and a quick resetting of the antennal receptors to perceive the next pheromone molecule (Leal 2005). In the case of vibrational communication, how the male locates the female by tracking vibrational signals back to the source is not yet clear for many species, including leafhoppers (Čokl et al. 1999; Virant-Doberlet et al. 2006). The signal active space network that is determined by calling signals (see Sect. 17.3.3) is not monotonous and variations of signal amplitude and frequency can easily occur in plant tissues depending on many factors (e.g., type of plant organ and its size and shape) (Michelsen et al. 1982; Mazzoni et al. 2014). In spite of this, the use of amplitude gradients by searching males as cues to locate the female has been proposed to explain accurate directionality toward the calling source (Mazzoni et al. 2014; Polajnar et al. 2014). Whatever the mechanism, studies on *S. titanus* (4–5 mm body length) (Polajnar et al. 2014) and on the planthopper *Hyalesthes obsoletus* (3–4 mm) (Mazzoni et al. 2014) showed good searching accuracy toward a signal source.

17.3.3 Signal Active Space

Pheromones are volatiles and can potentially travel for hundreds of meters in all directions (Fig. 17.3) (Baker and Roelofs 1981; Linn et al. 1987). This is because their diffusion is driven by environmental and landscape factors, among which temperature, the general direction of wind and landscape morphology play a major role (Baker and Roelofs 1981; Elkington et al. 1987; Linn et al. 1987; Suckling et al. 1999). Thus, the efficacy of PMD can be reduced to some extent, or even compromised, if some of these parameters prevent an adequate distribution of the pheromones in the treated area. Crop management is another important factor, in particular, the choice of the vineyard trellis system (Ioriatti et al. 2005). Although the type of formulation used sets the initial pattern of dispersion, the characteristic of the foliage canopy into which the disruptant is released greatly modulates its concentration in a crop (Karg and Sauer 1997). Early in the season, there may be few leaves in orchards and consequently disruptant released from point-source formulations may be transported downwind (and possibly out of the treated area) in relatively discrete plumes (Ioriatti et al. 2005), and aerosol can be adsorbed in the soil, as well. Foliage present later in the season will fragment and stir the plumes, so that their active space is more uniform close to the source, but may not extend as far downwind. Another phenomenon of interest is adsorption of pheromone onto foliage and its subsequent re-entrainment into the atmosphere (Wall et al. 1981; Karg et al. 1994). In the case of VMD, the vibrational signal diffusion is via substrate and the spreading efficacy has not much to do with environmental and landscape parameters, but depends almost exclusively on trellis architecture and plant habit (Polajnar et al. 2016). In this regard, the cultural practices, and also the continuous plant growth during the summer, will strongly affect the dispersion of the disturbance signal among treated plants. This is primarily due to increasing dissipation of vibrational energy, which is a function of several parameters, among which the way the vegetation (in terms of surface, volume, and weight) interacts with the trellis plays a major role. However, more research is needed to better understand this phenomenon and for finding technical solutions to maximize propagation.

17.3.4 Male Rivalry Behavior

The pheromone triggers scramble competition among males for access to females in moths (Cardé and Baker 1984). Males do not emit any rivalry signal but they simply jostle for position as they mate. In contrast, leafhopper males can compete by emitting specific disturbance vibrations aimed at interfering with already established duets (Mazzoni et al. 2009a, b; Derlink et al. 2018; Kuhelj and Virant-Doberlet 2017; Nieri et al. 2017). Physical competition involving kicks and abdominal lashing can also occur (Mazzoni et al. 2009b); however, the use of natural disruptive signals is the most important factor in gaining access to the female by causing delay or by misleading the competitors.

17.3.5 Insect Spatial Dispersion

PMD has been spectacularly successful for some species of moths, even in initially dense populations, and consequently this technique has been quickly incorporated into IPM programs used for these pests (Cardé and Minks 1995; Ioriatti and Lucchi 2016). However, PMD has proved to be effective in preventing crop damage only if populations were below specific thresholds of population density (Charmillot and Pasquier 2000; Louis and Schirra 2001). Similarly, VMD success could depend on population density. Leafhoppers can constitute high-density populations so that two or more individuals may end up on the same surface at short distances (i.e., same leaf or stem) (Bosco et al. 1997; Maixner 2003). In such conditions, all plants should be covered with the disruptant signal over the security threshold to maximize the VMD efficacy. Another possible reason for PMD failure is the high dispersal capability of some moth species, whose mated females can come into the vineyard from outside the treated area (Cardé and Minks 1995). On the contrary, it is generally admitted that leafhoppers' dispersive capability is comparatively limited. These insects fly only occasionally and spend most of the time dwelling on the host plant. In the case of *S. titanus*, movement range of less than 30 m outside the vineyard was reported (Lessio and Alma 2004). Longer distance movements can occur in those species (such as two grapevine typhlocybinae species, *Empoasca vitis*, and *Zygina rhamni*) that migrate from and to overwintering sites; although, the exact range of these migrations is not yet established, and it is not clear whether they mate at the overwintering sites or not (Mazzoni et al. 2001; Böll and Herrmann 2004).

17.3.6 Insect Phenology

The number of pest generations is also an important factor to consider. In the case of grapevine moths, it is crucial to start the pheromone application before the onset of the first (out of the typical three) flight (Ioriatti et al. 2005). This strategy is recommended to enhance the efficiency of the method by reducing mating success even on a flight responsible for a virtually harmless generation. *Lobesia botrana*, the European Grapevine Moth, is in fact polyvoltine and the generation originated by the first flight is often not treated with insecticides because it does not attack grape bunches but inflorescences (Ioriatti et al. 2011). Polyvoltinism implies the occurrence of multiple mating windows during the season that are narrow, however, when compared with the mating window of a univoltine species. The reproductive season of *S. titanus* is potentially uniform and uninterrupted from July to September, with a peak between the second half of July and first half of August, when most of the adults are present in the field (Chuche and Thiéry 2014). However, if we consider a sum of the three generations for *L. botrana*, the reproductive period lasts from April to September and is characterized by three peaks with a span of 10–15 days each, and periods of virtually absent mating (Ioriatti et al. 2011). As for polyvoltine leafhoppers, such as *Empoasca vitis*, which also develops three generations per year in Southern Europe (from May to September), the parallels with phenology of *L. botrana* are evident (Decante and van Helden 2006). The presence of reproductive individuals in the field for long periods creates the need for a constantly present disruptant signal. Energy consumption, and thus costs, to maintain an active VMD system for a long period of time can dramatically increase. However, the activation of the device according to environmental parameters (e.g., conditions of sexual inactivity due to temperature thresholds, rain, winds, etc.) and the adoption of duty cycles can reduce energy consumption. Moreover, computer science can benefit the VMD, enabling the production of automated transducers with integrated environmental sensors (e.g., thermometer, barometer, and anemometer).

17.3.7 Mechanisms of Action

Various authors have been debating the mechanisms of PMD (Cardé and Minks 1995; Sanders 1997; Howse et al. 1998; Miller et al. 2006; Millar 2007), still the principal mechanisms of action for even some of the most successful programs, such as codling moth (*Cydia pomonella*) in pome fruit, are not all perfectly identified (Witzgall et al. 2008). The dominant hypothesis is that PMD success is the result of multiple physiological and bio-ethological effects that are not mutually exclusive and can work synergistically or sequentially for the same insect under different conditions. Miller et al. (2006) reported analytical procedures and criteria whereby mechanisms of PMD can be differentiated in two main categories: noncompetitive (camouflage, desensitization, and sensory imbalance) vs. competitive mechanisms (false-plume following):

(a) *Camouflage* occurs when the female's pheromone plume is masked by a uniform presence of synthetic pheromone (Cardé 1990; Sanders 1997). In this situation, the males can no longer distinguish the natural pheromone emitted by a female from the background.
(b) *Desensitization* prevents males from responding to normal emissions of the natural blend and is caused by constant exposure to high pheromone concentrations. Bartell (1982) defines this mechanism as: (I) adaptation of antennal olfactory receptors (i.e., reduction in the efficiency of the olfactory sensilla after prolonged exposure to the pheromone) and/or (II) central nervous system habituation (i.e., reduction in the insect's response to the pheromone due to some change in the central nervous system).
(c) *Sensory imbalance* disrupts mate finding by interfering with the male's ability to perceive (i.e., identify) the specific sex pheromone. This can be due to the use of only one component of the natural blend (e.g., the main component) or to the use of "parapheromones" (antagonistic compounds, agonists, pheromone mimics, and synergists), which affect the behavior or the physiology of the insect's communication system (Renou and Guerrero 2000).
(d) *False-plume-following*, known also as false-trail-following, is regarded as a competitive mechanism, because it causes direct competition between calling females and synthetic dispensers. This results in a decrease in the proportion of females mated and/or in a delay of mating, since males spend time and energy locating "false females" (Anfora et al. 2008).

Despite the still low number of applicative studies of biotremology in general, and the lack of specific investigations on the mechanism of action, it is already clear that a similar classification also could be applied to the concept of VMD. The transmission of disturbance noise through the plant tissues can effectively camouflage the mating signals naturally emitted by individuals on the plant and prevent signal perception and/or interpretation. However, the most important difference between PMD and VMD is that the disturbance signal used in VMD does not mimic the leafhopper mating signal, but is another signal that covers the same amplitude range and frequency span used for mating communication by individuals (Eriksson et al. 2012). Therefore, we can exclude hypotheses of desensitization or sensory imbalance, because the mating signal is masked by noise that also covers its frequency pattern, or at least the dominant (i.e., carrier) frequency. A different situation would occur when using a disturbance signal that mimics a mating signal. This approach would make the VMD method more similar to the PMD, in that vibrations would rely either on noncompetitive or competitive mechanisms. Some recent experiments seem to demonstrate this. Playback of a female calling signal was successfully employed to disrupt glassy-winged sharpshooter (*Homalodisca* *vitripennis*) mating in semi-field conditions (Gordon et al. 2017); in another case, the female calling signal was used to attract Brown Marmorated Stink Bug (*Halyomorpha halys)* males toward specific signal sources in contact with an arena surface (Mazzoni et al. 2017). The latter case can be regarded as a false-trail-following (the same as in pheromone traps for monitoring); whereas, the former cannot yet be classified in either category without further investigation. At any rate, what is clear is that the use of the same strategy for different species does not seem feasible. For example, given the extreme complexity of the temporal pattern of the *S. titanus* mating duet, a female signal played back into the grapevine tissue has no chance of attracting a male unless quite sophisticated electronic devices are implemented for detecting, interpreting and replying in the proper time window and amplitude (Mazzoni et al. 2009b; Mankin et al. 2013). On the other hand, a competitive strategy should be preferred when males can be driven by the female signal and their search can be accomplished without the establishment of a duet (Mazzoni et al. 2017). Therefore, studies on the behavior of the target species are crucial to identify the best management strategy.

17.3.8 Assessment of the Method Efficacy

A direct assessment of the efficacy of mating disruption treatment is to measure crop damage (Baker and Heath 2005; Ioriatti et al. 2005). As long as damage remains below the economic threshold level for the targeted species, then mating disruption is considered to be successful (Baker and Heath 2005). To determine whether PMD actually interferes with mating behavior of the target pest, sentinel, or feral females in the treated area are dissected to assess mating status (Ioriatti et al. 2005). Sentinel females are females located in the crop on plants or on mating stations with clipped wings to prevent their escape, and after exposure they are retrieved for dissection to determine mating status (Evenden et al. 1999; Baker and Heath 2005). Mating disruption is often deemed ineffective if a high proportion of sentinel females positioned in the treated area is mated (Knight 1996; Schroeder et al. 2000). However, the recovery of mated sentinel or feral females from pheromone-treated plots does not necessarily indicate treatment failure as significant damage reduction can occur even with the presence of some mated females in the pheromone-treated crop (Rothschild 1975; Trimble 1995; Sharov et al. 2002). Lowered damage in the presence of mated females can be the result of reduced mating frequency in pheromone-treated plots, which results in fewer eggs laid and fewer larvae to damage the crop. On the one hand, the small size of most leafhoppers makes it difficult to use sentinel females; although, the trials conducted by Eriksson et al. (2012) with individuals released into net-sleeves could provide an important feedback. Furthermore, if the VMD is effective the number of virgin females caught in the field should be significantly higher than in its absence. Development of methodology for the assessment of females' mating status will enable direct efficacy assessment of VMD. On the other hand, monitoring of population density and measuring of crop damages can be used for both VMD and PMD.

17.4 Open Questions and Perspectives

The establishment of the first vibrational vineyard in 2017 might represent a milestone in the field of applied biotremology toward the transfer of a theoretical idea to a commercial product. Still, there are some general questions that need to be thoroughly investigated to assess the feasibility of the method and to obtain general knowledge comparable with that of PMD.

At this stage, side effects are not yet known, but their knowledge is common to all biologically based management approaches. Even if VMD is not a risk for human health and does not produce residues, it can still have some side effects on other organisms. Therefore, future studies should investigate in depth the effect of vibrational noise on nontarget species, and also on plant physiology, to unveil and solve potential risks for the environment and production.

17.4.1 Beneficial Arthropods

Vibrational communication is widely spread among arthropods; among them, there are several beneficial species. For instance, it is known that vibrations play an important role in mating communication of Chrysopidae (Henry et al. 2013) and spider's ability to locate their prey (Virant-Doberlet et al. 2011; Wu and Elias 2014). Yet, spiders are not the only beneficial species exploiting leafhopper's vibrations as locating cues. Numerous species of parasitoids can be attracted by vibrations as well (Mitter and Dorn 1998; Meyhöfer and Casas 1999). Beside pests, these beneficial species can also be negatively affected by an artificial continuous noise transmitted to the environment. So far, the effect of a DN on beneficial arthropod populations has never been taken into account in the development of a vibrational mating disruption method. Thus, now that the vibrational vineyard, which is a large-scale experiment, has being established, it gives us the chance to test the effect on both pests and beneficial species.

17.4.2 Plant Physiology

From the agroecosystem point of view, we should not forget about plants. The effect of low-frequency vibrations on plant physiology is poorly investigated (Jaffe 1973; Qi et al. 2010). However, the impact of a VMD method should be carefully considered, because it can affect the orchard production and potentially decrease the economic advantage of a biological approach (Polajnar et al. 2016).

17.4.3 Power Supply

Another important issue is how to bring the power supply for the shakers into the field, which is still demanding clear and sustainable solutions. In Europe, electric energy sources are rarely available in the vicinity of vineyards. The vibrational vineyard of San Michele all'Adige was established after the whole treated area has been wired; this was feasible because the electric supply/generator was relatively close to the experimental vineyard (i.e., lamp posts situated on the same side of the road). However, this solution is not general and more practical solutions should be invented. Solar panels seem to be an option, but their size and position should not interfere with standard management practices of the vineyard. Furthermore, if they are directly coupled with the mini-shakers in the row, the growing vegetation during the season could cover them.

17.5 Conclusions

To conclude, it is clear that a considerable amount of research is still needed, not only to improve the efficacy of VMD technology, but also to definitely demonstrate its applicability into the field. The replication of the system in different environments and vineyards with different management practices will also help to standardize the method.

We want to emphasize that when the energetic issue is solved, an unbelievably high number of new utilities could be added to the mini-shaker prototype, thus making a vineyard a smart tech project. Recently, the number of smart technologies is increasing in all fields of human activities, from everyday life to highly professional duties. One example is the growing number of electronic hives, which are able to detect the health level of the honeybee colonies and to advise the beekeeper on the best practices to adopt (Struye et al. 1994; McNeil 2015; Meikle and Holst 2015). In agriculture, drones and robots are already commonly used in greenhouses (Wang et al. 2006; Aqeel-Ur-Rehman et al. 2014). In this regard, it seems that our development of a specific tool for the vineyard is just one aspect of a much wider applicability. The implemented tool can be transformed into a customized solution, where the farmer can choose relevant optional add-ons, such as environment sensors (temperature, pressure, and humidity). These can be extremely useful for activities linked to the grape growing, and also for monitoring diseases (e.g., downy mildew, powdery mildew) (Pertot et al. 2017), thus contributing to increase the efficacy and the economic impact of the VMD. In our opinion, the parallel advance of biological and technical studies will work in synergy to provide customized support for growers that will enable timely responses to practical problems.

Considering that the development process of VMD can benefit from the lessons learned in PMD, and that VMD still has considerably fewer bureaucratic issues (in contrast with insecticides, and also pheromones, no registration is needed for VMD, since no chemicals are applied in the environment), we can assume that even if applied biotremology has begun to be studied only recently, the attention of the scientific community, stakeholders and common public will grow exponentially in the next few years.

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Chapter 18
Mating Disruption by Vibrational Signals: Applications for Management of the Glassy-Winged Sharpshooter

Shira D. Gordon and Rodrigo Krugner

Abstract The glassy-winged sharpshooter (GWSS), *Homalodisca vitripennis*, is a generalist insect and a major pest of grapevines. GWSS is a vector of the bacterium *Xylella fastidiosa*, causal agent of Pierce's disease that can lead to grapevine death within few years after infection. This chapter discusses the problem and current GWSS control methods. Then, the focus changes to efforts in developing a novel control method that uses synthetic vibrational signals to disrupt mating and, thus, population growth. A step-by-step method for creating effective playback signals is described and discussed. The method was termed "D.I.E.," which stands for Describe, Identify, and Execute. The first step is to describe the basic biology of the insect pest with emphasis on communication behaviors. From there, one can begin identifying which candidate signals disrupt communication. Finally, execution tests are conducted to determine which signals effectively disrupt mating in laboratory, and more importantly, in the field. While there are still steps needed for large-scale implementation in the field, the basic biological questions related to whether synthetic vibrational signals can disrupt mating are answered affirmatively. The next direction will be to develop a mechanism of signal transmission across large areas. In addition, season long field trials are needed, taking into consideration natural insect movements into and out of treated areas.

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18.1 Introduction

Modern farm-ecosystems encompass primary producers, such as crop plants, crop pollinators, herbivores, associated natural enemies, and lastly the crop consumers—people. Weighing in all of the factors to increase crop productivity while reducing inputs, as well as environmental impacts, leaves scientists with the task of developing new methods to control herbivorous insects. Insecticide applications are relatively inexpensive and effective in reducing pest population densities, but insecticide resistance has been reported from numerous species. Furthermore, some insecticides cannot be used when pollinators are foraging on crops or shortly prior to harvest for human consumption. Therefore, methods such as using vibrations may be an environmentally friendly approach for pest management. This chapter focuses on one case study—the glassy-winged sharpshooter—and alternative methods being developed to reduce its impact on grape production.

18.1.1 The Problem

The glassy-winged sharpshooter (GWSS), *Homalodisca vitripennis* (Germar) (Hemiptera: Cicadellidae) (Fig. 18.1a), is a xylem fluid-feeding species that transmits *Xylella fastidiosa* (Wells et al. 1983) (Fig. 18.1b), a xylem-limited bacterium that causes Pierce's disease of grapevines (Fig. 18.1c) (Davis et al. 1978). Grapes are considered to be one of the most economically important crops in California ($5.5 billion/year) with over 340,000 ha of vineyards (wine, juice, table, and raisin grapes, combined) distributed throughout the state (USDA-NASS 2017). Pierce's disease was first detected in California vineyards in 1884 in southern California and the first records of the disease in the San Joaquin Valley occurred in 1917 (Hewitt et al. 1949). For several decades, disease management practices have included removal of infected grapevines and control of native insect vectors, such as the cicadellids red-headed sharpshooter (*Xyphon fulgida* Nottingham), green sharpshooter (*Draeculacephala minerva* Ball), and blue-green sharpshooter (*Graphocephala atropunctata* (Signoret) (Freitag and Frazier 1954; Goodwin and Purcell 1992). However, in 1990 an established GWSS population was found in California (Sorensen and Gill 1996). After a rapid population growth and range expansion, GWSS became established in the San Joaquin Valley (Kern, Tulare, and Fresno Counties) and most of southern California, as well as in some northern areas of the state (CDFA 2016).

18.1.1.1 GWSS

GWSS is a highly mobile (Blackmer et al. 2006; Krugner et al. 2012) polyphagous species with over 100 known hosts (Turner and Pollard 1959; Hoddle et al. 2003).

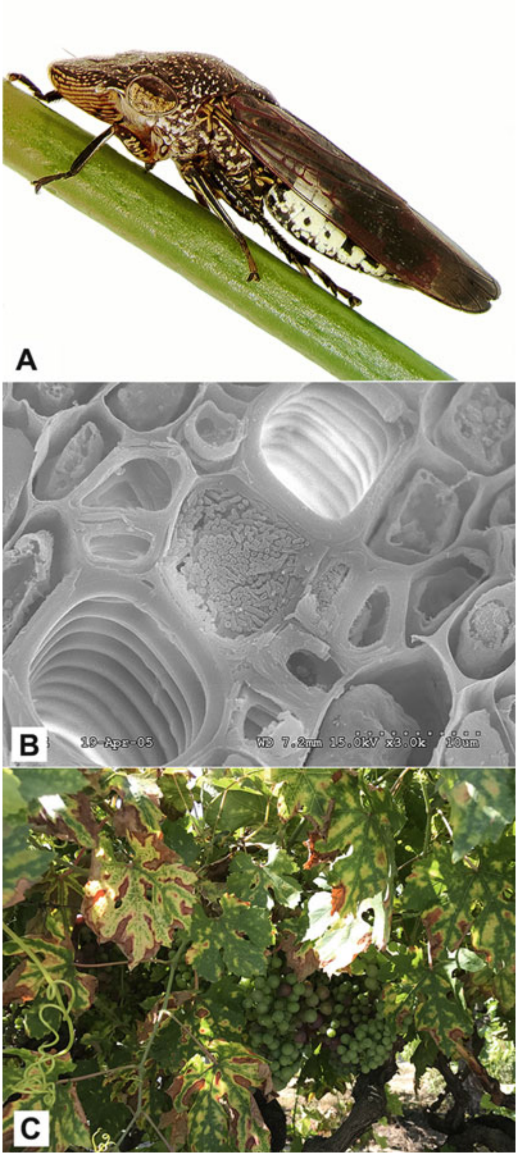

Fig. 18.1 (**a**) Glassy-winged sharpshooter, with its stylets inserted into the plant. (**b**) *Xylella fastidiosa* cells in a xylem vessel, and (**c**) Symptoms of Pierce's disease of grapevines. Photo of *X. fastidiosa* cells in xylem courtesy of Dennis Margosan

During its feeding process, GWSS stylets are inserted into the plant's xylem vessels and many microorganisms may be both acquired from and inoculated into xylem fluid by the sharpshooter (Bextine et al. 2005; Wu et al. 2006; Katsar et al. 2007). In greenhouse tests, GWSS was shown to transmit virulent strains of *X. fastidiosa* to several economically important host plants, such as peach, almond, grapevine, and citrus (Turner 1959; Almeida and Purcell 2003a, b; Purcell and Saunders 1999; Damsteegt et al. 2006). Therefore, controlling GWSS is of upmost importance for reducing the spread of *X. fastidiosa*. While spread of insect-transmitted plant pathogens is widely recognized to be a function of vector abundance, many aspects of GWSS reproduction are poorly understood (Sisterson and Stenger 2016). On grapevines in California, GWSS reproduce from spring to fall, producing at least two generations per year. Research on GWSS has determined that adult females emerge without mature eggs (Sisterson 2008) and must feed to produce mature non-fertilized eggs (Sisterson 2012). In laboratory studies, the highest longevity and fecundity for an individual female was 296 days and 967 eggs, respectively (Krugner 2010). Furthermore, mated females can exhaust sperm reserves for egg fertilization (Krugner 2010), and as such, re-mating may be required for some individuals. In fact, polyandry was recently observed from GWSS females in the laboratory (Gordon and Krugner, unpublished data).

18.1.1.2 *Xylella fastidiosa*

X. fastidiosa is a fastidious xylem-limited bacterium that infects economically important horticultural plants. About 145 plant species examined in California could be potential hosts of *X. fastidiosa* strains (Hewitt et al. 1949; Freitag 1951; Raju et al. 1980, 1983; Hopkins and Purcell 2002; Costa et al. 2004). In the Americas, besides Pierce's disease, it causes vascular occlusion diseases such as alfalfa dwarf (Goheen et al. 1973; Davis et al. 1978; Hewitt et al. 1956), almond leaf scorch (Mircetich et al. 1976; Davis et al. 1980), phony peach disease (Davis et al. 1981; Wells et al. 1983), plum leaf scald (Raju et al. 1982), pecan leaf scorch (Sanderlin and Heyderich-Alger 2000), blueberry leaf scorch (Oliver et al. 2015), and citrus variegated chlorosis (Chang et al. 1993). It should be noted that *X. fastidiosa* does not cause disease in most reported host plants. Based on genome comparisons (Van Sluys et al. 2003; Chen et al. 2010) and multilocus sequence typing analysis (Scally et al. 2005; Yuan et al. 2010), four subspecies of *X. fastidiosa* have been characterized (subsp. *multiplex*, *fastidiosa*, *pauca*, and *sandyi*). Diseases associated with *X. fastidiosa* also have emerged in Taiwan (Leu and Su 1993; Su et al. 2013), Iran (Amanifar et al. 2014), and Europe (Cariddi et al. 2014).

18.1.2 The Solution

All commercially grown *Vitis vinifera* L. varieties used for wine, table, and raisin grape production in California are susceptible to Pierce's disease. However, traditional breeding conducted by geneticists with the USDA-Agricultural Research Service and University of California has introgressed Pierce's disease resistance into *V. vinifera* accessions (Riaz et al. 2009). In the future, it is expected that Pierce's disease-resistant grape varieties will be deployed in California, but until new varieties become commercially available, disease management strategies are likely to depend on insecticide applications to suppress vector populations, removal of diseased grapevines to reduce source of inoculum, and avoidance of planting near vector habitats. This section describes some of the methods currently being used or developed to control GWSS.

18.1.2.1 Insecticide Applications

A key component in Pierce's disease management has been an area-wide insecticide application program to suppress GWSS populations in vineyards, citrus orchards, and urban areas (Wendel et al. 2002; Hix et al. 2003; CDFA 2006; Park et al. 2006). Citrus (*Citrus sinensis* L.) is one of the most common overwintering and reproductive hosts of GWSS in California (Blua et al. 1999) and it plays an important epidemiological role in Pierce's disease incidence in adjacent vineyards (Perring et al. 2001; Tubajika et al. 2004) because it influences the dispersal (Blua and Morgan 2003) and spatial distribution of GWSS populations (Park et al. 2006). The systemic neonicotinoid imidacloprid has been the primary insecticide used to control GWSS populations, but despite constant surveys and insecticide applications re-infestations by GWSS are commonly reported (CDFA 2016). In addition, GWSS resistance to imidacloprid has been reported from populations under aggressive insecticide treatments (Redak et al. 2016). Moreover, insecticide applications to suppress GWSS populations in citrus orchards have the potential to eliminate the GWSS egg parasitoids (Lauziere and Elzen 2007) and to disrupt biological control of citrus pests such as the cottony cushion scale, *Icerya purchasi* (Williston) (Hemiptera: Margarodidae) (Grafton-Cardwell and Gu 2003).

18.1.2.2 Mass Release of Egg Parasitoids

The search for effective parasitoids throughout the United States and Mexico resulted in the collection of several species of mymarid and trichogrammatid egg parasitoids (Triapitsyn and Phillips 2000; Triapitsyn et al. 1998, 2003; Hoddle and Triapitsyn 2004; Goolsby et al. 2006). Among these egg parasitoids, the mymarids, *Cosmocomoidea ashmeadi* (Girault), *C. fasciata* (Girault), *C. morrilli* Howard, *C. triguttata* (Girault), *C. walkerjonesi* (Triapitsyn), and *Anagrus epos* Girault have been mass produced and released in California to suppress GWSS populations (CDFA 2003; Morse 2006). *C. ashmeadi* was found to be the most common egg parasitoid of GWSS in California, Florida, and Louisiana (Triapitsyn et al. 1998) and currently exhibits a high potential for suppressing GWSS populations during summer months. However, the scarcity of GWSS egg masses during late fall to early spring (Krugner et al. 2009), the absence of alternative insect hosts (Boyd and Hoddle 2007) and the unfavorable low winter temperatures in California, which appear to be deleterious to *Cosmocomoidea* spp. (Chen et al. 2006; Pilkington and Hoddle 2006), impair their rapid increase in numbers and performance in suppressing GWSS populations during the first (spring) generation.

18.1.2.3 Interference with GWSS Communication

Vibrational playback is now being investigated as an alternative method to suppress GWSS population growth. As discussed in other chapters in this book (see Chaps. 17, 19, 21), there are several examples supporting the use of vibrations as a novel control method (e.g., *Diaphorina citri* (Mankin et al. 2013); *Scaphoideus titanus* (Eriksson et al. 2012; Polajnar et al. 2016)). Based on experimental methods described in these studies, work has begun experimenting with different types of vibration emitters to reproduce GWSS mating signals in plants (Fig. 18.2). In laboratory trials, the commercially available 4810 emitter (Bruel and Kjaer, Naerum, DK) produced great results in transmitting GWSS vibrational signals to plants. The emitter was adapted with a fine-point metal "stinger" that screws into the emitter and contacts the plant at a punctate point, similar to an insect on the plant (Fig. 18.2a). In addition, GWSS signals have been successfully replicated in plants by firmly clamping the emitter to a wire in contact with the plant (Fig. 18.2b). However, this emitter is not suitable for long-term use under field conditions because it is not weather resistant (rain and dust) and is relatively expensive for large-scale vineyard operations. To circumvent these problems, a private company (CBC Europe) has manufactured prototypes of emitters for field application of vibrational playback. These emitters were taken for testing into a vineyard (Fig. 18.2c) and citrus orchard (Fig. 18.2d) and reproduced a candidate disruptive signal in the frequency range required for interfering with GWSS communication. Equipment limitations that need to be overcome are power for the devices and long distance signal transmission.

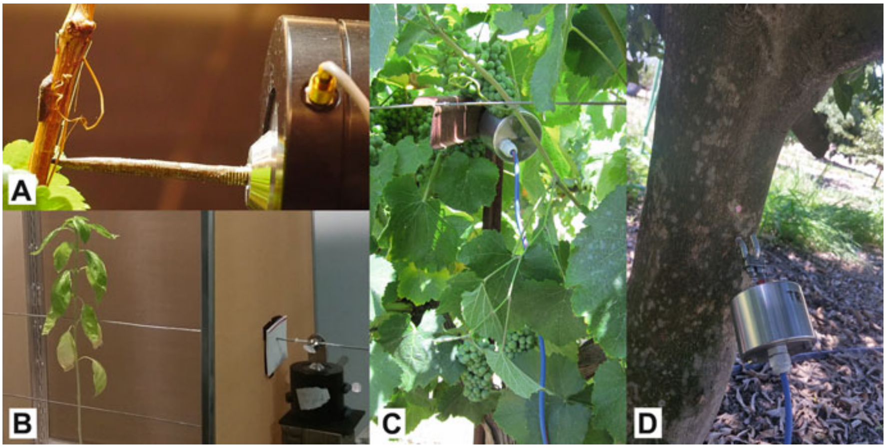

Fig. 18.2 (**a**) Bruel and Kjaer emitter with a stinger tip screwed to the emitter and a point tip to transmit signals to a grapevine. (**b**) Bruel and Kjaer emitter clamped to a wire in the laboratory. Custom built emitter clamped to a (**c**) trellis post for grapevines and (**d**) clamped to a screw in a citrus tree

18.2 The Three-Phase Process: D.I.E.

Before any pest control practices are implemented, a deeper understanding of an insect pest within its environment is required. Knowledge of pest behaviors and biological characteristics are important for efficiently controlling the insect pest, while reducing impact on the environment and beneficial insects in the system, and not wasting efforts in less productive practices. Therefore, a three-phase approach was designed for ensuring the necessary factors are considered. Each phase has its own objectives, but in general the phases focus on the description of insect behaviors, identification of candidate disruptive signals, and execution of the method in field conditions. The three-phase approach has been referred to as D.I.E.: Describe, Identify, and Execute (Fig. 18.3). This section walks through the D.I.E. approach, highlighting work conducted with GWSS. Future work on other insect pests can expand upon the methods described below.

18.2.1 Description

Describing pest biology and behaviors in its system can take many forms and will largely be influenced by characteristics of a particular system. However, rather than be daunted by the unknown communication style, steps may be taken to determine which method works the best. The first step is to determine whether the target pest uses vibrational signaling as a communication mode. To accomplish this task, a researcher could place multiple field-collected individuals together on the same host plant and record vibrations traveling through the plants using a non-contact laser Doppler vibrometry system. However, this approach may not be applicable for species that mate once in their lifetime or those that depend on age-related factors to emit signals, because mated or young individuals may be less likely to emit mating signals. In such cases, recordings should be conducted using non-mated insects of known age from laboratory colonies.

Fig. 18.3 This model represents the D.I.E approach where phase 1 is to describe the basic biology and behaviors of the target pest. While in the descriptive phase, weak links in pest behaviors and biology are identified and selected for vibrational playback as a possible tool for interfering with pest communication (Phase 2). Signals that provide satisfactory results in phase 2 are then tested in more complex environments for the execution of the disruptive method, phase 3

By conducting recordings of a male and female individually placed on host plants, the observer can determine the types of signals, signaling rates, and signal parameters in the absence of a potential mate or rival. Signals emitted by naïve insects alone on the plant are presumably those used for species identification, advertisement, and/or to determine whether a potential mate is reproductively active. Virgin and naïve individuals are recommended for use at this stage because experienced individuals may not emit mating signals at all, or they may behave differently. After identifying the repertoire of virgin individuals alone, the next step is to pair the individual with a conspecific, preferably of the same age. The same analytical methods used for identifying signals and signaling patterns of individual insects should be used for pairs or groups of insects, though it should be noted that with more than two insects on the plant it becomes difficult to determine which of the insects is emitting the signals, especially if new signals are now being emitted. Finally, combining multiple individuals with an individual of the opposite sex on the plant would determine whether rivalry signals are used by competitors to gain access to mates. A sufficient number of observations (replicates) will give a basic understanding of the pest communication strategy.

18.2.1.1 Behavior

GWSS mating communication was characterized through the process described above (Nieri et al. 2017). Briefly, three main phases of GWSS mating communication were identified: species identification, far-field courtship (localization and advertisement), and near-field courtship (final stages within a few body lengths) (Fig. 18.4). In the identification phase, a GWSS female usually initiated signaling and invested more energy than the males (and females when compared in later phases) by signaling more frequently and using longer signals. Over 75% of females placed alone on plants emitted signals; whereas, only 25% of males emitted signals during the trials. Furthermore, active females usually emitted more than one signal, while most of the calling males only called once in the whole trial. When two

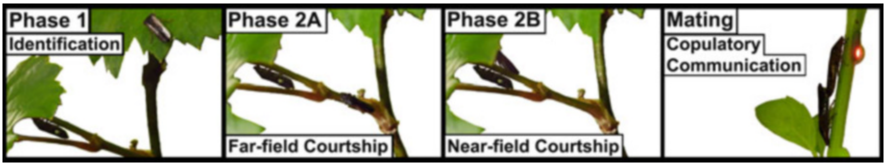

Fig. 18.4 Phases of GWSS mating communication. Phase 1, identification, occurs when the insects initially begin communication and duets are primarily led by the female. Phase 2A, far-field courtship, is when the male is searching for the female on the plant and presumably advertising his qualities. Phase 2B, near-field communication, is when the insects are within a few body lengths of each other and new signals occur during the final courtship stages. Mating is the outcome of successful communication, but also contains vibratory copulatory communication between males and females

individuals were on a plant together, during the identification phase, the female led a duet where the female–male pair called close to a 1:1 ratio. Then during the far-field courtship phase, the roles were reversed and the male usually called first and much more frequently than the female. The male was the one searching the plant to localize the stationary female. When the individuals were in a close proximity of a few body lengths, near-field courtship began with the addition of new male and female signals. At this point, the female sometimes still rejected the male, by raising the hind legs in the air, preventing the male from mounting her. Vibrational communication has been observed during copulation (Gordon and Krugner, unpublished data), but the purpose of exchanging signals during this period is still unknown (but see Chap. 6, this volume).

One characteristic of GWSS communication that is not fully understood is that it often results in loop phases during courtship (Nieri et al. 2017). One hypothesis is that the male has difficulties finding the female due to plant architectural properties. Another hypothesis is that signal composition becomes distorted, making one or both individuals less attractive. In a few cases, the entire communication process leading to mating lasted a few minutes, whereas in other cases it lasted several hours. As of yet, it has not been determined whether plant conditions, insect conditions, seasonal effects on insect activity, or any other component affects the duration of GWSS mating communication.

18.2.1.2 Signal Parameters

GWSS have distinctive male and female signals (Fig. 18.5) (Nieri et al. 2017). The female signal primarily consists of a relatively intense harmonic series with a fundamental that starts at 80 Hz and gradually increases to 120 Hz over the course of 1–4 s, with additional harmonics or overtones occurring at approximately every 100 Hz (Fig. 18.5a). This female signal (termed FS1) was found to be used during all phases of communication, but was significantly longer in phase 1 than in phase 2. The second signal emitted by GWSS females (FS2) was relatively short, compared to FS1, on average less than 0.5 s, with a more broadband frequency component, though with the dominant frequency lower than FS1 (Fig. 18.5b). Female signals are presumably produced by rapid movements of abdominal muscles.

The main male signal, MS1, can be divided into two components (Fig. 18.5a), both presumably produced by abdominal vibrations. The first part has a harmonic series with a dominant frequency slightly lower than the female's, starting at about 75 Hz then sharply increasing at the end to 110 Hz; this signal also has harmonics approximately every 100 Hz. The second half of the signal is fragmented and composed of a broadband frequency with a dominant frequency at the approximate upper end of the first half of the signal. Starting in the courtship phase, an additional element, observed sometimes at the beginning of the male signal, is produced by a rapid dorso-ventral movement of the body and opening of the wings. Because of this extra element, the signal was termed MS2. Another signal termed "quivering" (Fig. 18.5b) appears in the near-field courtship phase. This signal is produced by pulses of

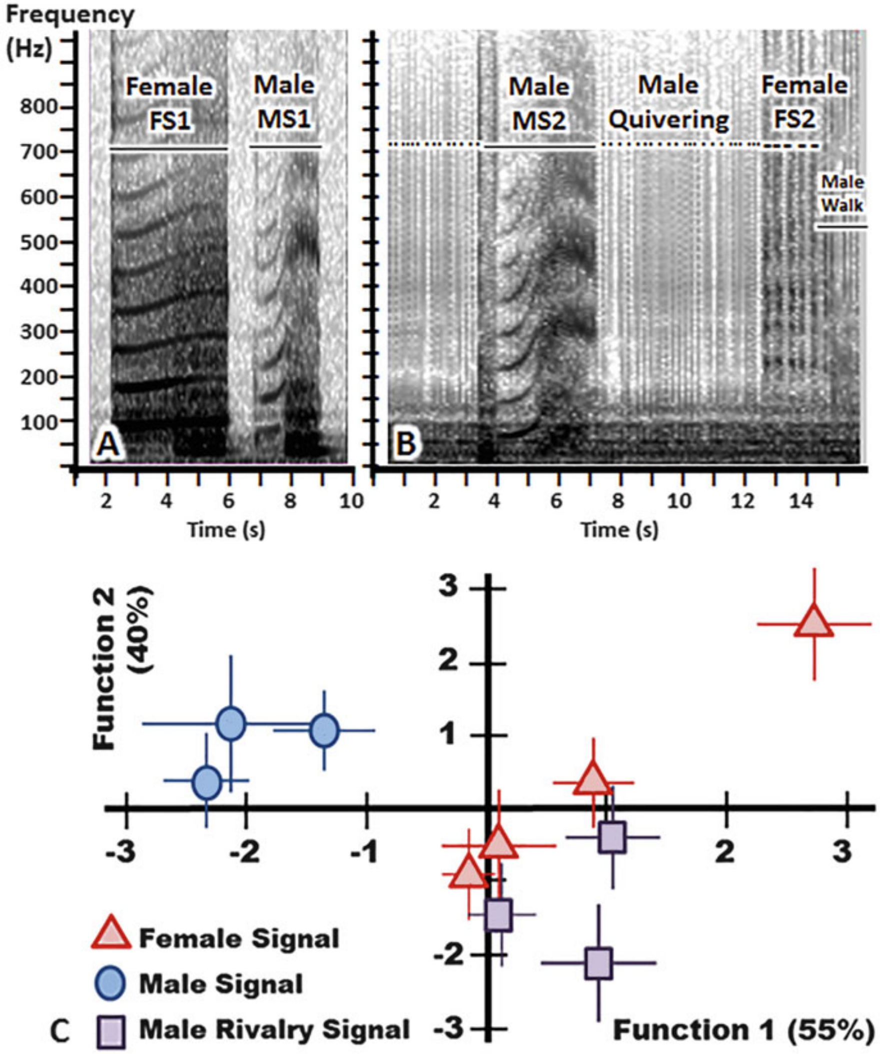

Fig. 18.5 (**a**) Male (MS2) and female (FS1) signals in a duet. MS2 appears identical to MS1 except for the short broadband signal at the beginning of the signal. (**b**) Male quivering follows MS2 and results in emission of the female response with an FS2 signal. (**c**) A discriminant function analysis using several signal parameters was used to statistically group the different signal types (adapted from Nieri et al. 2017)

the abdomen and is likely a form of tremulation. Emission of the quivering signal by males eventually triggers emission of the female signal (FS2) that precedes mating.

With the addition of another male to the plant, male rivalry occurs. Behaviorally, the female usually stops responding to male signals while the two males engage in an exchange of rivalry signals. Based on several components of rivalry signals, including frequency composition and duration, the male rivalry signals (MRS) are distinct from MS. Interestingly, two out of three of the rivalry signals mimic some attributes of FS, as determined by a principle component analysis (Nieri et al. 2017) (Fig. 18.5c).

18.2.1.3 GWSS Communication

Understanding the mating behavior and associated signal components was fundamental to initiate investigations in the second phase of the D.I.E. approach. Key factors learned from the descriptive phase of studying the GWSS mating behavior were that (1) females emit signals significantly more often than males in the beginning of communication, (2) females lead phase 1 of the communication system, and (3) with more than one male present on the plant, there were two male rivalry signals that mimic the female signal.

18.2.2 Identification

Identifying a potential disruptive signal can take many directions. A disruptive signal can have effects ranging from masking natural signals to distracting the sender or receiver (Naguib 2013). Synthetic signals can completely block the frequency range used by the target pest competing with natural signals (i.e., competitive signal) or interfere with pest behaviors through a myriad of other mechanisms (i.e., non-competitive signal) (Miller and Gut 2015). Ideally, non-competitive signals are the best type of signals to use, as these are more targeted and less likely to interfere with non-target species. However, identifying the range of effective signals is a good first step.

18.2.2.1 Competitive Disruption (Broad)

The first attempt at disrupting GWSS communication was with playback of a broadband white noise signal in the frequency range used by GWSS (Gordon et al. 2017). An FFT of the female signal with white noise showed that the white noise was intense enough to overpower the frequency range of the female signal. However, trials with females determined that comparing female signaling rate before and after the noise (during the trial was not possible) actually increased female signaling activity, with over 55% responding within 10 s of the noise cessation. This type of response is likely due to a behavior referred to as gap-detection, which is when animals signal more in response to the end of noisy conditions (McNett et al. 2010). At a first glance, broadcasting white noise seems promising as a method to suppress signaling activity, but should the playback system fail, it could result in the reversed effect of stimulating communication. In addition, mating and foraging behaviors of non-target species, such as natural enemies that use vibrations in the frequency range of the noise, could be affected.

18.2.2.2 Competitive Disruption (Narrow)

Signaling activity of GWSS males in response to playback of natural female signals were tested in the presence and absence of a narrow competitive signal disruption (Mazzoni et al. 2017). Specifically, a continuous playback of a pure tone signal at 80 Hz, which is the starting frequency of the first and more intense harmonic of female signals, completely suppressed male signaling response to playback of female signals.

18.2.2.3 Non-competitive Disruption

Non-competitive disruption involves using playback of natural insect signals with the purpose of interfering with signaling activity. Two methods were tested. First, pre-recorded natural female signals were played to individual females (Gordon et al. 2017) to evaluate the effects of playback on female signaling activity. In this scenario, females emitted signals in response to the playback (Fig. 18.6), with the signaling rate both during and after the playback increasing compared to silent control. In these trials, the playback was intentionally terminated to quantify female signaling rate in response to a factitious signaling female. In a scenario where the playback is continuous, it is expected that a GWSS female would not have sufficient

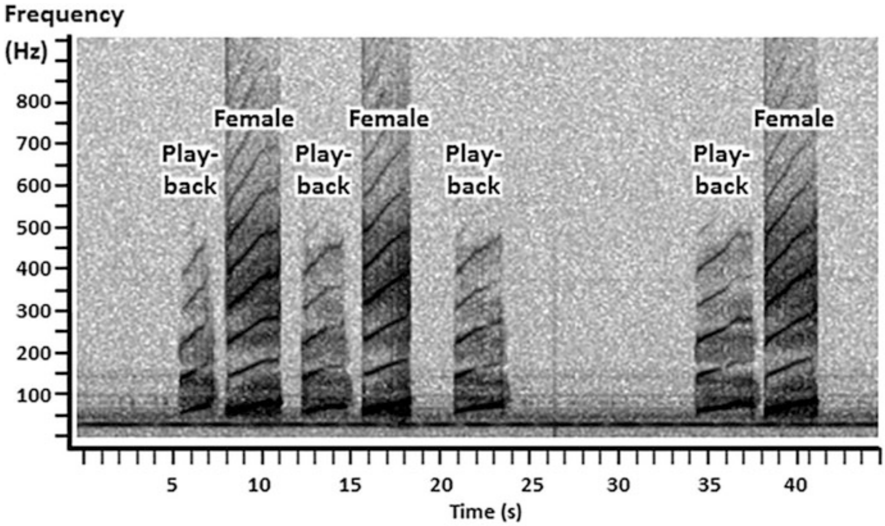

Fig. 18.6 Female response to playback of a female signal via an emitter touching the plant

energy to compete with the synthetic playback and as such would cease signaling and/or search for a quieter host plant. One hypothesis is that female–female duets occur in the context of rivalry to build a female hierarchy on the plant before arrival of a potential mate. Although the mechanistic and evolutionary explanations for female–female interactions in GWSS are still not known, female signals were selected as a candidate disruptive signal to be used for disruptive playback.

In the second method, the female signal used to stimulate male replies was modified by either reducing the intensity or deleting frequency components of the signal (Mazzoni et al. 2017). Results showed that male responses to playback of modified female signals were significantly reduced by 60–75% when part of the female signal spectral components above or below 400 Hz were deleted. Simply reducing the intensity of frequencies above 400 Hz was not sufficient to affect male's response compared to control.

18.2.3 Execution

Once candidate signals have been identified, the next step is to evaluate the effects on insect mating activity. Field testing of candidate signals is labor intensive and subjected to a number of potential effectors, such as wind, presence of natural enemies, horticultural practices, and environmental noise. Therefore, testing signal efficacy in more controlled conditions in the laboratory is advised prior to expansion into field scale trials. For GWSS, both competitive and non-competitive methods described above were evaluated initially in the laboratory.

18.2.3.1 Laboratory

Mating disruption trials using competitive signals, such as white noise and a frequency-tuned female noise (overlapping female signals), as well as non-competitive signals (i.e., natural female signals), were successful at disrupting mating of GWSS (Gordon et al. 2017). In these trials, about 20% of insect pairs exposed to the silent control mated, whereas only 1 out of 31 pairs mated when exposed to the female signal and no pairs mated in white noise or female noise treatments. With female noise, observations continued after the signal was turned off to determine any posttreatment effect on mating activity. After the female noise was turned off, insect pairs treated with the noise mated at a rate similar to those in silent control treatments. Since the frequency composition of the female noise spans a range similar to white noise, albeit less intense in parts of the spectrum, it could also cause deleterious effects on natural enemy populations. Therefore, a modified version of the female signal was used in the field trials described below.

18.2.3.2 Field

The objective of the field study was to evaluate the efficacy of a vibrational signal playback in disrupting mating in GWSS. The signal used in the field mating disruption trials was obtained from a previously recorded GWSS female (Nieri et al. 2017) and modified to include six different female signals with an average gap of 2.20 s between signals. Experiments were conducted in a vineyard (*Vitis vinifera* L.) with a trellis system that consisted of steel posts and wires to support a drip line irrigation system, the bilateral vine cordon and spurs, and canes. Disruptive signals were transmitted to wires used in the vineyard trellis by a custom-made electronic playback system consisting of a control unit and tuned emitters (CBC (Europe) Srl—Nova Milanese, Italy) specifically designed for research studies in vibrational mating disruption. In these trials, a total of 28 (out of 134) male–female pairs mated in the control treatment (silence) and only one (out of 134) pair mated when treated with the vibrational signal playback. Playback of vibrational signals through vineyard trellis was affected by distance from signal source, with frequency composition and relative amplitude (dB) being the highest at the signal source and lowest on vines positioned away from the source. Frequency composition in canes housing test insects decreased exponentially as distance from the source increased, whereas relative amplitude of analyzed frequencies decreased linearly (Krugner and Gordon 2018).

18.3 Concluding Remarks

The progress made on development of a vibrational control method to suppress the GWSS population growth was remarkable given the duration of the project. In a period of less than 3 years, GWSS mating communication and behaviors were described, putative signals for vibrational disruption identified, and proof of concept demonstrated. However, further research is needed prior to implementation in commercial farming operations. One challenge for mechanical engineers is to design signal delivery systems for application over large areas, whereas a challenge for entomologists is to design energy-efficient and environmentally safe signals. From the perspective of professionals responsible for mitigating the impact of insect pests in agricultural production, the ideal signal playback system would have a uniform coverage throughout the targeted area at the lowest intensity, narrowest frequency range, and shortest duration required for disruption of insect mating activity. Although further analysis is needed to determine the costs and benefits of vibrational control methods relative to current broadcast insecticide applications, the short-term results reported here continue to support development of the vibrational control method for integration with other control methods for GWSS and other pests.

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Chapter 19
Can Vibrational Playback Improve Control of an Invasive Stink Bug?

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Abstract Improved understanding of the function of insect vibrational signals has spurred development of a vibrational method for mass-trapping the brown marmorated stink bug, which is currently one of the most notorious invasive insect pests. We outline the ongoing research program, which started with the basic description of close-range sexual behaviour that is mediated by vibrational signals, and continued with testing of a promising female vibrational signal that proved to be considerably attractive to males in playback trials. On this basis, a bi-modal trap was constructed, comprising an aggregation pheromone dispenser, the vibrational signal playback and a device for electrocuting the attracted animals in a pyramid trap design. Preliminary field trial results are discussed in the context of the interplay between chemical and vibrational modalities during reproductive behaviour in stink bugs, and the potential for achieving environmentally friendlier control of this pest.

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19.1 Introduction

Biotremology as a (sub)field has in the past few decades progressed to a point where application of the amassed knowledge to solve "real-world" challenges is becoming feasible. More specifically, increasing understanding of the vibrational environment and its effect on organisms, particularly insects, is opening interesting new possibilities for agricultural systems whose performance currently relies on large-scale use of plant protection products. The need to maximize production has led, over the years, to practices that increase risks of pests (i.e. insects) and consequently to a strong dependence on pesticides (Metcalf 1994; Lamine et al. 2010). At some point, consumers became aware of this situation and demanded safer food and protection of environmental quality. Nowadays, the general public expects production systems to be more sustainable, also preserving biodiversity. As a consequence, in 2009, the EU issued the new directive on the sustainable use of pesticides (European Commission 2009a) and adopted a new legislative "pesticides package" (European Commission 2009b). This significantly decreased the range of active ingredients available to the farmers and incentivized research and application of new integrated pest management (IPM) tools. In essence, IPM implies a shift from relying almost exclusively on chemical pesticides to using a combination of methods in order to manage pest populations at acceptable levels. In this view, pests must be seen as components of agro-ecosystems, interacting with plant, soil and various biotic components under the influence of a variety of interdependent drivers (e.g. mechanical, physical, genetic, biological and chemical). Given these premises, behavioural manipulation by means of vibrational signals fits perfectly within the concept of IPM, or, more specifically, "biorational" pest control, even if definitions of these concepts tend to focus on chemicals (pheromones, natural products, semiochemicals, etc.; Horowitz et al. 2009). Applied biotremology is a newborn concept that is still far from achieving its full capacity. However, our conviction is that the first field applications are close to emergence, given that many studies are in progress worldwide, on different subjects and using diverse approaches (Mankin 2012; Polajnar et al. 2015).

In this chapter, we describe the research so far conducted to find a method for sustainable control of the brown marmorated stink bug (*Halyomorpha halys* (Stål, 1855); Heteroptera, Pentatomidae), in agricultural settings. The chapter outline is based on the two main papers published on this subject so far, Polajnar et al. (2016a) and Mazzoni et al. (2017a), a similar concept to the review by Polajnar et al. (2016b), which outlined the research on mating disruption of the leafhopper *Scaphoideus titanus* Ball, 1932 (Heteroptera: Cicadellidae). We added a brief report on a preliminary field test with a prototype multimodal trap, and plans for future research as well as expanded discussion on topics mentioned in the aforementioned papers, in the hope of stimulating development of other applied solutions, enabled or at least inspired by biotremology.

19.2 Background

19.2.1 Biology and Pest Status of the Brown Marmorated Stink Bug

The current status of the brown marmorated stink bug, or BMSB, as one of the most notorious invasive insect species of global importance is well deserved (Haye and Weber 2017). This member of the family Pentatomidae is native to East Asia, specifically China, Japan, Korean Peninsula, and Taiwan (Hoebeke and Carter 2003; Lee et al. 2013). It is thought to have been primarily introduced into the United States in the late twentieth century (Xu et al. 2014). It was first sighted in Europe 10 years later; the first report from Switzerland in 2004 (Haye et al. 2014) was followed by reports from Liechtenstein, Germany, Greece, France, Italy, Hungary, Romania, Russia, Austria, Serbia, Georgia, Spain, Slovakia and Slovenia (EPPO Reporting Service 2017). After about a decade of scattered sightings, the American mid-Atlantic population suddenly exploded and was subsequently recognized as a significant agricultural and nuisance pest (Rice et al. 2014). In 2015, a population outbreak was also observed in Italy where BMSB started causing damage to fruit orchards in the Po Valley area (Maistrello et al. 2017). The species' potential range includes most regions of the world with moist tropical, sub-tropical, Mediterranean and warm-temperate climates, so it is expected to invade large new areas even without considering the influence of global climate change (Kriticos et al. 2017).

As a generalist herbivore, the species is incredibly polyphagous, with reports on feeding from over a hundred host species included in 45 plant families in the native range alone (Lee et al. 2013). In the introduced range, preference for cultivated plants from the families Rosaceae and Fabaceae has been recorded (Nielsen and Hamilton 2009; Maistrello et al. 2016) (Fig. 19.1), but BMSB feeds on a wide variety of crops, ornamentals and wild hosts, and normally requires different hosts throughout the season to complete its development. Sub-populations therefore regularly migrate between suitable hosts present in an area, making them even more difficult to control (Rice et al. 2014; Leskey and Nielsen 2018). It is uni- to bivoltine in the mid-Atlantic US states (Nielsen et al. 2008), univoltine in central Europe (Haye et al. 2014) and bivoltine with overlapping generations in northern Italy (Costi et al. 2017). The second main issue is the conspicuous tendency of BMSB to invade human habitations in large numbers in the search for protected overwintering sites, making it a severe nuisance in affected areas (Rice et al. 2014).

Management of BMSB is challenging due to the high reproductive potential (Costi et al. 2017), the great mobility of both adults and nymphs (Lee et al. 2014; Lee and Leskey 2015), the multifaceted invasion dynamics of the pest (Malek et al. 2018) associated with high polyphagy that implies frequent movements among crops and from crops to wild plants, and the scarcity of available insecticides, due to low initial knock-down effects and short residual activity (Leskey et al. 2014). Thus, presently, BMSB control in infested areas relies on frequent applications of broad-spectrum insecticides such as pyrethroids, neonicotinoids and organophosphates

Fig. 19.1 Two adult BMSB feeding on a pear, which shows severe deformation due to piercing. Photo: Robert Malek

(Leskey et al. 2012a), due to the lack of alternative methods of pest management. The non-target action of these compounds has negatively affected existing IPM programs against other pests, as well as raised concern about environmental toxicity (Leskey et al. 2012b). A more sustainable approach applicable in orchards is the behaviourally based tactic IPM-CPR (Crop Perimeter Restructuring) (Blaauw et al. 2015) that focuses on perimeter applications of insecticides, exploiting the border-arrestment behaviour of BMSB by controlling them at the orchard edge, thus reducing damage throughout the block and the total amount of insecticide usage. New perspectives are offered also by the use of long-lasting insecticide-incorporated nets (Kuhar et al. 2017).

There is some hope that native and/or exotic parasitoids recorded incidentally from BMSB eggs may contribute to the control of this invasive pest in the introduced ranges, both in North America and Europe (Abram et al. 2017). Haye et al. (2015) investigated whether generalist egg parasitoids of native European Pentatomidae develop on BMSB. Their study concluded that the European platygastrids in the genera *Trissolcus* and *Telenomus* develop poorly on fresh BMSB eggs, while the eupelmid *Anastatus bifasciatus* can successfully parasitize them, thus making it the only potential candidate for augmentative biological control in Europe. As for predators, some orthopterans, ground beetles, lacewing larvae, ladybird beetles and predatory hemipterans have been shown to consume BMSB eggs and young nymphs (Abram et al. 2015; Morrison et al. 2016b; Pote and Nielsen 2017). A laboratory study showed that the ant *Crematogaster scutellaris* can efficiently predate all nymphal instars but cannot consume BMSB eggs (Castracani et al. 2017).

Cultural tactics such as trap cropping are still subjects of research, in order to determine their effectiveness against BMSB. Nielsen et al. (2016) concluded in a recent study that sorghum (*Sorghum bicolor* L. Moench) and sunflower (*Helianthus annuus* L.) have a great potential as trap crops, in that their period of BMSB attraction is considerably longer than other crops and they can harbour the highest seasonal densities of stink bugs. Another option could be the use of essential oils extracted from clove, lemongrass, spearmint and ylang-ylang that were demonstrated to almost completely block the attraction of BMSB, both nymphs and adults, at release rates of 14–80 mg/day (Zhang et al. 2014). However, future research should provide additional information about the appropriate size and the spatial arrangement of trap crops or the way to incorporate essential oils as pest control tools in a vision of IPM strategy.

19.2.2 The Use of Vibrations for Pest Control

Millar et al. (2002) originally proposed exploiting vibrational communication to improve the control of pentatomid bugs, and Čokl and Millar (2009) reviewed the theoretical background for such a method, but this idea was not put into practice until recently. The more recent review by Laumann et al. (2017) also explored the possibility to control stink bugs by vibrational signal playback, either via disruption or via attracting biological control agents; however, they mention trapping only for the purpose of monitoring.

Even more generally, the use of vibrations for any kind of insect pest management is still in its infancy, but two main strategies are emerging: detection and behavioural manipulation (Mankin 2012; Polajnar et al. 2015). Automatic detection of vibrational emissions in the field has been proposed as a reliable method of pest identification, particularly in cryptic conditions such as inside plants and stored plant products (Potamitis et al. 2009; Mankin et al. 2011; Mankin 2012; Zorović and Čokl 2015); however, most of the methods that have been tested detect incidental vibrations and rely on other information to identify the pest unequivocally. Recognition of species-specific vibrational signals requires advanced computational methods and has only been attempted in laboratory conditions so far (Lampson et al. 2013; Korinšek et al. 2016; Mankin et al. 2015; Lujo et al. 2016). While such a technique could greatly benefit decision support systems for more mobile pests such as stink bugs, practical issues like complexity, cost and ensuring stable recording in the field (see Chap. 8, this volume) limit its applicability for now.

Behavioural manipulation, on the other hand, works by presenting artificial stimuli that exploit sensory biases and elicit desirable behavioural effects on the target organism, in order to protect valuable resources. Two broad classes of approaches exist: attract-and-kill and push/pull, either attracting pests to target areas where they can be conveniently eliminated, repelling them from protected resources, or disrupting key behaviours such as host finding, feeding, mating and oviposition (Foster and Harris 1997). Their use is commonly associated with the chemical modality that has been historically prevalent—the use of synthetic pheromones for mating inhibition or mass trapping is now the most widely recognized alternative to pesticides (Witzgall et al. 2010). Sound has also been used, mostly in the form of playback of loud noises to deter vertebrate pests (Bomford and O'Brien 1990; Gilsdorf et al. 2002); however, this method is non-specific. Some reports exist on the use of intense sound to disrupt physiological processes in insects, particularly stored product pests, by eliciting destructive vibrations in their tissues (Kirkpatrick and Harein 1965; Mullen 1975; Kiruba et al. 2009), but without any practically applicable outcome so far. The potential of subtler behavioural effects of sound and vibrations on insect pests is even less explored, even though Saxena and Kumar (1980) first proposed using playback of sound picked up by plants to disrupt mating of leafhopper and planthopper pests decades ago, but several lines of study are now active to pick up the slack and hopefully provide a useful alternative to pesticides in the near future. All three approaches (attracting for detection or mass trapping, repelling and disruption) have been tested at least in laboratory conditions in different pest species, depending on the situation. Disruption of *S. titanus* with playback of male rival signals has been tested in small-scale field conditions (Polajnar et al. 2016b, c), and a similar approach using playback of synthesized disruptive noise was later also tested in the glassy-winged sharpshooter (*Homalodisca vitripennis* [Germar, 1821]) (Mazzoni et al. 2017b). Mankin et al. (2013) first attempted to develop a vibrational reply mimic to attract and trap male Asian citrus psyllids (*Diaphorina citri* Kuwayama, 1908), but that group later started to focus on mating disruption, with some success in the laboratory (Mankin et al. 2015; Lujo et al. 2016). They chose a more complex approach, implementing automatic recognition of male calls and playback of vibrational noise that overlaps the (expected) female reply in a single package, consisting of a contact microphone, a microcontroller and a piezo buzzer. Finally, playback of stridulation signals has been used to deter pine bark beetles (*Dendroctonus* spp.) from logs and disrupt their reproduction (Hofstetter et al. 2014, 2016).

All the above-mentioned behavioural manipulation studies build on comprehensive basic knowledge about the target species' biology, especially vibrational communication, and additional pest species are being studied with the same goal (Nieri and Mazzoni 2018; Nieri et al. 2017). Such a firm foundation is important to ensure efficiency; it is true that exploitation of sensory processes is possible even with an imperfect knowledge of underlying mechanisms (Cardé 1990), but poor understanding precludes constructive modification in case of failure or low efficiency (Foster and Harris 1997). As the *S. titanus* example demonstrates (Polajnar et al. 2016b), observations and recording of vibration-mediated mating behaviour may reveal exploitable signals or their properties, but other aspects of the pest's biology need to be taken into account, as well, in order to be able to choose a viable approach. A major consideration is that vibrational playback has a limited range, so, for example, mating disruption is viable only when dealing with accessible pests—i.e., those that are specialized to feed on a single, spatially limited resource and that cannot easily move out of reach of the playback apparatus (Polajnar et al. 2015).

Another important aspect of stink bugs in particular is that their mating communication is multimodal, involving long-range pheromones, short-range vibrational signals and contact chemical signals. The general pattern was elucidated by experiments on the model species *N. viridula* and others (Virant-Doberlet and Čokl 2004): long-range chemical signals are produced by males and function as aggregation pheromones, attracting both males and females, as well as late-instar nymphs. Additionally, they stimulate females to start producing low-frequency vibrational signals (Zgonik and Čokl 2014), which in turn stimulate males to increase pheromone production (Miklas et al. 2003) and respond with their own vibrational signals to further elicit the females to continue "singing" (Čokl et al. 2000; Čokl and Virant-Doberlet 2003). Vibrations emitted in species- and sex-specific patterns are used both for precise source localization and mate recognition (Čokl et al. 1999; Virant-Doberlet and Čokl 2004); males, as the more active partners, then start actively searching for stationary females (Ota and Čokl 1991; Čokl et al. 1999), and after arriving in close proximity, the partners switch to the last phase of vibrational courtship, which is then followed by copulation itself (Borges et al. 1987; Čokl et al. 1999; Čokl and Virant-Doberlet 2003). Before the work of Polajnar et al. (2016a) and Mazzoni et al. (2017a), Khrimian et al. (2014) confirmed that the BMSB follows the same pattern regarding aggregation pheromones. Kawada and Kitamura (1983) described some aspects of short-range courtship, but other aspects of short-range communication were unknown.

19.3 Basic Tremology and Associated Sexual Behaviour

As implied above, the research program on the potential of using vibrational playback for behavioural manipulation of BMSB had to start from point zero. The rich world of vibrational signals used for intraspecific communication alongside pheromones in the family Pentatomidae was of course recognized long ago (reviewed in Čokl and Virant-Doberlet 2003; Virant-Doberlet and Čokl 2004), with abdominal vibration of the Southern Green Stink Bug (*Nezara viridula* [Linnaeus, 1758]) a model for the whole family (Virant-Doberlet and Čokl 2004). The basic hypothesis that this species is no exception was therefore self-evident. In the light of this, it is surprising that despite hundreds of papers published in the past two decades on various aspects of BMSB behaviour, ecology, development, life cycle, etc., vibrational communication—a major driver of reproductive behaviour in this family—has not been described earlier. Even more, Lee et al. (2013) and Rice et al. (2014) did not even hint at the possibility in their comprehensive reviews of BMSB biology, ecology and management, while Harris et al. (2015) recognized it as a possible reason for poor performance of BMSB in Y-tube bioassays using pheromones as attractants, but did not follow up with multimodal trials. This omission is a clear testament to how overlooked vibrational communication still is outside biotremology (Hill and Wessel 2016).

Kawada and Kitamura (1983) were the first to focus on close-range courtship in BMSB (under the synonym *H. mista*), recognizing it as an important aspect of the pest's biology and following early examples of such studies (e.g. Harris and Todd 1980). They conducted observational trials and described seven distinct behaviours from the actual physical encounter until copulation. Perhaps more understandably, they too omitted vibrational communication, which was far less known at that time, instead stating that "the male walks around randomly searching for a mate"—although a more careful observation would surely show that the approach is non-random, even without knowing about vibrations. The close-range courtship of BMSB, as described by Kawada and Kitamura (1983), starts with the male chasing the female, which is followed shortly by the male head tapping on the substrate and directly on the female's body, then by antennation. The male then positions himself for genital coupling with distinct sideways ("crab-like") movement towards the female's abdomen, lifts the female's abdomen with his head and, finally, turns around and commences the genital coupling. Male's "tapping" on the substrate in this description may be understood as percussion-producing substrate-borne vibrational signals, although Kawada and Kitamura (1983) did not record or characterize any vibrational emissions.

A series of observational trials was first set up to record and unravel the postulated vibration-mediated courtship in this species (Polajnar et al. 2016a). Early trials were performed using a variant of the standard setup for recording substrate-borne vibrations emitted by animals (Elias and Mason 2014): a laser vibrometer recording from the substrate near experimental subjects, thus detecting vibrations already filtered by the mechanical properties of the substrate, similar to what the receiver(s) would perceive. Two types of substrates were used, a non-resonant loudspeaker membrane and a small bean plant (*Phaseolus vulgaris* L.) with two developed leaves, again following the example of existing studies on *N. viridula* and other stink bug species (e.g. Miklas et al. 2001; McBrien et al. 2002; Čokl et al. 2005). Different combinations of animals (single male, single female, male with female, two males and two females) were placed on those two substrates to decipher any recorded signals (Polajnar et al. 2016a).

The basic hypothesis was duly confirmed; males spontaneously emitted one signal type soon after being placed on any substrate, which elicited female response. As in other stink bug species, several types of male and female vibratory emissions were recorded (compare e.g. Čokl et al. 2001; Blassioli-Moraes et al. 2005). Also in line with other stink bug species in which reproductive behaviour has been described, males are the more active partners, initiating vibrational communication

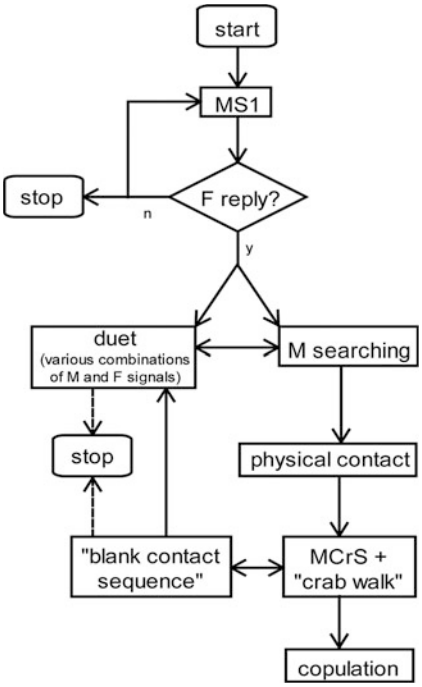

Fig. 19.2 Diagram of behavioural sequence during close-range sexual behaviour of BMSB. MS1 and MCrS denote male signal types, and "blank contact sequence" is an expression of the female's rejection of a male's mating attempt (Polajnar et al. 2016a)

and actively searching for the source (Fig. 19.2). The close-range sexual behaviour starts with a male's emission of the initial vibrational signal type, termed MS1 or, putatively, Male Calling Song (MCS). MS1 consists of a single long, steady and almost pure-tone vibrational pulse with low peak frequency (around 60 Hz) and prominent harmonics. Pulses with duration of up to 30 s were recorded in trials by Polajnar et al. (2016a), which is by far the longest signal reported from any stink bug species so far. For comparison, existing literature lists signals of 0.1 s to several seconds in duration, with at most slightly over 10 s in *Eurydema oleraceum* (Gogala 2006; Čokl et al. 2014; Shestakov 2015), a value which MS1 of BMSB exceeds several times. A receptive female replies to MS1 with her own signal, initiating a duet. This duetting phase is highly variable in terms of duration, signal emission and outcome, but MS1 is most often followed by FS1 with similar properties, followed in turn by FS2—a series of approximately one second long and regularly repeated pulses with downward frequency modulation, but just as narrow-band as MS1 or MS2 (Fig. 19.3). FS2 is effective in eliciting male searching behaviour, during which a male approaches the signal source with characteristic jerky motion, walking during pauses between successive pulses and staying still (presumably "listening") during pulse emission. FS2 sequences can be several minutes long and contain hundreds of pulses, enabling the male to locate the source from a distance. Other vibrational emissions in this phase include short and regularly repeated male pulses (MS2), which may be emitted during FS2 and partly overlap female pulses, and a rarer

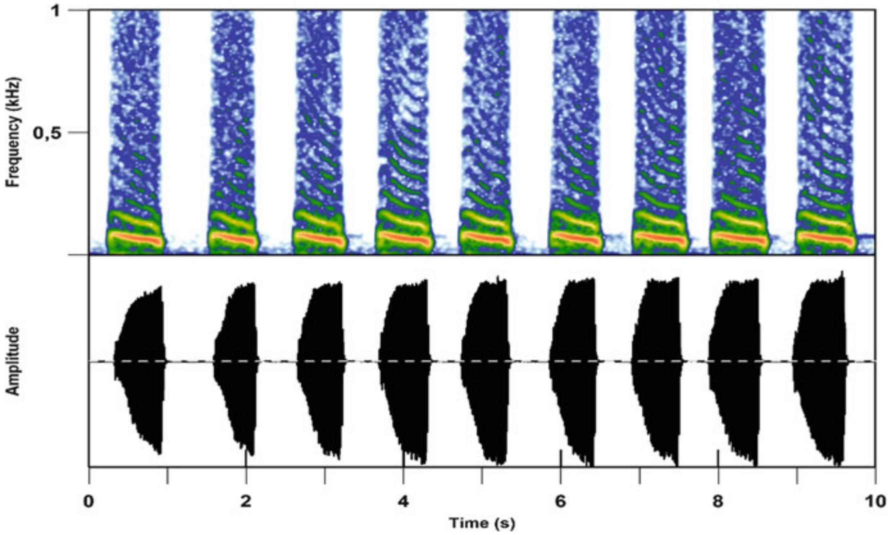

Fig. 19.3 Oscillogram and spectrogram of a pulsed-type vibrational signal emitted by females (FS2). Such pulse trains may contain hundreds of pulses and last several minutes (Polajnar et al. 2016a)

signal with unknown function, termed "coo" for its sound; however, any signal type other than MS1 may be absent in male–female interactions (Polajnar et al. 2016a).

In other combinations (male–male, female–female and lone animals), MS1 is the only signal type emitted; females almost never start signalling spontaneously and no rival signals have been detected. Another interesting observation by Polajnar et al. (2016a) is that males regularly emit MS1 every minute or two, but tend to avoid overlapping each other; however, only pairs of males were systematically tested. A laser pointed at a rearing cage with multiple males recorded continuous vibration over several minutes, with back-to-back MS1 signals from different males (J. Polajnar, unpublished data); however, this phenomenon has not yet been studied further.

When the male encounters the female, the last male song type follows, termed Male Courtship Song or MCrS, in analogy to other late-stage signals in stink bugs. Abdomen vibration pattern in this phase is similar to MS2, i.e., a train of short pulses with slight downward frequency modulation, but are interspersed with short bouts of whole body tremulation, presumably what Kawada and Kitamura (1983) described as head butting against the substrate and the female's body. According to observations by Polajnar et al. (2016a), this behaviour does not necessarily involve striking the substrate, but is true tremulation (*sensu* Claridge 2014), with rapid sideways shaking of the body. The male continues to emit MCrS while positioning himself for copulation, along with antennation and coercing the female to raise her abdomen by wedging his head between her and the ground. If the female is not receptive, she will refuse to raise her abdomen and instead move away slightly. The male might crawl over her in this case and eventually find himself away from direct contact, in which case he will restart the vibrational communication sequence or abort the mating attempt completely (Kawada and Kitamura 1983; Polajnar et al. 2016a).

Several properties of recorded songs merit attention, from the perspective of both basic and applied science (Polajnar et al. 2016a):

- Extreme duration of basic male signals (MS1), which is far longer than any previously recorded stink bug signal;
- Extreme narrow-band (almost pure-tone) character of vibrational emission, especially in MS1 and FS1 pulses (spectral width in MS1 was 3 Hz at −20 dB below the dominant peak, which is an order of magnitude less than signals in other species that have been described as narrow-band; Čokl et al. 2001; Blassioli-Moraes et al. 2005);
- Low frequency of all signal types, which, although not exceptional, is at the lowest end of the range reported for Heteroptera (Čokl and Virant-Doberlet 2003; Čokl 2008);
- Substantial overlap in duration measurements between MS1–FS1 and MS2–FS2, to the extent that it is impossible to reliably distinguish between recordings in absence of additional information;
- Continuous transitions between signal types in both sexes (Pulsed songs may be emitted with increasingly short pauses over time, fusing completely at the end into a longer signal with the frequency modulation pattern still visible.)

Slight but highly significant differences in the dominant frequency were observed between signals emitted on the bean plant and on the non-resonant loudspeaker membrane (Polajnar et al. 2016a). Significance of such differences in the order of one Hertz is dubious, but opens an intriguing question about tuning of vibrational songs to mechanical properties of the substrate. According to a physical model, the frequency of plant stem vibration faithfully reflects vibration of the attached insect at low frequencies (Miles 2016), but vibrating the substrate at its resonant frequency maximizes energy efficiency and there is an indication that stink bugs are capable of actively modifying their output frequency according to the properties of the substrate they encounter (Polajnar et al. 2013). The BSMB with its extensive and diverse host range may be convenient as a model species to explore these questions further.

19.4 Behavioural Manipulation in the Laboratory

19.4.1 Choosing the Approach

During basic observational trials, two signal types emerged as promising candidates for development of a behavioural manipulation technique that might be used in the field: the basic male song (MS1) and the pulsed female song (FS2). Therefore, several tests were designed to evaluate their effectiveness in attracting BMSB males and females, with the emphasis on FS2 (Fig. 19.3) because MS1 playback did not perform well in preliminary trials (J. Polajnar, unpublished data).

Artificial signal playback is a standard technique in studies of animal communication. In biotremology, it is performed using specialized minishakers or improvised electromagnetic/piezoelectric actuators ("shakers"; Cocroft et al. 2014). Although it is generally difficult to maintain signal fidelity across many different substrates in biotremology, sharp frequency peaks of BMSB signals alleviates this issue and simplifies both playback and construction of traps. An electromagnetic shaker's driving current is proportional to the output acceleration (Cocroft et al. 2014), but laser vibrometers measure velocity of the substrate oscillation, which could lead to overrepresentation of low-frequency components in playback (Norton and Karczub 2003). Since bandwidth of MS1 and FS2 signals is narrow and frequency modulation is only slight, this was not considered a major issue.

Disruption was considered a less feasible option. Polajnar et al. (2016a) did not record any rival emissions on which to base stimulus design. The work by Polajnar and Čokl (2008) indicated that stink bugs are able to avoid disruption by changing their frequency away from pure-tone noise, while constant white or broadband noise would be inefficient and probably even unable to mask temporal structure of almost pure-tone BMSB signals. Appropriating the chaotic and broadband rivalry signal from *S. titanus* (Polajnar et al. 2016c) might overcome this problem, but the impossibility of reaching all the potential resting sites of this incredibly versatile and mobile species precludes feasibility of mating disruption even in theory. Thus, attractiveness of naturally emitted vibrational signals was tested with the goal of improving the existing pheromone traps. Vibrations would represent the hypothetical missing link between long-range but imprecise attraction by aggregation pheromones and physical contact with the signal source.

19.4.2 Experimental Work

Four sets of experiments were designed to test the attractiveness of BMSB vibrational signals. The sets consisted of different setups to verify the robustness of directional response across different substrates, an important issue due to the large variability of microlocations stink bugs occupy. Setups were not designed to mimic real-world situations at this point, but featured diverse geometry and substrate types, thus presenting different challenges to the bugs' localization abilities. The setups were as follows (Mazzoni et al. 2017a):

- Trap: a cubic net cage with an "acoustic trap" in a no-choice scenario. Vibrations were transmitted through the cage's opening on one side, where a funnel was placed to prevent the bugs from returning. Three hours stimulation.

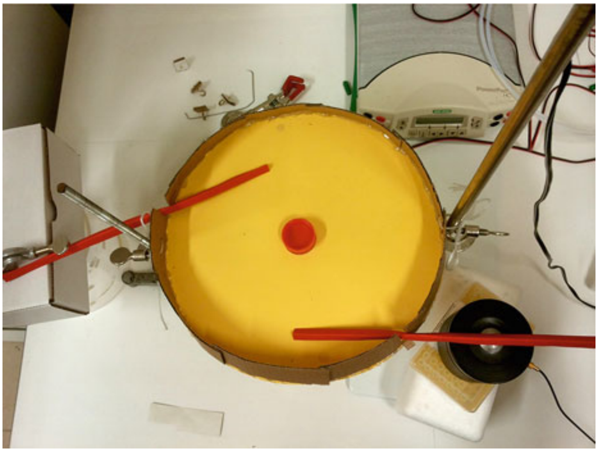

Fig. 19.4 Circular arena with ramps as used for one of the tests of male attraction by playback of female vibrational signals (Mazzoni et al. 2017a). Playback was applied to one of the ramps and the male was released from the centre of the arena

- Arena—point source: cardboard circle with raised edges. A single animal was placed in the centre of the circle, and stimulation was applied to a point near the edge. Three minutes stimulation.
- Arena—ramp (Fig. 19.4): as the previous arena, but with two inclined ramps leading away from the surface, the distal end of one of them being vibrated. Three minutes stimulation.
- Host plant: two small bean plants, each with a pair of developed leaves, were placed together so that the pairs were perpendicular. A male was placed on a random leaf and the shaker was attached to another leaf. Ten minutes stimulation, plus five minutes if the male found the target leaf.

Various tests were conducted within these sets and a number of parameters were measured. As the most general measure, roughly three-quarters of males were active—they left the releasing point—and one-half to two-thirds of males reached the point of stimulation where the shaker was attached. The number of active males was not significantly different in control trials without vibrations, but fewer than one-tenth reached the stimulation point (Table 19.1) in most cases, presumably by random movement. One exception was the arena with the point source where almost half of males reached the stimulation point even in control trials, but this was probably due to random movement: stimulation point was closer to the release point and more accessible than in the other sets, so the difference between control and treatment became prominent only when repeated crossings of the stimulation point were considered (Mazzoni et al. 2017a).

The tendency of males to continue the characteristic jerky motion after locating the FS2 source was prominent. Males circled around this location for a prolonged period, thus remaining in the vicinity, unlike those who only approached the shaker

Table 19.1 Proportion of active males and males that reached the point of shaker attachment in experiments by Mazzoni et al. (2017a)

	Active		Reached the stimulation point	
	Control	FS2 treatment	Control	FS2 treatment
Trap	NA	NA	5%	65%
Arena—point	58%	73%	48%	73%
Arena—ramp	75%	90%	10%	55%
Plant	46%	77%	4%	61%

attachment point in control trials. We dubbed this "loitering" effect, the term borrowed from military terminology (i.e. circling around the target area, waiting to strike). We realize that introducing new terms might be controversial, but this effect is distinct from what is described as arresting (ceasing motion entirely, as in e.g. Aluja and Prokopy 1992) and lingering (sharply reduced motion, as in e.g. Ibrahim et al. 2004), which describe inhibition of movement in response to a stimulus, but not necessarily near the source. Conversely, BMSB males continued to search at full speed after locating the shaker attachment point, lacking other key stimuli to switch to the final courtship stage (Mazzoni et al. 2017a). Cuticular hydrocarbons are presumably the factor responsible for inducing the switch, as indicated by antennectomy experiments of Toyama et al. (2006) and the fact that the presence of a "dummy"—a dead female washed with dichloromethane—did not have a measurable behavioural effect (Mazzoni et al. 2017a).

Measurements of the vibrational amplitude field revealed a rather complex pattern of peak amplitudes within the setups, without a monotonous amplitude gradient from the furthest point to the stimulation point (Mazzoni et al. 2017a). As shown by Polajnar et al. (2012), narrow-band signals are particularly prone to amplitude fluctuations with distance from the source, due to resonance. Nevertheless, this did not prevent the males from localizing the source, which is another (indirect) proof that stink bug males primarily use time difference in arrival of the stimulus to receptors located in all legs to orient towards the source, as postulated already by Čokl et al. (1999) and demonstrated recently by Hager et al. (2016). However, larger 2-D surfaces did present a challenge to the BMSB males' localization ability, such as in trials using arenas with ramps where the males kept walking in circles around the ramp attachment point until they touched the ramp itself (Mazzoni et al. 2017a), indicating that they are not adapted to locating the source by triangulation as are some beetles and stoneflies (Abbott and Stewart 1993; Goulson et al. 1994).

19.5 Development of Vibrational Traps

A first prototype vibrational trap (Biogard®, CBC Europe S.r.l.; Fig. 19.5) was tested in summer 2017 in a pear orchard located in Carpi (44°43′46.8″N 10°52′30.1″E, northern Italy). Two "vibrotraps" with the addition of a commercial aggregation

Fig. 19.5 A prototype bimodal trap with a pheromone dispenser, female vibrational signal (FS2) playback and a device administering electric shocks for killing the attracted bugs. Photo: Aya Ibrahim

pheromone dispenser (Pherocon® BMSB dual lures, Trécé Inc.) were installed in an orchard naturally infested with BMSB. As control, two transparent sticky traps (Pherocon® Stink Bug, Trécé Inc.) and two commercial pheromone traps (Dead-Inn Pyramid Trap—4 ft. height, AgBio Inc.) were placed nearby. The vibrotrap (Fig. 19.5) was pyramid-shaped (1 m in height), with a square base (40 cm in width). In concept, the prototype vibrotrap involves the emission of: (1) aggregation pheromone (2), the playback of female courtship song (type FS2) that has previously shown significant loitering effect (i.e. males tended to keep searching in the close vicinity of areas stimulated by this signal) (Mazzoni et al. 2017a) and (3) an electric shock sufficiently strong to kill a stink bug, triggered every 1 min. Both emissions (pheromones and vibrations) were generated at the apical part of the trap. The males were attracted to the trap's external surface by the pheromone and then driven inside cavities in the head of the trap where they were electrocuted; finally, the dead bugs fell into the cardboard base. Our hypothesis was that if the vibrotrap FS2 playback was effective, then the male–female ratio of captured stink bugs would have been

Table 19.2 Capture success of “Vibro”, sticky and pyramid pheromone traps in a pear orchard in North Italy

	“Vibro” trap + Agg Ph	Sticky trap + Agg Ph	AgBio + Agg Ph
Working days	3	7	4
Captures/trap/day	8.3	0.8	9.75
M:F capture ratio	11.5:1	0.6:1	1:1

much higher than in the control traps. Table 19.2 summarizes the captures by the three utilized traps along with the corresponding working days of each.

Promising preliminary results showed a male–female capture ratio of 11.5:1, which was substantially higher than those of both the commercial Pyramid trap (1:1) and the sticky traps (0.6:1). The observed effect clearly indicates that FS2 signal is very attractive to BMSB males and can be regarded proof of concept for specific action of vibrations, since signals of other modalities are not sex-specific. On the other hand, the relatively low absolute number of captured females might be due to either a disrupting effect of FS2 signal that would repel females from the vibrational trap, or rather the use of electricity (one shock/minute) would be less effective than the trapping system. Both hypotheses must be assessed in further laboratory and field trials. Another interesting observation to mention is that only a few non-target insect species were found in the tray of the vibrational trap, thus indicating a good selectivity. This result may represent additional value of the prototype, particularly in terms of specificity against BMSB.

19.6 Perspectives

As a result of the work described herein, the role of vibrational communication in BMSB biology and its potential for the development of alternative pest control techniques is starting to gain attention in the wider community (Weber et al. 2017; Leskey and Nielsen 2018).

Efficiency will be a key issue in development of a useful solution. Male-produced pheromones are the closest to a universal stimulus, being able to elicit positive taxis in all adults and late-instar nymphs (Khrimian et al. 2014); however, precision of the aggregational effect is insufficient for trapping, as described in the introduction. Thus, playback of vibrational signals in conjunction with synthetic pheromone lures seems to be the only way to combine long-range with short-range attraction. An obvious problem is that Polajnar et al. (2016a) failed to uncover vibrational signals that would attract females, and the proportion of captured males in laboratory trials ranged between one-half and two-thirds (Mazzoni et al. 2017a). In principle, it is necessary to remove a very high proportion of males from an insect population in order to achieve a significant impact on subsequent generations, because removing males is generally less efficient than removing females (Lanier 1990). This is undoubtedly also true for the BMSB in which both males and females are able to mate repeatedly, in rapid intervals (Kawada and Kitamura 1983). While some synergistic effect can be expected from pheromone emissions of trapped males, if they are kept alive for some time after the capture, it will nevertheless be crucial to optimize the vibrational playback to achieve maximum attraction.

Several avenues for rational planning should be considered, in order to construct the most efficient trap from the outset. Among these are playback fidelity, use of the most representative female signals, and a trap geometry that would facilitate approach and capture. Judging by the model species *N. viridula*, stink bug vibrational receptors are broadly tuned to the whole range of frequencies used within the population (Čokl 1983), but there is a clear behavioural preference to middle values of both temporal and spectral signal properties (Žunič et al. 2011), and changing of those parameters due to transmission along different substrates may significantly affect male responsiveness (Miklas et al. 2001). Not much is known about the influence of higher harmonics on the responsiveness of stink bugs to vibrational signals; relative amplitudes of dominant and higher harmonic spectral peaks vary between signals and between locations on the substrate at different distances from the signalling animal (Čokl et al. 2007). Thus, higher frequency components are unlikely to play a major role; however, data on leafhoppers suggest that harmonic components nevertheless do affect behaviour (Mazzoni et al. 2015). This aspect requires further research to optimize playback. As far as geometry is concerned, placing the container with the lure on the top of the structure as in existing pyramid traps seems a logical choice to exploit the negative geotaxis exhibited by stink bugs (Tillman and Cottrell 2016). It may be advantageous to replace large flat surfaces used in pyramid traps with structures more conducive to searching by BMSB males, perhaps nets; however, this may reduce the attractive effect of visual cues (colour). At least the final approach, i.e., the last 10 or 20 cm, should be designed using rods or other such structures to guide the animals inside the actual trap. Material properties (thickness, stiffness) of structures guiding the insects inside the trap should be adapted to provide directional cues detectable by those insects, i.e., vibration propagation velocity in the range of 300 m/s at 60 Hz, which results in 0.5 ms delay of arrival to opposite legs touching the surface 15 mm apart. Such a delay is used by stink bugs as a cue for orienting in the direction of a “leading” leg (Prešern et al. 2018). Amplitude will need to be carefully adjusted as well; Mazzoni et al. (2017a) only tested attractiveness of signals in the natural amplitude range of BMSB vibrational emissions (Polajnar et al. 2016a), but stronger playback may be needed to ensure detectability in a larger pyramid trap. Response of males to such strong signals should therefore be checked. Arrestment area of pheromone-baited traps is confined to a 2.5 m radius around the pheromone dispenser (Morrison et al. 2016a), which is the theoretical limit for the bimodal trap, unless a method can be devised to distribute vibrations further.

The prototype bimodal trap uses electricity to generate playback and the shocks for killing the attracted bugs. In parallel with optimizing the structure of all the prototype’s parts (in terms of colours, shapes and materials), solar panels could be implemented to provide power, as a sustainable and ecologically sound option. It is important to underline the high selectivity shown by the vibrational trap in the preliminary trials. More extended field tests must be conducted to definitely assess the performance of vibrotraps as potential tools to be employed in agricultural settings. If this is confirmed, it will be vital to include vibrational stimuli together with olfactory (pheromones/kairomones) and perhaps visual cues (i.e. lights/colours) to maximize the efficacy of trapping devices in the framework of multimodal action which is a basic IPM concept.

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Chapter 20
Vibrational Trapping and Interference with Mating of *Diaphorina citri*

R. W. Mankin

Abstract Microcontroller-platform devices have been constructed that detect *Diaphorina citri* male vibrational communication calls and broadcast mimics of female vibrational replies. The devices successfully interfere with mating of virgin pairs of *Diaphorina citri* in 1-h tests on citrus trees, reducing the mating percentage significantly from 57% in the control to 13% in disruption tests. Video and audio monitoring of searching behaviors in laboratory bioassays indicate that males are attracted to the source of the female reply mimics. The percentage of mating may be reduced by the following: (1) interference of a louder and earlier reply mimic more attractive to the male than the female reply; (2) masking of the female reply by the louder mimic; or (3) reduction of female responsiveness in the presence of other female replies, or combinations thereof. In male *D. citri* trapping bioassays, the device has successfully trapped 45% of males stimulated to initiate search behavior in 1-h tests on citrus trees. Positive and negative effects of social, flush-seeking, and phototactic behaviors of males and females are discussed that may affect the utility of these devices in field applications. In addition, potential applications are discussed for low-cost, modified microcontroller-platform devices that discriminate insect-produced feeding and movement vibrations from background noise in field studies.

20.1 Introduction

Diaphorina citri (Liviidae) (Hemiptera: Sternorrhyncha) is a recent addition to the increasing count of insects for which biotremology, the study of vibrational communication signals, has been applied in development of trapping or mating disruption applications (Čokl and Millar 2009; Mazzoni et al. 2009, 2017; Mankin

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2012; Hofstetter et al. 2014, Polajnar et al. 2016; Nieri et al. 2017; Gordon et al. 2017). Vibrational communication has a long history of study in the Sternorrhyncha, including pioneering research by Ossiannilsson (1950), who reported that *Trioza* (*Bactericera*) *nigricornis* Förster communicates with wing vibrations. Courtship duets consisting of male vibrational calls followed by female vibrational replies have been characterized for several other Sternorrhynchans in subsequent studies, including those by Tishechkin (2006), Lubanga et al. (2014, 2016), Eben et al. (2015), Liao and Yang (2015, 2017), and Liao et al. (2016).

Because of the urgent need to develop improved methods of detecting and controlling *D. citri* in citrus groves (Sétamou et al. 2008; Hall et al. 2012), the possibility of vibrational communication in *D. citri* was investigated by Wenninger et al. (2009), who recorded and acoustically characterized male and female courtship duets. The recordings (Rohde et al. 2013) as well as synthetic mimics (Mankin et al. 2013) then were considered for their potential to elicit female replies and male searching behavior in citrus trees. These initial studies led to development of prototype signal-mimicking devices that disrupted mating (Lujo et al. 2016; Mankin et al. 2016b) and attracted male *D. citri* to traps (Hartman et al. 2017).

As the technology was being developed, it became apparent that successful deployment of *D. citri* vibrational mating disruption and trapping applications in citrus groves would be highly dependent on the structural features of trees, which affected transmission of courtship signals as substrate vibrations through branches, shoots, and leaves (Mankin et al. 2018a; Krugner and Gordon 2018). In addition, behavioral observations suggested that such applications would benefit not only from understanding and co-opting of mating behavior but also from co-opting of social (Kennedy et al. 1967; Lin 2006), flush-seeking (e.g., Sétamou et al. 2016), and phototactic behaviors (e.g., Sétamou et al. 2011). Finally, it became apparent that mating and dispersal behavior of both sexes are altered by weather patterns, barometric pressure, and other abiotic factors (Zagvazdina et al. 2015; Martini and Stelinski 2017; Udell et al. 2017). Implications of these behavioral and abiotic factors for deployment of mating disruption and trapping applications against *D. citri* and other insects are considered in sections below.

20.2 Spectral and Temporal Characteristics of *D. citri* Vibrational Communication Signals

As is frequently observed in the Sternorrhyncha, *D. citri* courtship includes vibrational communication signals produced by wing vibrations in a duetting pattern of male calls and female replies (Wenninger et al. 2009). The spectra of both male and female signals contain multiple harmonics of the 170–250 Hz wingbeat frequency (Wenninger et al. 2009; Mullen et al. 2016). Bae and Moon (2008) suggest that the flapping motion produces the fundamental frequency and the higher harmonics are produced by vortex scattering from the edge of the wing. Due to its small size, *D. citri* produces only weak acoustic signals, but the wingbeat vibrations are transmitted through the legs to the leaves, stems, and branches of the host tree as substrate vibrations that conspecifics (or commercially available vibration sensors) can detect over distances up to 1–2 m on the same tree (e.g., Ichikawa 1979; Michelsen et al. 1982). Several other members of the Psylloidea have rows of teeth on the axillary cords of the wing mesoscutellum and metascutellum that serve as a stridulatory organ for sound production (Heslop-Harrison 1960; Taylor 1985; Tishechkin 1989). Stridulatory organs are known to produce signals with high-amplitude fundamental frequencies and weak harmonics (e.g., Mankin et al. 2009). Because such spectral patterns are not observed in its signals (Mankin et al. 2016b), *D. citri* likely uses only wing-flapping and not stridulation as a sound-production mechanism.

Male *D. citri* initially signal advertisement calls intermittently to determine whether females are nearby. When a receptive female replies to a male call, typically within 0.3–1.2 s (Wenninger et al. 2009), the male initiates searching behavior, walking toward her and continuing to call at intervals of 9 ± 1.4 s (mean ± standard error [SE]) during the 15.9 ± 2.38 min period needed to find her (Lujo et al. 2016). For males actively searching along branches, movement speeds typically are >9 mm/min (Zagvazdina et al. 2015) between bifurcations and other transition points at which they pause, call again, and then move forward or change direction (Lujo et al. 2016; Hartman et al. 2017). The durations of male calls have been observed to range from 148 to 544 ms, and the durations of female replies from 331 to 680 ms (Wenninger et al. 2009).

There has been considerable investigation of the capability of insects to localize the directions and sources of vibrational signals (e.g., Virant-Doberlet et al. 2006). The important factor determining whether a psyllid can localize the direction of the source is whether it can stretch its legs enough apart or place them on different branches in a way that provides enough amplitude and/or time of arrival difference for the central nervous system to distinguish the difference (Virant-Doberlet 2004; Čokl et al. 2006; Virant-Doberlet et al. 2006). The ability to localize direction has been experimentally verified in Hemipterans (Čokl et al. 2006; Virant-Doberlet et al. 2006), sand scorpions, *Paruroctonus mesaensis* (Stahnke) (Scorpiones: Vaejovidae) (Brownell and Farley 1979), and *Macrotermes natalensis* (Haviland) (Isoptera: Macrotermitinae) (Hager and Kirchner 2014).

The large variations observed in call and reply durations, as well as in the relative amplitudes of different harmonics in male and female signals, suggest that these parameters are not under selection for species discrimination and that the presence of multiple harmonics of the wingbeat frequency in the duetting signals may be sufficient for species identification (Mankin et al. 2016b). The ability of the *D. citri* central nervous system to identify the fundamental frequency and its harmonics in vibrational signals has not been determined, but it is known that mosquitoes (Mankin 2012; Simões et al. 2016) and mammals (Simmons and Simmons 2011) can do so. The consistently short, <1.4 s, interval between the end of the male call and the female reply (Wenninger et al. 2009) also may be a potential indicator of species recognition. Preliminary studies (Rohde et al. 2013) suggested that the percentages of male searching in response to female replies decreases as the interval increases above 0.4 s. The duration of the interval between call and reply also has been reported to affect searching behavior in a leafhopper, *Aphrodes makarovi* Zachvatkin (Kuhelj et al. 2015).

20.3 Development of a Prototype Device to Mimic and Interfere with Vibrational Communication Signals

The first devices used to produce *D. citri* vibrational communication signals for behavioral studies were vibration exciters controlled by laptop computers that played back recorded or synthetic signals (Rohde et al. 2013). However, laptops, vibration exciters, and many other devices commonly used to assess and broadcast vibrations in the laboratory are difficult or costly to employ in field environments (Cocroft and Rodríguez 2005; Mankin et al. 2010, 2011). A search for portable, low-cost vibrational signal processing and playback devices led to consideration of a battery-powered, 8-bit-microcontroller platform (Arduino Uno, Arduino Inc., Ivrea, Italy) connected to a circuit board with amplifiers for an electret microphone (Model WM-63GNT, Panasonic, Newark, NJ) and a piezoelectric buzzer (9S3174, Taiyo Yuden, Tokyo, Japan). The microphone was clamped to the trunk or branch of a citrus tree to detect male *D. citri* vibrational signals. The piezoelectric buzzer was clamped 10–50 cm away on the tree to broadcast vibrations of synthetic mimics of female replies. It was found that use of either a recorded female reply or a synthetic female reply (Fig. 20.1) usually stimulated the tree structure to produce several additional vibrational harmonics that were not present in the original signal. However, these additional harmonics did not reduce either the male or female responses in comparison to their responses to vibrations produced by conspecifics (Rohde et al. 2013). Indeed, the additional harmonics possibly help mask harmonics of actual female replies.

It was anticipated that the microcontroller could be programmed to discriminate male calls from background noise automatically, and then broadcast a female reply mimic within 0.4 s to optimize the likelihood that the calling male would be attracted to the broadcast source. One way to initiate the process of signal discrimination was to compare spectrograms of incoming microphone signals with average spectrograms (profiles) of known male calls, accepting signals whose squared spectrogram amplitudes sufficiently matched the profile in the call's frequency range of greatest energy (Mankin et al. 2016b). An alternative would have been to adopt a procedure such as that used by Korinšek et al. (2016) that programmed a larger, 32-bit microcontroller platform (ARM Cortex M4, ST Microelectronics, Geneva, Switzerland) using more powerful algorithms, such as those based on linear prediction Cepstral coefficients and multilayer perceptron classifiers to distinguish male calls from background noise.

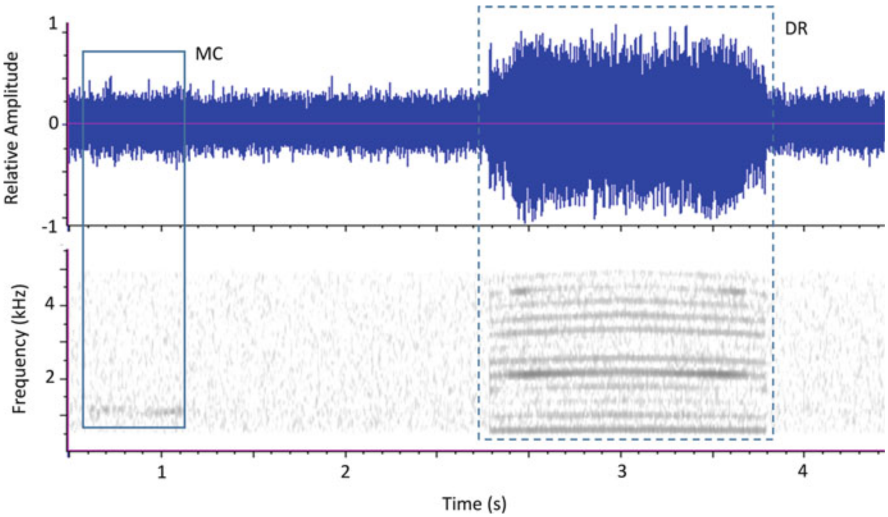

Fig. 20.1 Example of male call (in solid box, MC) that was detected by the prototype device, which then produced a synthetic female reply (in dashed box, DR)

The microcontroller was programmed to calculate a 128-point spectrum every 0.1 s from 256 time points sampled at 8 kHz. The spectrum was calculated using an open-source, Fast Hartley Transform algorithm (Bracewell 1984). Each time the spectrum amplitude rose above a preset threshold, the program inspected the last six spectra before the spectrum amplitude again fell below threshold. This 0.6 s duration was selected because it slightly exceeded the 0.15–0.59 s range of male calls reported by Wenninger et al. (2009). The six spectra comprised a spectrogram that could be compared against an average spectrogram (profile) of known male calls.

The male-call profile used for matching with incoming signals was constructed as an average spectrogram of a set of 460 calls recorded from six separate males on multiple citrus trees in the laboratory. Most of the non-background energy in these calls appeared between 600 and 2000 Hz, so only these frequencies were used in the spectrogram-matching process in the final version of the noise discrimination algorithm (Mankin et al. 2016b).

Previous experience with vibrational signals in field environments (Mankin et al. 2011), as well as reports about background noise in other field studies (Barth et al. 1988; Cornell and Hawkins 1995; Tishechkin 2007; McNett et al. 2010), suggested that the presence of wind-induced noise, vehicular noise, and bird calls would cause the greatest interference with automated identification of male calls. To consider the background noise in relation to *D. citri* communication vibrations, two 40-min recordings were collected simultaneously with an accelerometer and the prototype device from different *D. citri*-infested trees in an area with moderate interference from traffic and bird noise. Listeners identified individual signals from the record-

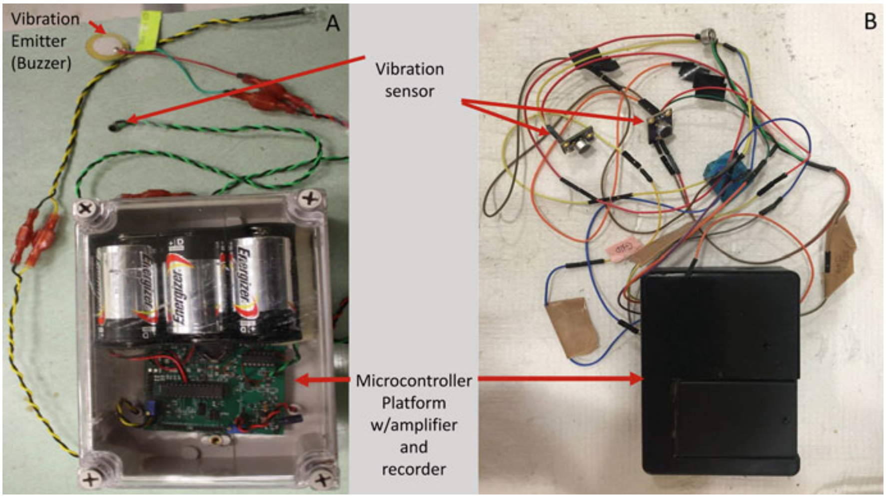

Fig. 20.2 (**a**) Original field-test version of prototype device showing microcontroller and batteries inside a moisture-proofed container, a microphone used to detect the signal that will be clamped to a branch or trunk of the citrus tree, and a vibration source that is clamped in the upper canopy of the tree; (**b**) a newer prototype with two sensors to cancel background noise

ings as male calls or noise and compared them with the predictions of the prototype device-discrimination algorithm. The listener vs. algorithm predictions about the above-threshold signals suggested that the algorithm had accepted incorrectly a high percentage of background noise signals (false positives). Consequently, the profile-matching process was optimized further by weighting specific spectral and temporal pattern features using a Matlab genetic algorithm (MathWorks, Natick, MA), described in Mankin et al. (2016b), that maximized the squared differences between the male call profile and the spectrograms of background noise. The optimized procedure was found to identify 77% of listener-identified *D. citri* calls correctly in the 40-min recordings of calls and background noise collected in infested trees, with 26% misidentification of background noise as *D. citri* calls.

The synthetic female reply mimic selected for broadcast by the prototype device was one that had been used successfully to elicit female behavioral responses (Mankin et al. 2013) and had been found also to elicit male searching behavior (Mankin et al. 2016b). The interval between the end of the male call and the initiation of the broadcast was governed primarily by the speed of the signal acquisition and discrimination algorithms and usually was <0.4 s. The signal measured on the tree at 10 cm distance from the buzzer was 1–5-fold greater than the typical amplitude of a female reply (Lujo et al. 2016).

Several devices of this prototype version were tested for efficacy of applications for *D. citri* mating disruption and male trapping. Figure 20.2 shows examples of two devices constructed for field use. The initial study to collect *D. citri* signals and background noise in the field was conducted using the device in Fig. 20.2a.

20.3.1 Mating Disruption Bioassays with Prototype Device

A series of tests additionally monitored by video and audio equipment was conducted to compare *D. citri* natural courtship behaviors with behaviors in the presence of disruptive signals broadcast by the prototype device (Lujo et al. 2016). Virgin males and females were placed on different branches of small citrus trees and the prototype system platform was attached lower on the trunk, with broadcasting either on or off. Times of calls, replies, and other behaviors were noted for analysis. The mating percentage was significantly lower in 1-h tests where the prototype device broadcast a reply mimic immediately after the male called (Lujo et al. 2016). In control tests without prototype device broadcasts, males were observed searching for replying females by walking rapidly along the branch, pausing, calling, and then walking forward or reversing direction. The pauses usually occurred at the end of a leaf or branch, a bifurcation, or other visually identifiable transition point. After pausing, the male frequently (although not always) walked toward the female reply. The duration before the male reached the female varied considerably, but on average was 15.9 min, and mating occurred in 57% of controls (Lujo et al. 2016).

In contrast, when the prototype device broadcast reply mimics, as in the example of Fig. 20.1, a majority of the males walked toward and remained near the synthetic signal source instead of walking toward the actual female's reply. The duration before reaching the female was significantly greater than in the control, 24.13 min, and mating occurred in only 13% of disruption tests (Lujo et al. 2016). It should be noted that the female often stopped replying after the buzzer had broadcast 1–3 reply mimics in response to the male call, which further reduced the likelihood of the male finding the female (Lujo et al. 2016). This phenomenon was observed also with *D. citri* by Wenninger et al. (2009), and with *Scaphoideus titanus* Ball by Mazzoni et al. (2009). Altogether, the observations suggest that the percentage of mating was reduced by one of the following three factors (or combinations thereof): (1) interference of an earlier and louder signal mimic more attractive to the male than the actual female reply; (2) masking of the female reply by the louder signal mimic; and (3) reduction of female responsiveness in the presence of other female replies.

20.3.2 Vibration Trap Bioassays with Prototype Device

A second series of 1-h tests using the prototype as a female mimic to attract virgin males was conducted on small citrus trees without a female present (Hartman et al. 2017). As in previous observations of natural courtship (Lujo et al. 2016), males which produced an advertisement call often began searching in response to the female reply mimic. They stopped briefly at transition points, called again, and then continued forward or reversed direction, frequently walking closer to the source of the reply mimic. Forty-five percent of males that initiated searching located the source (Hartman et al. 2017), only slightly below the percentage that mated in natural courtship (Lujo et al. 2016). In addition, the mean latency before initiation of calling and searching was significantly lower for those males that reached the broadcast source than for those that missed it.

The result that calling and searching latency were lower for successful males supports a hypothesis that the trapping efficiency may be affected by variability in male responsiveness to searching cues. Other reports of male responsiveness variability include Stockton et al. (2017a), who found variability in courtship behaviors of blue and orange color morphs. Variability in searching behaviors of male *D. citri* was observed by Zagvazdina et al. (2015), who noted effects of weather on the proportions of males who moved either > or <9 mm/min toward the synthetic female reply from the prototype device. To place this in behavioral context, we note that *D. citri* have been reported to walk toward different types of attractive light sources at rates of 10–80 mm/min (Paris et al. 2017).

Other behavioral factors may affect trapping efficiency also. Several factors are discussed in Sect. 20.5 below.

20.3.3 Extension of Prototype Device Usage to Additional Pest Detection Applications

A potential use of the prototype device that remains to be addressed is the detection and identification of insect pests without directly trapping them. Early detection of pest presence or identification of particular insect species is often an important use of acoustic technology but the cost and portability of currently available sound and vibration detection devices makes them difficult to use in large-scale field applications (Mankin et al. 2011; Potamitis and Rigakis 2015). In preliminary studies, the low-cost Arduino Uno microcontroller/amplifier platform has been tested in the field to consider its utility for detecting internally feeding stored product insects and hidden infestations of insects in wood. However insect-produced signals detected by device were less easily distinguished from background noise than signals recorded from commercial equipment. For this reason, recent tests also have been conducted using a 32-bit platform operated by an Atmel SAM D20 (Atmel Corp., San Jose, CA) microcontroller (Fig. 20.2b). The system includes a vibration sensor and amplifier to detect the insect feeding and movement vibrations, an SD memory card to record incoming signals, and software to discriminate insect-produced signals from background noise.

A rationale for use of a larger microcontroller platform for detection of insect vibrational signals in field environments is the improved capability to discriminate insect signals from background noise that is provided by the larger memory and the higher resolution analog-digital converter. Identification of particular insect species using either the Arduino or Atmel platform would depend on previous knowledge of empirically determined spectrum profiles of their vibrational signals. However, the capability provided by the larger microcontroller to employ linear frequency Cepstral coefficients, Gaussian mixture models, probabilistic neural networks, and multilayer perceptron classifiers (Bimbot et al. 2004; Ganchev and Potamitis 2007; Lampson et al. 2013; Korinšek et al. 2016) enables more powerful analysis and interpretation of the spectral and temporal patterns of insect-produced vibrations in trees (Mankin et al. 2016a, 2018a, b), stored products (Njoroge et al. 2016), and soil (Mankin et al. 2007), in addition to the spectral and temporal patterns of *D. citri* vibrational communication signals. Consequently, a third-generation prototype is now under development, designed to reduce costs and improve interpretation of insect-produced vibrations in field environments.

20.4 Host Plant and Abiotic Factors That Influence *D. citri* Vibrational Trapping and Mating Disruption

Diaphorina citri mate and develop on multiple plant species of different sizes and structural architectures in the rutaceous subfamily Aurantioideae (Halbert and Manjunath 2004) in a wide variety of geographical regions and environmental conditions (Liu and Tsai 2000; Nava et al. 2010; Hall et al. 2011, 2012; Grafton-Cardwell et al. 2013). Differences among these architectures result in considerable variation in vibrational signal amplitudes and in behavioral responses (Cocroft et al. 2006). Transmission of vibratory energy in trees, for example, depends on the natural frequencies, damping ratios, and modal shapes, which are determined by the mass distribution, stiffness, and morphology of the tree (e.g., Castro-Garcia et al. 2008; Mortimer 2017; Mankin et al. 2018a). Consequently, the amplitude of vibrational signals produced by either a female reply or a synthetic reply mimic does not attenuate uniformly with distance from the source. The vibration active space (Mazzoni et al. 2014) is a network of one- or two-dimensional spaces including the trunk, primary limbs, secondary branches, and twigs, which modulate vibration amplitude at each bifurcation point. Improved knowledge of such factors (Du et al. 2014; Gupta et al. 2015) may prove useful when attaching piezoelectric buzzers or waveguides operated by minishakers (Polajnar et al. 2016; Gordon et al. 2017; Krugner and Gordon 2018) to broadcast disruptive signals within individual trees or vineyard rows.

In addition, *D. citri* populations are known to be affected by elevation, and were found to be absent at elevations above 600 m in Puerto Rico, although citrus is found at those elevations (Jenkins et al. 2015). In future studies, it will be worthwhile to consider how environmental factors like elevation and biotic, host plant factors might affect implementation of vibrational trapping and mating disruption applications.

Previous studies of *D. citri* biology have found that adults and nymphs have the highest percentage of survival and greatest reproductive capacity between 11 and 28 °C (Liu and Tsai 2000). It is not certain whether temperatures outside the ideal range would directly affect mating behavior, or if they would significantly affect physiological processes that result in impairment of mating behavior. It should be noted, however, that extremes of weather have been found to reduce *D. citri* abundance (Catling 1970), as is commonly observed in insects when heavy winds or precipitation reduce foraging success or impair ability to mate (Cornell and Hawkins 1995). Such extremes typically are preceded by strong variation in barometric pressure (Zagvazdina et al. 2015), and it has been reported that mating and phototactic behaviors, as well as dispersal behaviors, are affected by barometric pressure variations. Mating behavior decreased but phototaxis increased with increasing barometric pressure (Zagvazdina et al. 2015), and dispersal increased with increasing barometric pressure (Martini and Stelinski 2017).

20.5 Behavioral Factors Influencing *D. citri* Vibrational Trapping and Mating Disruption

Both male and female *D. citri* exhibit phototaxis (Sétamou et al. 2011; Anco and Gottwald 2015) either by walking (Pregmon et al. 2016; Paris et al. 2017) or flying (Paris et al. 2015). Both sexes also are attracted to host plant odors (Hall et al. 2015; Beloti et al. 2017) and new leaf flush (Catling 1970; Hall and Albrigo 2007; Patt and Sétamou 2010; Sule et al. 2012; Sétamou et al. 2016). Mating occurs during photophase, primarily on new leaf flush (Wenninger and Hall 2007), which typically appears on the tree periphery. Part of the attractiveness of flush may be due to the limited ability of nymphs to probe through the thicker structure of leaf veins of older citrus leaves, compared to new flush (Ammar et al. 2013). Placement of traps near attractive phototactic or host odor cues may enhance trap effectiveness. It should be noted, however, that although females are attracted to feeding-damaged plants, they prefer uninfested leaves when they land at the tree (Martini et al. 2014).

Finally, it is relevant to note also that male *D. citri* alter their calling behaviors when they detect female odor (Wenninger et al. 2009) or male calls (unpublished, and observed also in *A. makarovi* Kuhelj and Virant-Doberlet 2017). Males display adaptive plasticity and “learn” to be attracted to female odors after they have experienced mating (Stockton et al. 2017b).

The effects of adaptive learning and biases toward female odor, flush, the tree periphery, and light are likely to be significant factors in the success of efforts to apply vibrational signals to disrupt *D. citri* mating. Such effects should be addressed in detail to optimize placement of vibration traps or sources for mating disruption broadcasts.

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Chapter 21
Vibrational Behavior in Bark Beetles: Applied Aspects

Richard W. Hofstetter, Nicholas Aflitto, Carol L. Bedoya, Kasey Yturralde, and David D. Dunn

Abstract Acoustic signals are used for intraspecific communication in bark beetles and a variety of stridulatory mechanisms have evolved within the subfamily Scolytinae (Coleoptera: Curculionidae). Bark beetles use stridulatory signals for communication at the tree surface and within tunnels inside tree tissues. Bark beetles produce a variety of call types that are broadband with frequencies ranging from 1 to 80 kHz. Not only are airborne and substrate-borne vibrations available, but every stridulation event produces both airborne and substrate-borne vibrations via the same action of the animal. Vibrations appear to be used during species recognition, premating interactions, pair formation, mate selection, intraspecies aggression, territoriality, and predator deterrence. No sound receptors have been located for bark beetles; however, we propose potential locations in this chapter. We provide an overview of acoustic communication and its use by adult bark beetles, describe their stridulatory structures, interpret how vibrations move within tree materials and how this affects the beetles' ecology and behavior, and present technical and applied applications of acoustic tools for bark beetle management.

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21.1 Introduction

Bark beetles (Coleoptera: Curculionidae: Scolytinae) are an ecologically and economically important subfamily of weevils that colonize tree phloem and other plant parts such as seeds and stems (Raffa et al. 2015). Over 6000 species of Scolytinae have been described (Hulcr et al. 2015) and can be found throughout the world wherever trees are located (Vega and Hofstetter 2015). Several bark beetle species are capable of altering large scale forest patterns over time via their selection of particular trees and resulting tree mortality (Eidmann 1992; Raffa et al. 2008; Bentz et al. 2010). Most bark beetle species utilize tree materials where they mate, lay eggs, and complete larval development (Raffa et al. 2015). Life history strategies can be monogamous or polygamous with regard to mating, and solitary or gregarious with regard to feeding (Kirkendall 1983; Wermelinger 2004). Bark beetles are highly adapted to life within trees and thus are adapted to boring and communicating within tree material. Adult beetles bore into phloem making cylindrical tunnels that often lack light (i.e., complete darkness) and may contain high levels of plant defensive compounds such as monoterpenes (Raffa et al. 1993). Signals from air- and substrate-borne vibrations become important once beetles are within tunnels or at the tunnel entrance (Rudinsky and Michael 1972, 1973; Ryker and Rudinsky 1976a; Swaby and Rudinsky 1976; Rudinsky et al. 1978 and many others).

Host tree selection and mate location involve chemical cues via gustation (e.g., tasting tree tissues), olfaction (e.g., detection of pheromones related to beetles within tree tissues), and possibly sound (Rudinsky and Michael 1974; Ryker 1984; Raffa et al. 2015). Acoustic cues have been proposed for host tree location (Mattson and Haack 1987), and some evidence suggests that they can hear and respond to the sounds resulting from tree cavitation in response to drought conditions (Kaiser 2014). Multimodal communication, such as chemical and acoustic are likely required to convey species-specific and individual information to conspecifics (typically of the opposite sex) within the tree (Rudinsky and Michael 1972; Rudinsky et al. 1973; Ryker et al. 1979; Birch 1984).

Bark beetles produce sound by rubbing body parts or body-substrate friction (Barr 1969; Lyal and King 1996) called stridulations (Wessel 2006). There is great diversity in the types of structures employed in stridulation by bark beetles among genera, species and between the sexes (Fig. 21.1) (Barr 1969; Ryker 1988; Lyal and King 1996; Kerchev 2015). Interestingly, stridulatory structures, regardless of the location of the body, are often sexually dimorphic and less-developed or absent in the sex that initiates tunnel construction (i.e., pioneer or colonizing sex) (Barr 1969).

Bark beetles produce a variety of call types that vary in temporal characteristics. General call types appear somewhat consistent within genera (Rudinsky and Michael 1974; Lyal and King 1996; Yturralde 2013); however, intraspecific differences occur between chirps produced in different contexts (Michael and Rudinsky 1972; Fleming et al. 2013). Signal characteristics in bark beetles show that both air- and substrate-borne vibrations are present and potentially detectable by conspecifics at distances within a few centimeters (Fleming et al. 2013), and

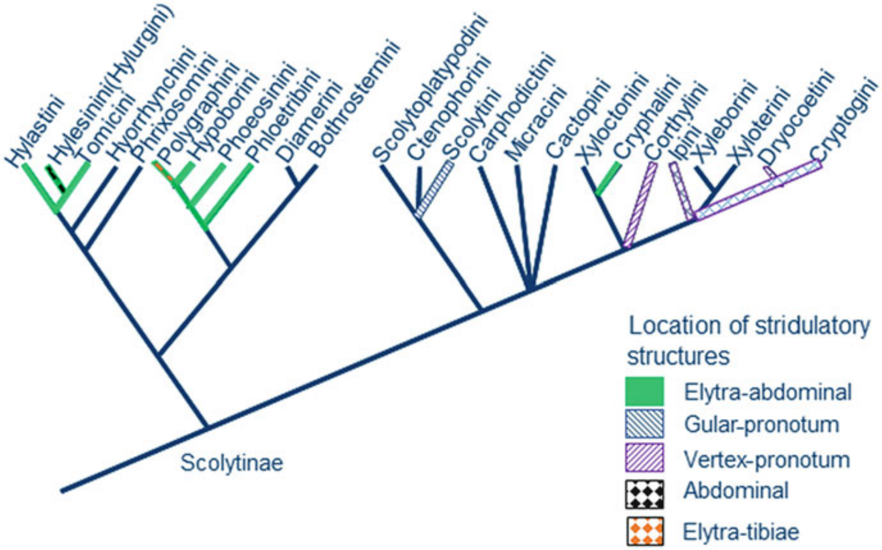

Fig. 21.1 Phylogeny of Scolytinae modified from Wood (1982) and Kirkendall (1983) and location of stridulatory structures based on review of stridulatory structures by Lyal and King (1996) and more recent publications on individual species. Some tribes have more than one stridulatory mechanism (e.g., Hylurgini, Polygraphini, and Cryptogini)

these close signals could be detected using a variety of receptors (Yack 2004, 2016). However, no sound receptors have been located for bark beetles; here, we propose potential locations.

Bark beetle acoustic communication remains one of the least studied and underappreciated forms of communication in this group of insects. Despite the ubiquity and purported importance of acoustic signals in bark beetles (Rudinsky 1969; Rudinsky and Michael 1972; Ryker 1984), little is known about their physical properties and how these properties vary among behaviors and under different tree substrate conditions. Furthermore, nothing is known about possible sound or vibration receptors. Here we summarize the current knowledge of acoustic communication in bark beetles and hope to advance our understanding of the potential role of vibrations in bark beetle systems.

21.2 Sound Production and Structures

Air- and substrate-borne vibrations produced via stridulation are known to occur in most bark beetle genera, and vibrational signals are proposed to play important roles in their life history (Barr 1969; Ryker 1988; Lyal and King 1996; Kerchev 2015). Like most coleopterans, sounds are delivered via stridulation, which involves the use of two structures, the ‘plectrum’ or the ‘scraper’ that is moved across a ridged surface commonly known as the ‘file’ or ‘pars stridens’ (Wessel 2006; Rosado-Neto and dos Santos 2010). Additionally, it is possible that some beetle species rub or scrape their exoskeleton against substrates to evoke vibrations (Drosopoulos and Claridge 2006). Within the bark beetle subfamily Scolytinae, there are five known stridulatory mechanisms. These include the (1) gular-prosternal, where the pars striden is located ventrally on the head and is scraped against the plectrum, consisting of a single or multi-ridged structure at the anterior end of the prosternum; (2) elytral-abdominal (Fig. 21.2), where the pars stridens located on the ventral side of the elytra (usually more prominent on one elytron) is scraped by the plectrum (sclerotized peg) located on the seventh segment of the abdominal tergite. A slightly different elytral-abdominal mechanism is proposed for some female *Dendroctonus* beetles in that an elytral file, similar to that found in males, is located on the sutural margin of the right elytra and a sternal plectrum is located on the inside wall of the last sternite (Rudinsky and Michael 1973); (3) vertex-pronotal (Fig. 21.3), where the pars striden, an elongate, ridged structure present on the vertex of the head, is scraped against the plectrum, a multi-ridged structure present at the ventral anterior side of the pronotum (Barr 1969); (4) abdominal, where a sclerotized peg present on the eighth abdominal segment is scraped against a pars stridens on the posterior region of the last sternite (Rudinsky and Michael 1973); and (5) elytral-tibial, where the pars stridens on the outer margin of the elytra, starting at the level of the boundary between abdominal sternites III and IV, is rubbed by the plectrum, which is a large acicular spine on the inner surface of the hind tibiae (Sasakawa and Yoshiyasu 1983; Kerchev 2015). Each of these mechanisms produces somewhat distinct acoustic patterns and frequency components. One factor that can affect acoustic frequency is body size, but only if the mechanism relates

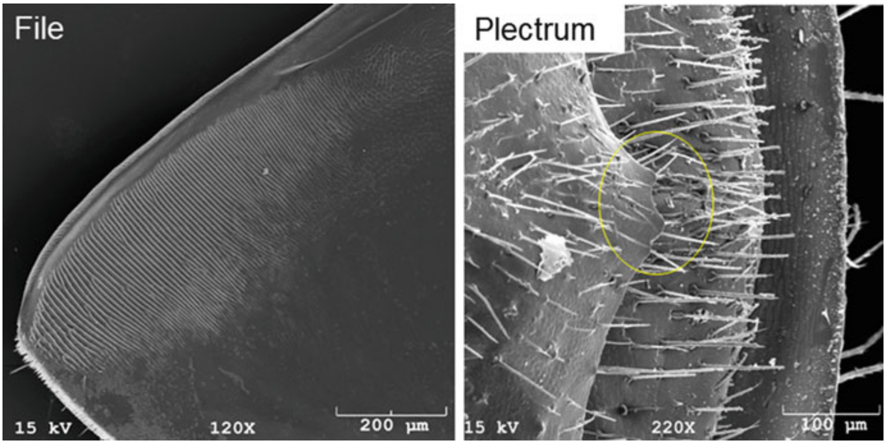

Fig. 21.2 File (underside of elytra) and plectrum of *Dendroctonus approximatus*. Picture by K. Yturralde, Scanning Electron Image, Northern Arizona University

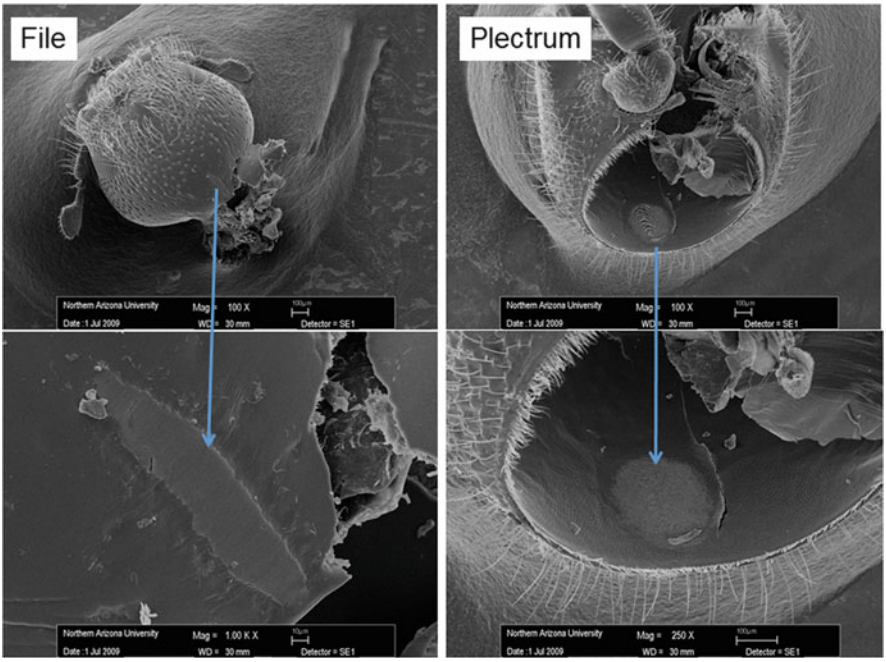

Fig. 21.3 File (anterior dorsal head) and plectrum (dorsal underside of pronotum) of *Ips pini*. Picture by K. Yturralde, Scanning Electron Image, Northern Arizona University

proportionally to body size, or if body cavity size directly influences frequency (Yturralde 2013; Lindeman 2016). Studies have shown that beetles using the elytral-abdominal stridulation method (e.g., *Dendroctonus* beetles) have an inverse correlation between body size and frequency, but other stridulatory methods such as the vertex-pronotal stridulation method (e.g., *Ips* beetles) are not correlated with frequency.

The extent to which beetles stridulate and the physical mechanism employed often differs between the sexes within a species, depending on which sex initiates the construction of the nuptial gallery (Barr 1969). For instance, the vertex-pronotal mechanism (Fig. 21.3) is generally found in non-host selecting females of polygamous species in the genus *Ips* and *Gnathotrichus* (Wilkinson 1962; Wilkinson et al. 1967; Barr 1969; Swaby and Rudinsky 1976). The elytral-abdominal type of stridulatory mechanism (Fig. 21.2) is observed in non-host selecting males of monogamous species in the genus *Dendroctonus*, *Hylesinus* and *Polygraphus* (Vernoff and Rudinsky 1980; Ryker 1988; Kerchev 2015). While the gular-prosternal mechanism can be observed in both sexes of some monogamous (e.g., *Scolytus* spp.) and polygamous (e.g., some *Ips* spp.) species (Barr 1969). In some species, one of the sexes may have two stridulatory mechanisms, such as *Dryocoetes autographus* females, which have the elytral-abdominal and vertex-pronotal stridulatory mechanism (Sasakawa and Yoshiyasu 1983), or *Cryphalus* *fulvus* males, which use the elytral-abdominal mechanism during aggression with other males, but use the vertex-pronotal mechanism during male-female interactions (Sasakawa and Sasakawa 1981).

The mechanics of sound production have only been described for a few bark beetle species. Lindeman (2016) determined that chirp production (both simple and interrupted) in *Dendroctonus* beetles was produced by elastic potential energy, like a stretched spring. Potential energy is stored as the plectrum locks onto the file and remains stationary while the abdomen moves posteriorly, resulting in an increased angle between the plectrum and abdomen (Lindeman 2016). Thus for the elytral-abdominal stridulation mechanism, sound is produced during the down stroke of the plectrum against the pars stridens. Sound that occurs on the upstroke is termed ‘trailing chirps’, which are infrequent but may occur (Lindeman 2016). For intermediate calls, the intervals between phrases occur from a stop in movement in the down stroke of the plectrum against the elytra. This was further confirmed by Lindeman (2016), who determined that the number of teeth on the pars stridens match closely the number of pulses (strikes). A similar elastic mechanism works for species that use the gular-prosternal or vertex-pronotal stridulation mechanisms. As the head prepares to move backward or forward, potential energy is stored as the plectrum begins to push against the pars stridens.

21.3 Sound Perception by Bark Beetles

Given that beetles stridulate and produce a variety of purported call types (see Sect. 21.4), it can be hypothesized that beetles have receptor organs (see Figs. 21.4, 21.5, 21.6). However, no receptor organs have been located in bark beetles. Surprisingly, receptor organs have only been described in a few Coleoptera species. For example, a Johnston’s organ has been described in whirligig beetles (Gyrinidae) (Kolmes 1983; Bendele 1986) and tympanal hearing organs in tiger beetles (Cicindelidae) and scarab beetles (Dynastinae) (Yager and Spangler 1995). In beetles with tympana, the hearing organs act mainly as sense organs for recognizing the ultrasonic sounds from predatory bats (Forrest et al. 1997). Like many other species living within wood and trees (e.g., termites, social wasps, bees, and ants), or living on surfaces similar to the phloem (plant stems; e.g., leaf hoppers), bark beetles likely possess sensitive vibration detectors. More insects use the vibratory channel than use airborne sound for communication (Michelsen et al. 1982; Virant-Doberlet and Čokl 2004; Yack 2016).

Bark beetle stridulation sounds are broadband, exceeding 85 kHz in some recordings (Yturralde 2013; Fleming et al. 2013). The high sonic and ultrasonic frequencies of bark beetle signals provoke questions about a hearing mechanism capable of perceiving these signals. However, the range at which beetles hear is not known. Here we present results of a playback study, where male *D. adjunctus* beetles were placed in phloem sandwiches (Aflitto and Hofstetter 2014) and subjected to artificially generated calls of different frequencies and call durations. Playback calls

Fig. 21.4 Blue arrows point to potential hearing organs on the wings and abdomen of *Ips pini* and *Dendroctonus adjunctus*. Pictures by R. Hofstetter, Northern Arizona University

ranged in band frequencies of 1–100 Hz, 100–5000 Hz, 5000–10,000 Hz, 10,000–25,000 Hz, and 25,000–40,000 Hz and durations of 1, 10, 40, 160, and 640 ms. We found that beetles would call back only to sounds in the band frequencies of 100–5000, 5000–10,000, and 10,000–25,000 Hz and durations of 10, 40, or 160 ms. Although this is not a perfect test of what beetles can hear, it does give some insight into the call characteristics that beetles may be responsive to or are capable of hearing. There is a clear need for more advanced research into the functions, characteristics and receptor mechanisms of the acoustic communication in bark beetles, and beetles in general.

Fig. 21.5 Interior of pronotum with head removed of *Dendroctonus adjunctus*. Arrows point to potential sound receptor organs within the body. Picture by R. Hofstetter, Northern Arizona University

21.4 Acoustic Ecology and Use by Bark Beetles

Given that bark beetles communicate in small galleries within trees, beetles might be hypothesized to communicate by near-field airborne sounds and solid-borne vibrations. Bark beetle stridulations typically produce sounds that are broadband, with multiple peak frequencies ranging from 1 to 80 kHz (Fleming et al. 2013; Lindeman and Yack 2015). Many species are reported to signal in more than one behavioral context, and sounds are often assumed to be used during species recognition, premating interactions, pair formation, mate selection, intraspecies aggression, territoriality and predator deterrence (Barr 1969; Rudinsky 1969; Rudinsky and Michael 1972; Rudinsky et al. 1973; Rudinsky and Ryker 1976; Ryker and Rudinsky 1976a, b; Yandell 1984; Ryker 1988; Lindeman and Yack 2015). Bark beetles typically produce three call forms: single clicks, simple chirps or interrupted chirps. Single clicks are usually produced by the sex that has less pronounced stridulatory structures (e.g., female *Dendroctonus* or male *Ips*) and the stridulation mechanism is poorly understood. Clicks usually occur as a single pulse, but multiple consecutive pulses can be produced. Unlike clicks, chirps contain many pulses (i.e., tooth strikes). Both interrupted and simple (uninterrupted) chirp forms

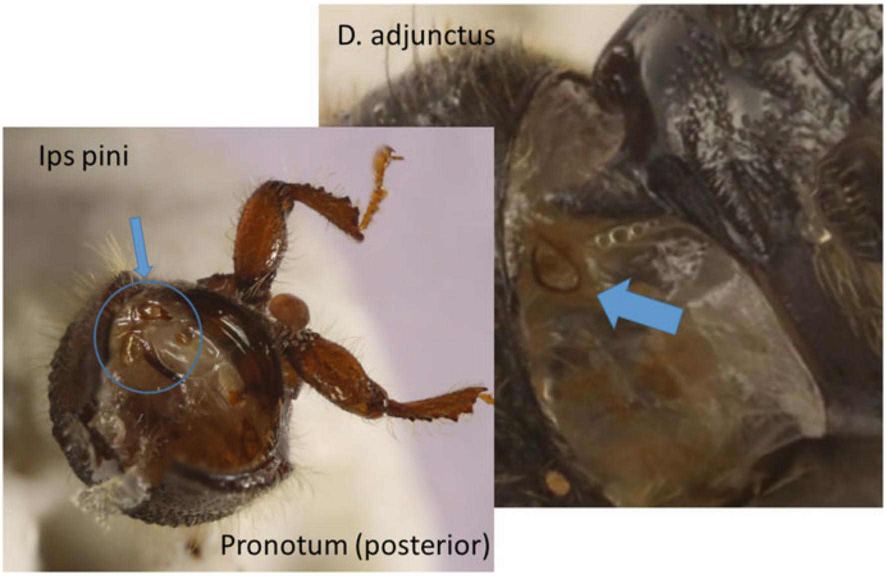

Fig. 21.6 Posterior of pronotum of *Dendroctonus adjunctus* and *Ips pini* (with abdomen removed). Blue arrows (and circle) point to spiracles, which may serve as sound receptor organs. Picture by R. Hofstetter, Northern Arizona University

(Fig. 21.7) may occur within wave trains; however, in some genera, interrupted chirps may be rare (as in *Ips pini*; Dobai et al. 2018).

Simple chirps are significantly shorter than interrupted chirps (Fig. 21.7), with chirps containing one set of tooth strikes and interrupted chirps containing two to five sets of strikes within a phrase (e.g., Michael and Rudinsky 1972). Lindeman and Yack (2015) quantitatively defined chirp type produced based on the minimum inter-tooth strike interval that could be considered a “gap” to classify chirps as interrupted. They found that simple chirps contained inter-tooth strike intervals less than 5 ms, while the interrupted chirps also comprised inter-tooth strike intervals less than 5 ms, but more than one quarter (~28%) were greater than 5 ms. Both chirp types can have a similar number of tooth strikes, although interrupted chirps tend to include more strikes (Fleming et al. 2013). The interrupted chirps typically have significantly lower mean tooth strike rates and higher mean inter-tooth strike intervals (Fleming et al. 2013). Within a beetle species, simple chirps usually have lower dominant peak frequencies than interrupted chirps (Yturralde and Hofstetter 2015; Fleming et al. 2013).

Whether simple or interrupted chirps vary between contexts is poorly understood for most species (Fleming et al. 2013; Lindeman and Yack 2015; Yturralde and Hofstetter 2015). Past studies refer to the chirp types as “attraction,” “premating,” “rivalry,” or “distress” chirps (Barr 1969; Ryker and Rudinsky 1976b; Oester et al. 1978; Ryker 1988; Michael and Rudinsky 1972); however, chirp characteristics may differ between contexts and require verification for many species. Understanding

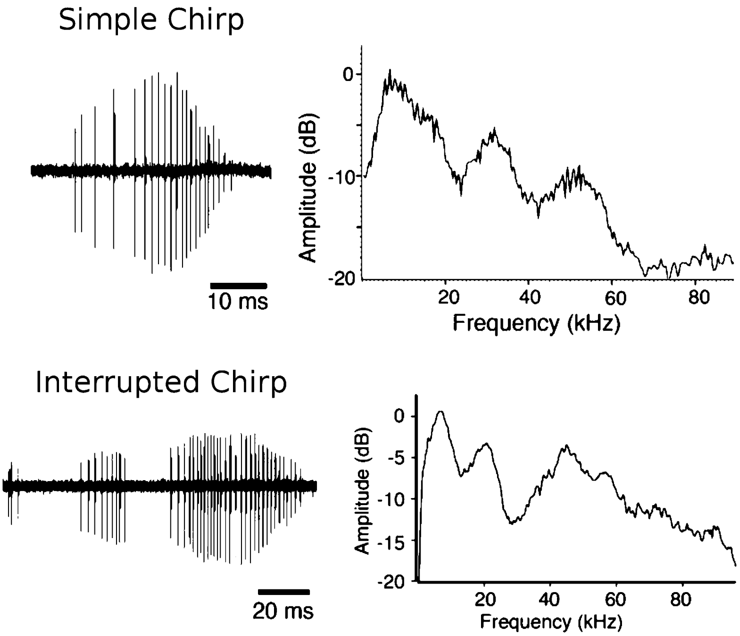

Fig. 21.7 Simple and interrupted chirps showing individual tooth strikes and power spectrum for each chirp type of *Dendroctonus ponderosae*. Adopted from Fleming et al. 2013. © 2008 Canadian Science Publishing or its licensors. Reproduced with permission

how signals vary between contexts can be further complicated in the literature, as signals were recorded under artificial settings that may not represent natural conditions (Wilkinson et al. 1967; Swaby and Rudinsky 1976; Yturralde and Hofstetter 2015). Additionally, beetles appear to produce a variety of calls during encounters or under different situations. Several authors have found that beetle individuals produced both simple and interrupted chirps, but vary in the ratio of interrupted to simple chirps under a variety of situations (Fleming et al. 2013; Lindeman and Yack 2015; Yturralde and Hofstetter 2015). Beetle condition or body size may also influence the ratios of simple and interrupted chirps produced or the characteristics of the chirps (e.g., larger male *Dendroctonus valens* tended to produce interrupted chirps with more components; Lindeman and Yack 2015).

Acoustic signals appear to mediate pheromone production in many of the aggressive tree-killing bark beetles (Rudinsky and Michael 1972; Pitman and Vité 1974; Ryker and Rudinsky 1976a, b; Pureswaran et al. 2016; Liu et al. 2017). Acoustic communication indirectly functions in moderating aggregation by inducing the release of anti-aggregation or masking pheromones in *Dendroctonus* species (Rudinsky 1969). Males stridulate at the entry hole and induce females to release anti-aggregation pheromones. This consequently results in the loss of attraction by males to the gallery (Rudinsky 1969). Males stridulate in response to pheromones released by virgin females, and females respond by altering (i.e., reducing attractiveness) their pheromone composition (Liu et al. 2017).

It is unclear whether acoustic signals are used to distinguish sympatric bark beetle species. Several studies indicate that acoustic signals may not contain enough information on species identity. In a laboratory cross-mating study, Lewis and Cane (1990) found that the acoustic signals of four closely related *Ips* species, although unique in their characteristics, were not effective in preventing *forced* heterospecific pairings. This suggests that acoustic signals may not serve in species recognition. Alternatively, Pureswaran et al. (2016) found evidence that sympatric *Dendroctonus* species produce acoustic chirps that differ and could potentially be used for mate location and differentiation by males. For example, chirps of *D. brevicomis* females (Fig. 21.8) are longer, more frequent and contained more tooth strikes than those of *D. frontalis* (Fig. 21.8). They also found that males could distinguish between conspecific and heterospecific females when given the choice of pairs of females within tree material. Acoustic call characteristics could be used by males to decide whether or not to enter a gallery. Once inside the female's gallery, a male may use information from female acoustic signals (or other male signals) to decide whether to remain in the gallery. Differences in female chirp parameters may therefore be reinforced by selection (Pureswaran et al. 2016).

Chirp characteristics and type (e.g., simple or interrupted chirps) appear to play a role in mate acceptance. For instance, male *D. valens* that produce interrupted chirps have greater success of entry into female galleries (Lindeman and Yack 2015). In each of the trials where males performed exclusively simple chirps, including those where the male was eventually accepted, females actively resisted entry of the male (Lindeman and Yack 2015). Sivalinghem (2011) found that only *Ips* females that produced acoustic signals were admitted into the gallery (by the male). With *Hylastes* spp., the number of interrupted chirps increases, while the simple chirps decline prior to mating (Sapkota 2017). Lindeman and Yack (2015) suggest that for *Dendroctonus*, a male's acoustic performance may provide the female with information on his vigor, and that gaps in interrupted chirps are produced by a more complex motor performance than required for simple chirps. This more challenging action may be a reliable indicator of fitness (Byers et al. 2010). In any case, premating signals likely provide information about the physical attributes of the signaler, whether it be female (e.g., *Ips*) or male (e.g., *Dendroctonus*) (Byers et al. 2010; Lindeman and Yack 2015).

Female signals may function to mediate spacing and territoriality between conspecifics. In most bark beetle species, galleries rarely collide with each other, and in some cases, galleries nearing collision show a sudden change in direction (Rudinsky and Michael 1973; Byers 1989, 2007; Davis and Hofstetter 2009). It is possible that tunneling beetles produce vibrations, either from stridulation or friction via chewing transmitted through phloem substrate, that announce their presence to neighboring beetles. Such sound vibrations may only be transmitted within 1 cm of the gallery but this is an effective distance to deter traversing and touching of galleries. Additionally, larvae could use chewing sounds to space themselves while tunneling, thus reducing potential competition or harm to each other. Rudinsky and Michael (1973) showed that the distance of nearby conspecific adult females affects female stridulation patterns. *Dendroctonus brevicomis* females emitted significantly

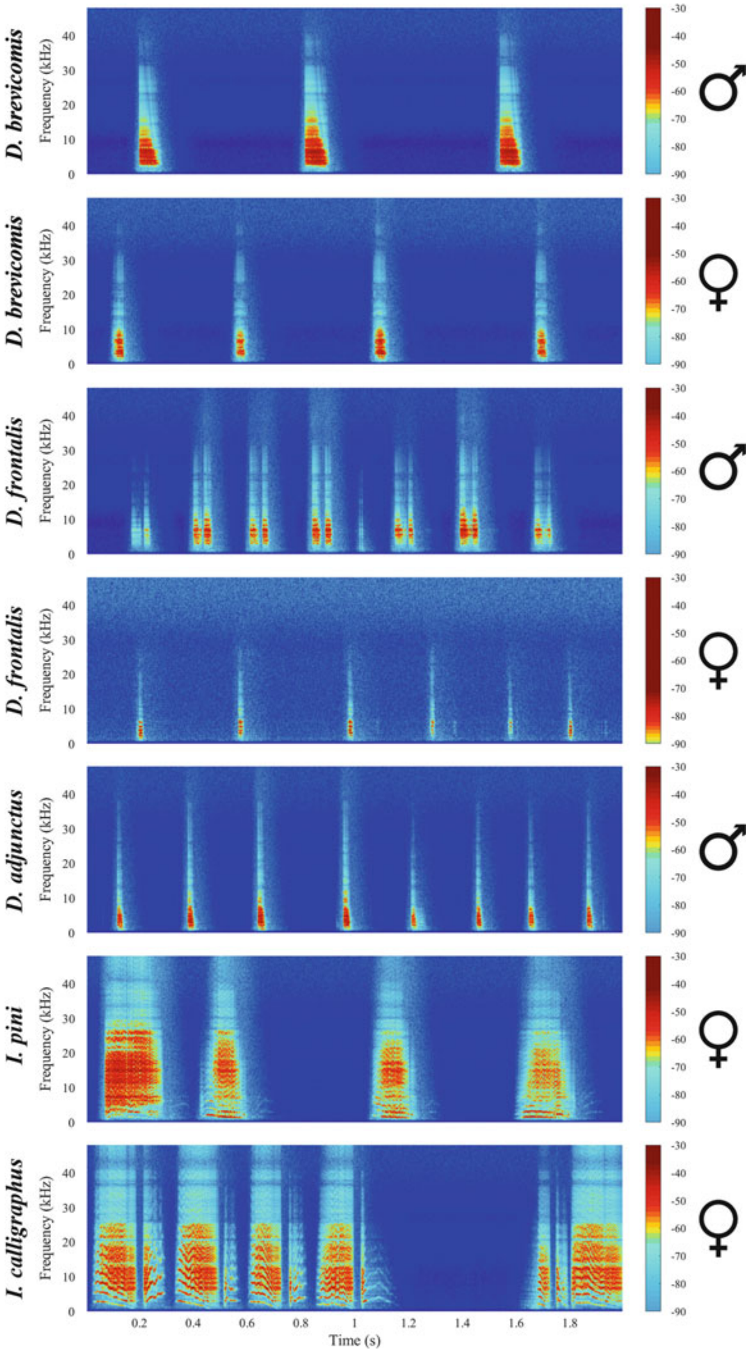

Fig. 21.8 Spectrograms of stridulatory sounds produced by three *Dendroctonus* and two *Ips* species. Color bars in dB. *Dendroctonus* species generate stridulations using an elytro-abdominal stridulatory mechanism; *Ips* species (last two spectrograms), possess a vertex-pronotal organ. No stridulatory sounds have been found in *D. adjunctus* females, and *I. pini* and *I. calligraphus* males. Recordings by C. Bedoya of beetles collected in Flagstaff AZ, USA

more chirps when (two) conspecific females were within 10 cm compared to the number of chirps emitted by solitary females. *Dendroctonus pseudotsugae* females were slightly less sensitive to nearby conspecific females (Rudinsky 1969). Interestingly, neither species changed their vibrational signals when in the presence of heterospecific females at distances of 1–5 cm.

Male-male aggression is common in some bark beetle genera, and males will often produce intense stridulatory vibrations in the presence of other males within their gallery (Rudinsky and Michael 1974; Pureswaran et al. 2016). Studies of *Dendroctonus frontalis* show that males emit a chain of chirps (with a combination of simple and interrupted types) when placed with other males or in response to males entering an already male-occupied gallery. These chirps (sometimes called rivalry chirps) are accompanied by aggressive behavior by both males. A resident male will respond to an intruding male with intense chirping, biting and pushing. When males are confined together in a gallery, long chirp trains occur and intense pushing and biting ensues (Pureswaran et al. 2016). Once out of the gallery, the resident male may continue to chirp and push the other male. Similar behavior has been observed for many *Dendroctonus* species (Rudinsky and Michael 1974) and also between sympatric species of *Dendroctonus* (Pureswaran et al. 2016).

It is unclear whether natural enemies use bark beetle stridulations to locate their prey. Woodpeckers are common predators of many bark beetle species (Schenk and Benjamin 1969; Wegensteiner et al. 2015), and Ramp (1965) showed that the auditory range of the hairy woodpecker had an upper limit reaching 18.5 kHz, which overlaps the frequency of many bark beetle signals (Fig. 21.8). However, attraction of predators to specific beetle stridulations has not been tested. Lewis and Cane (1990) and Sivalinghem (2011) tested whether stridulation by bark beetles would deter or reduce predation events. Lewis and Cane (1990) showed that signaling *Ips calligraphus* females were dropped significantly more often than non-signaling males by a natural beetle predator, *Thanasimus dubius*. Alternatively, Sivalinghem (2011) demonstrated that acoustic signals during predation events were not effective in causing predators to release prey, and the results do not support the "startling function" hypothesis proposed by Lewis and Cane (1990). It is possible that the difference between the studies was due to the differences in beetle size (Lewis and Cane 1990 studied a larger *Ips* beetles), the relatively low sample size in the studies, or that the data may not have been independent as each predator was used more than once in the Lewis and Cane (1990) study. Frazier et al. (1981) investigating predator-prey interactions between *Dendroctonus frontalis* and *T. dubius* found that handling time was significantly higher for male *D. frontalis* than for females. Since male *D. frontalis* produce chirps, sound production may have been a key variable contributing to the longer handling time of males versus females.

Emerging bark beetle progeny or over-wintering adult beetles may use stridulation or other substrate vibrations to coordinate emergence from host trees. No formal studies have looked at the cues or behaviors associated with beetle emergence on trees. Recordings (R.W. Hofstetter, pers. comm.) in the field of overwintering *Ips* and emerging *D. valens* progeny show that beetles may stridulate within the bark prior to emergence.

Mattson and Haack (1987) hypothesized that bark beetles may locate weakened or drought-stressed trees by exploiting the ultrasonic acoustic emissions released by cavitation (Haack et al. 1988). Several studies have shown that when trees experience long periods of dehydration, the water columns in the xylem tissues cavitate, releasing ultrasonic sounds with dominant frequencies ranging from 60 to 300 kHz (Tyree and Dixon 1983; Pena and Grace 1986; Tyree and Sperry 1989). Mattson and Haack (1987) hypothesized that bark- and wood-boring insects could exploit these acoustic cues during host-plant localization. The ultrasonic frequencies of bark beetle signals (Fig. 21.8) implies that bark beetles may be capable of hearing these frequencies, which indirectly supports Mattson and Haack's (1987) hypothesis. Kaiser (2014) tested whether beetles preferred host material that emitted (synthetic) cavitation sounds. He found a greater number of pioneering female *D. ponderosae* chose host material that had high acoustic emissions (produced by ultrasound tactile speakers) versus host material that did not emit ultrasonic sounds. The ability of beetles to identify water-stressed hosts via acoustic cues may be critical to their success at low population densities.

21.5 Vibrations and Movement Within Tree Materials

Many insects use solid-borne vibrations to communicate (Markl 1983; Cocroft et al. 2014; Yack 2016). Bark beetles are capable of producing solid-borne vibrations, but few studies address this specific mode of communication (Fleming et al. 2013; Lindeman 2016). Beetles likely produce two types of vibrations, passive cues produced during chewing of wood or movement within tunnels and active signals produced via stridulation, which were previously referred to as chirps. Vibrations from non-signaling behavior are likely received by predators such as woodpeckers and predatory beetles, as well as neighboring bark beetles and competitors. Sound produced by stridulation, or through friction with the substrate (e.g., mandible-substrate stridulation), by bark beetles conveys messages and is typically stereotyped and conspicuous (Fleming et al. 2013). In most situations with vibrations in wood, the type of vibrations used for communication is almost exclusively restricted to Rayleigh waves (combined longitudinal and transverse waves) or bending waves (Hill 2008). Identifying the type of vibration would provide information on how a given signal would be transmitted (Hill 2008).

We know little about the transmission properties of the phloem in living, dying or dead trees. The phloem's transmission properties are influenced by wood density, deterioration by bacterial, fungal or other boring agents, and moisture content. Phloem and xylem characteristics affect frequencies differently through filtering or by attenuation (Hebets et al. 2008). Bark beetle acoustic behavior and signal properties are likely adapted to accommodate the sound properties of phloem. For example, the broad-band spectra of bark beetle calls may restrict communication to a close range (e.g., Čokl et al. 2004). Close range communication could be an advantage to reduce eavesdropping by predators, limit unintended signals from conspecifics in non-neighboring galleries, and provide a convenient mechanism for limiting overlapping galleries.

Fleming et al. (2013) observed that higher frequency signals (e.g., interrupted chirps during male-male interactions) could be detected by a laser vibrometer several centimeters away from the beetle, but lower amplitude signals were not detected by a laser at distances of 1 cm. Of those chirps that were detected at 1 cm, the vibrations were low amplitude, with a velocity of ~2.7 mm/s. Fleming et al. (2013) notes that the poor signal quality of substrate-borne vibrations compared with airborne sounds could be due to attenuation through the wood but could also be attributable to recording method (i.e., using a laser). Studies (Fleming et al. 2013; Lindeman 2016) show that both air- and substrate-borne vibrations are available to conspecifics at the distances they would normally be interacting, and these close signals could be detected using tympanal ears, near-field sound detectors (e.g., Johnston's organs), or vibration receptors (e.g., subgenual organs) (reviewed in Yack 2004).

We conducted an experiment to evaluate the attenuation effects of the phloem tissue on bark beetle calls (Fig. 21.9). The experiment consisted of recording the sounds produced by individual *Hylastes ater* inside a freshly cut *Pinus radiata* log. To achieve this, an accelerometer was located on the phloem layer of the log at nonlinearly spaced distances from the sound source. Figure 21.9 shows the averaged power spectral densities and energies obtained from five *H. ater* individuals. With distance, the energy decays nonlinearly and the bandwidth shrinks toward the spectral centroid. The phloem tissue acts as a low-pass filter, thus, audible and ultrasonic components above 15 kHz are heavily attenuated regardless of the distance.

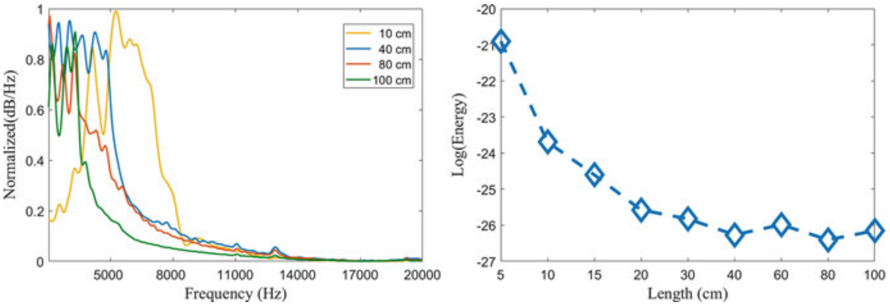

Fig. 21.9 Normalized power spectral density (left) and energy estimated from recordings (right) of *H. ater* calls collected at several distances (10, 40, 80, 100 cm) using an accelerometer located on the phloem tissue of a *P. radiata* log

21.6 Acoustic Technology and Potential Applied Applications

With the exception of olfaction (Borden 1989), the sensory system of bark beetles, along with many other insects, has yet to be leveraged as a management tool. Since bark beetles are more reliant on air- and substrate-borne sounds inside of trees, a place where other sensory modalities are restricted, the application of acoustic-based treatments has the potential to modify behavior in this insulated environment. While the use of vibrations has been largely limited to the detection of wood-infesting insects (Mankin and Moore 2010; Mankin et al. 2011), a few studies have illustrated the efficacy of acoustic treatments that alter behavior.

In one of these studies, Hofstetter et al. (2013) tested the effects of acoustic signals on the tunneling and oviposition of *D. frontalis.* Two sound treatments were administered to a phloem sandwich assay (see Aflitto and Hofstetter 2014): modified *Dendroctonus* beetle calls and an FM radio station. Daily tunneling length was the same in the control (no sound) and radio treatments, averaging 2.1 cm per day. This is contrasted by the modified beetle treatment, which reduced daily tunneling to 0.4 cm per day. The beetle sound treatment also had a strong negative effect on oviposition and only one egg was laid in 15 replicates over seven days compared to 204 eggs from 13 control replicates and 117 eggs from ten radio treatment replicates. Reducing the amount beetles tunnel and oviposit is an important part of the life cycle to target since tunneling contributes to the failure of the tree's vascular system (Bridges et al. 1985; Franceschi et al. 2005).

Automatic acoustic detection and identification of bark beetles is another relevant and understudied area with potential applications (Mankin and Moore 2010; Mankin et al. 2011). Acoustic approaches could be used to study bark beetles without disrupting their natural environment, or to detect them in cases where conventional detection procedures (e.g., visual inspection) are impractical. Additionally, acoustic features could be used as a rapid method of species identification. The wide variety of shapes, sizes, and stridulatory organs makes the call of each bark beetle species unique (Fig. 21.8), and ultimately, a potential taxonomic character. Nonetheless, there is very limited research activity in automatic acoustic bark beetle detection and identification (Lindeman 2016), and no works have addressed the use of these types of methods in the previously mentioned contexts.

Targeting host selection behavior is another aspect of the bark beetle life history where acoustic treatments may be applied. Aflitto et al. (2014) tested whether beetle entry into logs could be affected by acoustic treatments. A choice test assay was used to observe the response of three bark beetle species to four sound treatments: conspecific stress and attraction calls (interrupted calls), longhorn beetle stress call and abiotic tones. The sound treatments affected bark beetle species differently, but the greatest response was found with *D. frontalis* to their stress call, where entry into logs was reduced by 72%. An interesting part of *Dendroctonus* beetle host selection behavior is the use of multimodal communication. For example, *D. pseudotsugae* females colonize a host and quickly begin releasing aggregation pheromones to attract males. Once she identifies a mate via his attraction call, she begins releasing anti-aggregation pheromones to reduce competition for her offspring (Rudinsky et al. 1976). There is potential to hasten the release of these repellent semiochemicals by sonically treating trees with the attraction sounds of male beetles. More research is needed to understand the mechanisms behind how beetles receive acoustic cues and how played-back sounds travel through tree material before it can be used.

There are several challenges to overcome before acoustic treatments are deployed. The current research has tested treatment effects only on portions of trees (e.g., logs, phloem sandwiches). Applying the technology to entire trees will require more testing and inevitably additional modifications. Further, the application of acoustic treatments for stand or landscape-scale outbreaks pose additional challenges such as an efficient way to administer treatments and powering audio devices.

The variety of acoustic tests that have been performed, both under controlled laboratory conditions and in the field, have strongly suggested the efficacy of using sound to affect bark beetle (and other invertebrate) behavior. This research has led to successfully securing patent on a combination of acoustic technologies and associated protocols to disrupt and deter wood-infesting insects in trees and wood products (Hofstetter et al. 2010, Patent No.: US 9480, 248 B2). As an applied technology, the device and protocols are flexible enough to encompass a wide range of insects and other invertebrates but has so far been primarily applied to research upon members of the Scolytinae and Platypodinae tribes (Coleoptera: Curculionidae).

The patent describes the use of biologically relevant sounds derived from the normal signals produced by the insects themselves, modified biologically relevant sounds, synthetically produced complex sounds, and various combinations of all of these acoustic sources, played back into the acoustic substrates occupied by the target organisms (Hofstetter et al. 2013). The working hypothesis is that exposure to the biologically relevant sounds solicits perceptual attention and "neural" readiness that is forced to constantly shift in an unpredictable and exhausting manner since the sounds are presented as a random and quickly shifting playback. Responses to the playback of biologically relevant sounds can be both predictable and dramatic.

Synthetic sounds are generated from a novel network of electronic circuits based upon the mathematics of deterministic chaos (Hofstetter et al. 2013). These circuits produce constantly changing and non-repetitive complex sounds that have very large frequency and amplitude dynamics resulting from a hyper-chaotic state that is autonomous in its behavior. Once set in motion, the circuit network continues to produce novel sounds that appear to be highly disruptive to the target insects since they pass through so many constantly changing auditory behaviors (Hofstetter et al. 2010). Some of these sounds are reminiscent of the insects' own sounds, those of competitive species and potential predatory threats, others that are simply outside of their experiential domain but highly intrusive, and others that appear to mask the normal acoustic communication of the insects themselves. The most important feature of these circuits and their sounds is that they make habituation to the simultaneous presentation of all of the treatment sounds unlikely.

Further development of the patent toward a commercial prototype is ongoing. This research has been directed toward several areas of potential application. These objectives include the effect of sound at reducing bark beetle attacks and colonization on healthy trees, the effects of these sounds on bark beetle behavior within tree tissues, and the potential use of acoustic methods to reduce beetle reproduction and overall populations. Current work is being dedicated to coding both the playback of biologically relevant sounds and the chaotic circuit network into digital form appropriate for implementation as inexpensive and small digital devices that can be used for the protection and treatment of high-value individual trees, orchards and other agricultural contexts, and wood products. Deployment at the scale of large forests remains impractical at this time.

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Part VII
Outreach and Resources

Chapter 22

Shaking It Up in the Classroom: Coupling Biotremology and Active Learning Pedagogy to Promote Authentic Discovery

Carrie L. Hall and Daniel R. Howard

Abstract Active learning methods are instructional techniques that create an environment for increased student engagement in the process of learning. Whether employed in the lecture hall or in the teaching laboratory, these pedagogical methods have been shown to improve content learning, increase process skills, and positively affect psychosocial factors associated with the learning process. Additionally, because active learning environments have been shown to increase academic performance and lead to greater retention among students from under-represented groups, they hold the promise of harnessing untapped talent in STEM fields like biotremology. When implementing active learning pedagogies, educators can align student learning outcomes with Bloom's Taxonomy of Cognitive Domains to integrate both lower-order and/or higher-order cognitive skills development into the learning activities of the course. When teaching STEM courses, especially those seeking to integrate principles in biotremology, implementing research or inquiry-based active learning methods can ensure students have access to an authentic and inclusive research experience; this more accurately represents the process of science and leads to higher-order critical thinking skills. Research-based active learning methods such as project-based learning and course-based undergraduate research experiences (CUREs) are presented in three case studies that include a biotremology dimension. Each case study includes student learning outcomes, a guide for instructional implementation, tips for evaluating student learning, and considerations for pedagogical practicalities and plausible alternatives.

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22.1 Introduction

Lecture-style teaching is the most common pedagogical method used by instructors in institutions of higher education (Brockliss 1996). However, faculty, researchers, and instructors are being challenged to implement empirically validated pedagogical practices in Science, Technology, Engineering, and Mathematics (STEM) classes to improve undergraduate STEM teaching and learning. In the United States, national calls to reform science education (American Association for the Advancement of Science 1989, 2011; Handelsman et al. 2004) have resulted in research that investigates pedagogies that increase student engagement in lecture courses, provide instruction in higher-order cognitive processes, and involve undergraduates in authentic scientific research experiences.

Pedagogies that require students to engage in the learning process while in the classroom are collectively referred to as *active learning methods*. Compared to most traditional lecture formats that emphasize a unilateral exposition style of instruction, active learning methods improve content learning (Freeman et al. 2014) and positively affect psychosocial factors associated with the learning process (Hurtado et al. 2009; Eagan et al. 2013) by facilitating a multilateral learning environment. In a meta-analysis of over 225 studies of student performance in active learning courses compared to lecture-style courses, Freeman et al. (2014) found that, on average, students in active learning courses performed better by six percent (6%) on examinations and concept inventories than students in traditional lecture courses. Additionally, they found that students in lecture courses are 1.5 times more likely to fail than are students in active learning courses (Freeman et al. 2014).

Pedagogical research has revealed three general reasons why active learning has such significant effects on learning, retention of information, and conceptual understanding. First, active learning methods employ cognitive retrieval practice for recalling information from long-term memory. Retrieval practice leads to transferable learning of previously learned information, and the effectiveness of retrieval practice can increase when recall activities are challenging, accompanied by immediate feedback, and are temporally spaced (Karpicke and Blunt 2011; Brown et al. 2014; Roediger and Butler 2011; Felder and Brent 2016). For instance, when teaching a problem-solving method in lecture, rather than outlining the method, marching through the steps, and giving an example, educators who understand the efficacy of active learning might instead teach the method in small steps, following each step with a small activity that requires students to retrieve what was just taught, and then integrate it with previously learned material (another retrieval practice). With this approach, students are more likely to be able to use the method in subsequent tasks and in novel situations (Felder and Brent 2016). For example, in teaching basic concepts in biotremology, such as wave transmission through a substrate, an instructor might integrate new material with previously learned principles of acoustics related to airborne sound transmission, reinforced by an activity that demonstrates the wave property or contrasts the properties of substrate-borne and airborne waves. Second, active learning gives

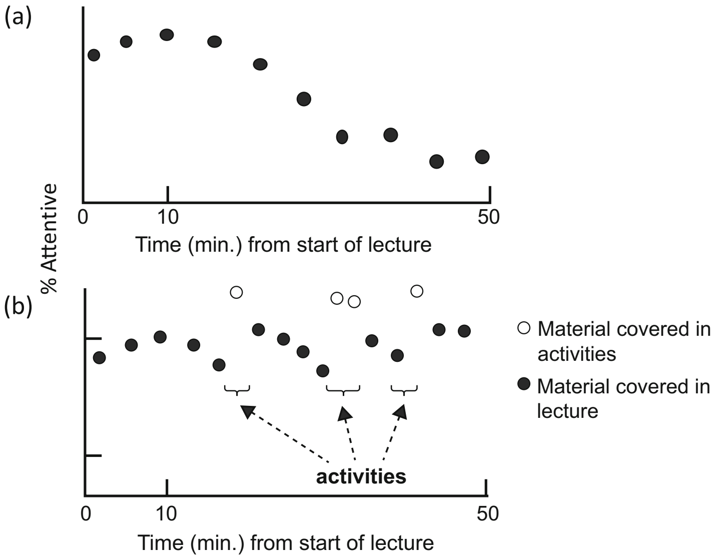

Fig. 22.1 Student attentiveness in lecture across a 50-min lecture class. (**a**) In pure lecture sections, student attentiveness (filled circles) peaks within the first 10 min of class, and decreases consistently for the remainder of the class period. (**b**) When active learning activities are interspersed (open circles), student attentiveness remains consistent (Adapted from Felder and Brent 2016, and used with permission)

working memory time and space to integrate new information into memory storage. Working memory has limited capacity for information; thus, content-heavy lectures overwhelm working memory by presenting new information at a rate faster than working memory can process and integrate. By interrupting lectures with frequent, active tasks that require students to use recently presented information, you increase the chances that new information will be stored in long-term memory (Felder and Brent 2016). Finally, active learning methods increase attentiveness throughout a class period. In a typical 50-min lecture, research has shown that attentiveness decreases past the first 10–15 min of class, and decreases continuously until the end of class (Fig. 22.1). However, when lecture is interspersed with active learning methods every 10–15 min, attentiveness remains high for the duration of the class period (Fig. 22.1). Fortunately, given the wealth of biotremology literature in the past decade, there are numerous examples of attention-grabbing case studies around which to build brief in-class learning activities or demonstrations to increase student engagement and learning.

Scientists across STEM fields are recognizing that, just like one's research should be informed by prior research and published findings, one's teaching approach also should be designed with evidence in mind (Handelsman et al. 2004). In the past decades, empirical studies of active learning methods have been published in both STEM education and disciplinary research journals. With this wealth of peer-reviewed insights into what works in the classroom, educators should no longer rely on anecdote or “gut feeling” alone to guide their pedagogical design (Bradforth et al. 2015). Education research reveals quantitative and qualitative evidence on topics ranging from small course discourse engagement to full-scale large course (>100 students) redesign, and can be used to justify why individualized and institutional-wide teaching reform should be prioritized across STEM academic units.

As the discussion surrounding the need for STEM education reform becomes more wide-spread, the stakeholder community paying attention to these changes grows larger and more diverse, as well. In many instances, administrators are working with faculty and promotion and tenure committees to design reward systems that recognize teaching reform in formal career advancement guidelines (Anderson et al. 2011). Universities are demonstrating valuation of excellence in teaching by devoting human and capital resources for educators to participate in training programs focused on evidence-based teaching approaches (Handelsman et al. 2004; Wood 2009; Anderson et al. 2011). These training programs approach teaching as a scholarly activity, integrating education theory and science of learning concepts, tested methodologies, and assessment methods. Perhaps most importantly for early career educators, these training programs can elucidate methods for translating learning theory into teaching practice (Anderson et al. 2011). If early career educators begin the course design process with the implementation of active learning methods from the outset of their careers, it is likely that their teaching skills will continue to develop during the first critical years of their higher education career; that administrators will appreciate their devotion to excellent teaching, and this effort will be recognized in career advancement; that early career faculty will build a community of scholarship that is focused on teaching; and that their teaching investment will serve as an example to new incoming faculty. Thinking of one’s perspectives on, and professional development in teaching as parallel to that of the forks in the road and refinements that occur in a research trajectory over a career may be useful.

The national reform movements urging science educators to implement active learning strategies that model scientific inquiry do so for two reasons. First, research shows that these methods help students connect abstract ideas to real-world applications (Allen and Tanner 2005). During this process, students gain useful skills that may help advance them through undergraduate education and into graduate training programs or careers in the STEM enterprise. This becomes especially important when considering the particular skill sets associated with the field of biotremology, which are somewhat unique and differ from those used in other biosciences. Second, students gain knowledge that persists beyond the course (Allen and Tanner 2005). Conceptual understanding, integration with applied knowledge, and skills development coalesce in an emergent way to produce an education of enduring worth. This is the critical link between higher education and fundamental research.

22.2 Active Learning for Engaging All Students

Participating in the scientific process and producing new knowledge are the fundamental goals of science. New ideas, unconventional approaches, novel collaborations, and interdisciplinary thinking are necessary for pushing the boundaries of science to make new discoveries and overcome uncharted challenges. Making strides toward these goals requires broad and diverse thinking. Research has shown that one of the most effective ways to stymie discovery and creativity is to rely solely on members of one gender, one race or ethnic group, one background, and one orientation to envision and create pathways to new knowledge and innovation. Herein lies the value of diversity and inclusion in the pursuit of scientific knowledge. Bringing together, and including equally, the voices of diverse groups of people, from diverse backgrounds and experiences, reinforces a commitment to social justice, benefits society, and broadens the talent pool that engages in and ultimately advances science (Intemann 2009).

Active learning methods increase learning and engagement for students from underrepresented minority groups, and for those from diverse and/or non-traditional backgrounds and experiences (Gándara and Maxwell-Jolly 1999; Summers and Hrabowski III 2006; Dirks and Cunningham 2006; Rath et al. 2007; Hurtado et al. 2009; Hrabowski 2011; Haak et al. 2011; Eagan et al. 2013; Freeman et al. 2014). For decades, U.S. agencies have been calling for an increase in the number of underrepresented minority students who complete degrees in STEM (see Haak et al. 2011) because of the high attrition rate of students from these under-served groups. In fact, underrepresented minority groups made up 28.5% of the U.S. population as of 2010, but only 9.1% of Americans with degrees in higher education (American Association for the Advancement of Science 2011). This loss of potential STEM talent has been attributed to many deficit factors (e.g., lack of preparation, including underperforming high schools that lag behind in STEM education), and colleges and universities have responded by creating programs that recruit underrepresented students and provide supplementary instruction, mentoring, social support, and financial aid, as well as additional instruction in challenging introductory-level courses and undergraduate research opportunities. Indeed, one of the most effective methods for increasing the participation, learning, and performance of students from underrepresented groups is through authentic research experiences and other active learning methods that can be applied in large lecture courses. Thus far, research that is examining these active learning and inclusive teaching methods is finding that no other method more effectively works to close performance gaps and retain underrepresented STEM talent more than active learning methods (National Academies of Sciences Engineering and Medicine 2016). Attracting and retaining students that carry with them diverse perspectives can advance discovery in biotremology, and should be a priority reflected in the learning environments that we create.

22.3 Implementing Active Learning Methods

Disciplinary-based education research (DBER), and more specifically, biology education research (BER), has shown that specific student-centered instructional strategies can improve students' learning and understanding. In lecture sections, active learning methods can be implemented to gather the attention of students, engage them in class discussions, incorporate problem solving, and synthesize content knowledge and apply learning to course content. For example, one strategy, *interactive lecture demonstrations*, requires students to predict the outcome of a demonstration performed during lecture by the educator. Students individually predict the result of a demonstration described by the educator, discuss their predictions with their peers, watch the demonstration, and then compare their predictions with the real outcome of the activity. This strategy helps improve conceptual understanding (Sokoloff and Thornton 1997). Other strategies that are simple to implement include asking open-ended questions in lecture and having students discuss their thinking with a peer or peer group; assigning student groups a set of questions or problems in class that require them to make predictions, or pose a way to test their ideas; using 2-min writing prompts at the beginning of lecture to probe students' understanding of previously presented material, or at the end of lecture to summarize and review material presented in class; and implementing collaborative learning activities. Felder and Brent (2016) and Handelsman et al. (2007) offer excellent guides to incorporating active learning strategies into undergraduate courses, as well as designing courses using empirically validated pedagogical strategies.

Active learning methods applied in laboratory sections or as independent research experiences can engage students in science-as-process learning. Methods that engage students in conceptual understanding (content), as well as those that develop specific scientific competencies (process), help students gain the comprehensive knowledge and skills to *be* scientists. And, while research posits that involvement in authentic research is "the purest form of teaching" (National Research Council 2003), the practical implications for involving all students in a research experience can be daunting. Since it is often untenable to provide all students with research apprenticeships in faculty members' labs, one way to achieve this teaching best-practice is to incorporate authentic research into lab courses (Auchincloss et al. 2014; Handelsman et al. 2004; Brownell et al. 2015). Active learning methods such as project-based learning and course-based undergraduate research experiences (CUREs), described below, have been designed for this purpose.

22.4 The Large-Enrollment Lecture Course Challenge

Despite the wealth of research showing significant learning gains and increases in student and educator satisfaction in active learning courses, many of these active learning methods that provide for the most learning gains (Edgerton 2001; Allen and Tanner 2005; Smith et al. 2005) were designed in small-class settings. Implementing these active learning methods into large-enrollment courses, such as those courses taught at the introductory level, is challenging (Brownell et al. 2015). But, given that these large-course formats are perpetually ingrained into our systems of higher education (Edgerton 2001), and although neither the students (Seymour and Hewitt 1997) nor the educators (Carbone and Greenberg 1998) thrive in this environment, educators should strive to deliver the most learning-rich experience possible for the students with whom they interact in these courses.

In their 2005 work, Allen and Tanner reviewed seven strategies for infusing active learning into the lecture portion of large-enrollment classes (six of these strategies are pertinent to biology-specific courses, while one is designed for non-majors courses). And, while the focus of their review was on biology courses, many of these active learning methods can be applied to chemistry, physics, engineering, and mathematics courses, as well (Allen and Tanner 2005). These strategies are not designed to replicate the scientific process, but are effective ways to implement active thinking and high-order cognitive skills required for scientific inquiry. In the context of teaching biotremology, or more broadly, animal communication, animal behavior, behavioral ecology, conservation behavior, etc., these methods can be applied as intended to supplement (or replace) pure lecture-based courses. Further, educators who teach biotremology in some context can test the application of these methods to understand the benefits of active learning for their students (Freeman et al. 2014). Educators can incorporate these six biology-applicable lecture section methods as appropriate for their course (for a full review, see Allen and Tanner 2005):

1. "Bookending" lectures with synthetic discussion-probing questions: Posing thought-provoking questions at particular intervals during lecture requires students to synthesize concepts and think more deeply. This is perhaps the easiest method to integrate when first attempting to depart from pure lecture (Allen and Tanner 2005). Educators can pose these questions as either open discussion, or as short writing exercises that take no more than a few minutes at the beginning and end of the course period. Complex, open-ended questions that push intellectual growth are the most effective for achieving desired learning outcomes (Freeman 1994; Felder 1997).
2. Using student response systems: Student response systems (clickers) can provide instantaneous feedback to discussion points, course content, or thought-provoking topics. The systems can be used for survey, practice, review, or formative assessment of course material. Concepts surveyed using these response systems need not be didactic lower-order thinking tasks, but can delve into the more complex and concept-level topics requiring deeper cognitive engagement.

Additionally, clicker use need not be limited to lecture sections. Sevian and Robinson (2011) found that student learning increased with use of clickers in multiple contexts, including laboratory sections. Increasingly, student response system apps are being designed for smart phones (see www.polleverywhere.com and the REEF polling option for www.iclicker.com), co-opting the ubiquitous devices for tools to diagnose student learning and engage them in the process of learning. Wood (2004) and Knight and Wood (2005) provide good studies of the use and implementation of these systems, and Caldwell (2007) provides an excellent review.

3. Student presentations and projects: Educators may opt to devote the entire class meeting times to student presentations and projects. While it is common in upper division undergraduate courses to assign summative end-of-course presentations to students or student groups, this method can be implemented across the term of the course to increase student ownership of content preparation and mastery. In this type of course, the educator's role becomes one of behind-the-scenes support for planning and providing feedback to student presenters. Eisen (1998) provides a foundation for this model, and an ambitious approach for implementing this strategy in second-year level cell biology course.
4. Incorporating learning-cycle models: As course instruction moves more toward active student-centered learning, rather than the comfortably passive lecture style to which most students have grown accustomed, students may express concern about their ability to direct their own learning. By incorporating learning-cycle instructional models, students' concerns can be allied without compromising learning goals (Ebert-May et al. 1997). One of the most commonly used learning cycle approaches, and one that the authors have employed with great success in several different courses, is the "5E" Learning Cycle. This constructivist learning model was originally proposed for elementary science programs in the 1960s (Atkin and Karplus 1962), and then well studied and applied to higher education in the following three decades. The appeal in higher education contexts is perhaps that the five phases are consistent with cognitive theories on how learning occurs. The five phases – Engage, Explore, Explain, Elaborate, and Evaluate – capture the interest of students, guide them through conceptual and skills-based learning tasks, expand the application of the key topics, and challenge students to apply the learning to new contexts, or understand the implications of the new knowledge in new real-world applications. Application of this model is fairly straightforward. For a thorough review of the application to large lecture courses, please see Ebert-May et al. (1997) and Llewellyn (2005). This model is particularly well suited for teaching core principles in biotremology.
5. Peer-Led Team Learning (PLTL): Peer-Led Team Learning is most often employed in foundational chemistry courses (Gosser and Roth 1998), but has been applied in introductory and upper division biology courses, as well. The premise of this model is cooperative group learning framed around enlisting the assistance of expert student peers (those students who have previously taken the course and performed well). Peer leaders work with cooperative learning groups to facilitate supplemental learning sessions for students who need additional

engagement with course content or skills development (Allen and White 2001), thereby extended learning opportunities outside of the classroom.

6. Using case studies: The case-study method has been widely used in medical and business education, and has celebrated success in post-secondary science education since the early 2000s. This highly adaptable method involves problem-based learning that promotes the development of analytical skills (Herreid et al. 2011). Course content is presented in the form of a narrative, and is accompanied by a series of questions, problems, or intriguing clues that students must think through to arrive at a logical explanation or conclusion. One of the most compelling reasons why students learn content through this approach is the connection between course content and real-world issues and applications (Bonney 2015). Educators report that case studies promote critical thinking, learning, and student participation, especially in terms of considering alternative perspectives, and integrating core concepts into applied problem solving (Yadav et al. 2007). The National Center for Case Study Teaching in Science (NCCSTS; http://sciencecases.lib.buffalo.edu/cs/) at the University of Buffalo hosts a collection of educator-authored peer-reviewed cases that span STEM topics that can be implemented in courses at the introductory level or in upper division courses. To assist in integrating case studies into a teaching repertoire, the NCCSTS offers a five-day summer workshop and a two-day fall conference to train faculty in the case method of teaching science. While the NCCSTS website does not currently list any biotremology-related case studies (as of December 2017), there are mechanisms for contributors to add new materials as these become available.

22.5 A Framework for Implementation of Active Learning Pedagogies

Regardless of whether active learning methods are applied in lecture sections or as laboratory investigations, instructors who decide to implement active learning need to make informed decisions regarding which methods to apply, and in what context these methods may be appropriate (Eddy et al. 2013; Bangera and Brownell 2014). While the application of particular active learning strategies in particular contexts is an emerging area of research, the following is a suggested framework for active learning application decision-making for educators (Fig. 22.2). This framework, with some modification, was first presented at the First International Symposium on Biotremology at the Fondazione Edmund Mach in San Michele all'Adige, Italy, in 2016. This framework is based on pertinent literature in the field of biology education research, and the research and applied work of the authors of this chapter.

When deciding which active learning strategies are appropriate for a given course, educators should first determine the experience level of the student population (here referring to undergraduate/post-secondary students). Novice students in introductory courses may require a balance of lower-order cognitive skills

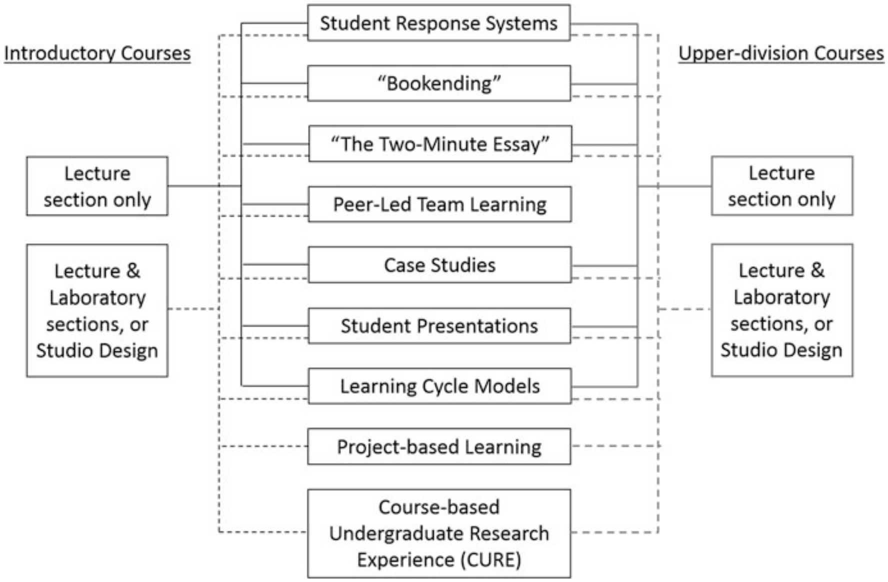

Fig. 22.2 Decision-making framework for implementing active learning. Educators may find it surprising that most active learning methods can be successfully implemented in both lecture and laboratory sections of both introductory and upper division courses. And, while literature examining the application of PLTL focuses primarily on introductory courses, some educators may find upper division PLTL an appropriate strategy. One distinction worth noting is that research-based methods (project-based learning and CUREs) are most easily implemented into laboratory sections, rather than lecture sections. Black solid and dashed lines indicate applications in introductory-level courses, while gray solid and dashed lines indicate applications in upper division courses (Figure credit: the authors)

(LOCS) and higher-order cognitive skills (HOCS) development, compared to more experienced, upper division learners who thrive in courses requiring analysis and evaluative thinking skills, along with creation of new knowledge as they engage in the scientific process. In teaching concepts in biotremology, this may be especially important given that students may have limited prior knowledge on the topic. Next, educators should determine whether the course will be structured as a lecture-only course, or whether a laboratory section will be developed. While it is not impossible, educators can more easily incorporate authentic research experiences into laboratory sections than into lecture-only courses.

Educators should also decide whether the learning outcomes for the course align with lower-order cognitive skills (LOCS), higher-order cognitive skills (HOCS) (see Zoller 2003), or a combination of each. Within biology, undergraduate courses, particularly at the introductory level, have been criticized for overemphasizing memorization of facts (American Association for the Advancement of Science 1989; Bransford et al. 1999; Wood 2009) at the expenses of teaching students how to engage in the process of science, and in critical thinking and problem solving.

To reverse this trend, educators can consider the cognitive level of knowledge students should achieve in a course, and can adopt active learning methods and develop assessment tools that span the hierarchy of cognitive domains described by the Bloom's Taxonomy of Cognitive Domains, hereafter referred to as "Bloom's." Bloom's is a well-vetted and broadly accepted tool for categorizing types of thinking into six different levels. In the original construct, these six orders, from the lowest order to the highest were knowledge, comprehension, application, analysis, synthesis, and evaluation (Bloom 1956). This tool was created to facilitate assessment of student learning levels, and to create a common language for assessment experts, and represents a continuum of cognitive tasks from simple and concrete, to complex and abstract (Bloom 1956). A revised version of Bloom's (Krathwohl 2002) converts these categories into active verbs – remember, understand, apply, analyze, evaluate, and create – and provides further subcategories for each of the constructs (Crowe et al. 2008). In general terms, the first two domain levels (remember and understand) align with LOCS, while the top three domains (analyze, evaluate, and create) require HOCS. The third level can be utilized as a transition between LOCS and HOCS.

Active learning strategies can be implemented to support students' learning in each of these cognitive domains, from lower-order to higher-order, and across Bloom's taxonomy. Typically, educators can implement most any active learning method when content requires students to recall facts and basic concepts, explain ideas, and apply information in new situations by demonstrating and interpreting knowledge in an analytical way (Bloom's taxonomy levels one through three). However, should educators decide that higher-order cognitive skill development is a goal of the course, and that students should synthesize, design, apply, analyze, and create original scientific work (Bloom's taxonomy levels four through six), then active learning strategies that provide authentic research experiences are appropriate.

22.6 Research-Based Active Learning Pedagogies

The opportunity for undergraduate students to participate in authentic research has traditionally occurred on a one-on-one basis working in a faculty research lab on an independent project. And, even though there is ample evidence supporting the benefits of engagement in any research experience, this one-on-one model necessarily limits opportunity and access for most students for logistical reasons. As a response to this challenge, national calls for reform have recommended integrating research experiences into the undergraduate curriculum (Kenney 1998; National Research Council 2003; American Association for the Advancement of Science 2011; President's Council of Advisors on Science and Technology 2012; Bangera and Brownell 2014). By implementing this course-based pedagogical change, all students are putatively able to participate in authentic research as an integrated part of their undergraduate degree program, and faculty are alleviated from the challenge of placing, supervising, and equipping multiple, and perhaps disjunct, independent projects at one time.

Two well-vetted methods for implementing authentic research experiences into laboratory courses at the undergraduate level are project-based learning (PBL) and course-based research, also known as course-based undergraduate research experiences (CUREs). Each offers the same cognitive and skills-development benefits, but differs in design and implementation. These methods have shown learning gains at the introductory and upper division course level, and can be designed thematically to meet the learning outcome goals of any course (Hall 2016), especially those focused on or including principles from biotremology.

22.6.1 Project-Based Learning

Project-based learning is a pedagogical method developed from constructivism theory, with which students learn content by actively participating in the learning process, particularly with respect to critical thinking and problem solving (Doppelt 2003; Frank et al. 2003; Richardson 2003). Students who experience project-based learning grapple with real-world problems pertinent to the course topic. Studies of project-based learning courses have shown that, when assessed appropriately, students gain knowledge that perseveres beyond the course (Doppelt 2003; Gulbahar and Tinmaz 2006).

Project-based learning (not to be confused with problem-based learning, or PBL), frequently used in engineering education, begins with a content-related assignment, frequently a research project, that leads to a final product, typically a written and/or oral report summarizing the process and revealing the findings of the research. The end product is usually the focus of the assignment, but since the project relates to the content of the course, content learning is developed during the research process. Like authentic research, projects are typically accomplished collaboratively (2–4 students per project), and projects emulate challenges that researchers would undertake in their labs. Students must formulate solutions, execute the experiment, and continually reevaluate their approach in the face of emerging data. In this context, students define their own "project." Depending on the preferences of the educator, student groups can be granted various levels of autonomy for their project (de Graaff and Kolmos 2003; Prince and Felder 2006). When well-orchestrated by the course instructor, this method can yield intended authentic research that is knowledge-generating and publishable. The case studies presented at the end of this chapter provide examples of project-based learning that met this criterion.

22.6.2 Course-Based Undergraduate Research Experiences (CUREs)

Course-based undergraduate research experiences are designed similarly to project-based learning and independent research experiences in that students explore scientific research questions that have no known answer. The data and knowledge gained by the students who engage in this process are, therefore, of interest to the broader scientific community (Auchincloss et al. 2014; Brownell and Kloser 2015). This new knowledge generation through engagement in the scientific process is the most authentic way students can participate in science, and thus this model also benefits the faculty member's research agenda (Kloser et al. 2011; Brownell and Kloser 2015). Additionally, CUREs are typically designed such that the students work collaboratively, much as a lab group of researchers would function.

Two types of CUREs have been developed (Shortlidge et al. 2015). The first model is that in which individual faculty members develop their own research agenda through integrating their line of investigation into the class(es) they teach. The students enrolled in the class directly contribute to the data collection, analysis, and synthesis of their findings during the semester, and in some cases, also contribute to the initial development of predictions and experimental design. Since the faculty member is pursuing their established research program, students typically do not contribute to the development of the research question or hypothesis development *per se*, though this does not have to be the case. The second type of CURE is that which contributes to a national network model. The curriculum for these network CUREs has been pre-developed and provides implementation support (e.g., training for educators and community expertise). Examples of these national network CUREs include the Small World Initiative (http://www.smallworldinitiative.org) and the Howard Hughes Medical Institute Science Education Alliances-PHAGES project (https://www.hhmi.org/developing-scientists/science-education-alliance).

For students, benefits of the CURE model include increased interest in science and research (Lopatto et al. 2008; Harrison et al. 2011; Bascome-Slack et al. 2012; Brownell et al. 2012; Jordan et al. 2014; Rhode Ward et al. 2014), improved science process skills (Kloser et al. 2013; Sanders and Hirsch 2014; Brownell et al. 2015), enhanced conceptual understanding of content (Rhode Ward et al. 2014; Shaffer et al. 2014), and increased self-confidence in conducting science (Bascome-Slack et al. 2012; Brownell et al. 2012). There is also some evidence that students' professional identity (Gilardi and Lozza 2009), self-motivation, and self-directed learning also are positively impacted (Pascarella and Terenzini 2005; Hu et al. 2008).

This model also benefits faculty in a number of ways. In a study by Shortlidge et al. (2015), faculty who implemented CUREs identified twelve benefits, and all faculty who participated in the study identified more than one of these twelve (Shortlidge et al. 2015). Five benefits were identified by 50% or more of the participating faculty and included the following: (1) CUREs are a way for faculty to connect teaching and research (76%), (2) faculty enjoy teaching CUREs (74%), (3) CUREs can contribute positively to promotion and/or tenure (68%), (4) CUREs can result in publications (basic scientific and/or science education research) (61%), and (5) students collect data in a CURE that benefit faculty research programs (61%).

Educators who are considering adopting a CURE model to improve their pedagogical practice, increase their research productivity, and increase student learning and involvement in authentic research should take into account the following considerations when developing their CURE (see Shortlidge et al. 2015). First, as all educators know, there is a time commitment when developing a course, and in involving oneself in teaching the laboratory sections. The same is true when transforming a traditional lecture and lab course into a CURE. Educators may need to step into the CURE lab more frequently than in traditional scripted lab sections that may have been previously taught by graduate student teaching assistants. Second, the logistics of CURE teaching, such as ordering supplies, arranging transportation (for field-based experiments), and allowing additional laboratory time for students to complete experiments, can be less scripted and more variable than with the traditional weekly labs that have predefined and unvarying schedules. Third, the financial cost of CURE labs can be greater than that of non-CURE lab sections. However, educators have noted that many of the supplies and equipment needed for the CURE research are typically part of the research laboratory of the faculty member. And, if the faculty member is willing to allow students to use their laboratory infrastructure – an even further extension of authentically involving undergraduates in research – then the cost consideration becomes lessened. Finally, CUREs that most successfully provide students with authentic research experiences, and contribute to the faculty member's research program, should run smoothly, with as little technical frustration as possible for students. In light of this consideration, Kloser et al. (2011) offer six recommendations when developing CUREs (Box 22.1). These suggestions range from lowering barriers to skill acquisition by making sure that technical tasks are appropriate for the students, to establishing due dates and making sure data are checked for accuracy by another student group, or by an expert researcher.

Box 22.1 Suggestions for Creating a Research-based Course Using a Faculty Research Program. (Adapted from Kloser et al. 2011, and used with permission)

1. Lower the barrier of technical expertise for students to collect data
    - Data collection should require minimal prior knowledge or technical skill.
    - Technically difficult procedures that cannot be mastered quickly by students can be executed by staff members, but demonstrated to students so that they understand the process behind the data collection.

(continued)

Box 22.1 (continued)

2. Establish checks and balances for student-collected data
   - Student-collected data should require either minimal expertise or be repeated by a second lab group as a check for data collection accuracy.
3. A diverse, but constrained set of variables for developing hypotheses
   - The given model system should have enough variables to allow for a variety of student questions.
   - The number of variables available to students should be constrained to limit the work of the instructional team and increase the scope of peer discussions that can occur.
4. Central database accessible to all students
   - A central database allows students to access data from other lab groups, and even from previous years.
   - The ever-increasing size of the database provides students with realistic sample sizes that could not be obtained if students only used data generated during the course.
5. Course assessments reflect authentic scientific communication.
   - The final paper (if part of the assessment plan for the course) should follow the format of an influential journal in the given field, and students should receive multiple iterations of feedback from peers and instructors.
   - Students should present their findings in a conference-like presentation format at the end of the course.
6. Research-specific expertise of faculty member.
   - The instructors should leverage their expertise with both general biological concepts and the specific research system to foster high-level discussions and provide effective feedback to students.

22.7 Active Learning in Biotremology

Biotremology, and other related courses such as animal behavior, animal communication, research methods in animal behavior, and others, are uniquely suited for teaching in an active learning framework. By transforming an undergraduate course into an active learning, research-based course, undergraduate students can learn course-related content while experiencing authentic research that contributes knowledge to the field. Following are three case studies of undergraduate courses that include both content and/or process skills related to biotremology. The content and process skills are integrated into the student learning outcomes of the course. Each is unique in the scope of training or scale of questions in which students engaged, but provides a basic idea of how the principles of substrate-borne communication can be woven into an active-learning environment.

22.8 Case Studies of Teaching Biotremology

22.8.1 Case Study #1: Singing Through the Ground; Exploring Animal Seismic Communication by Measuring and Characterizing Substrate-Borne Signals in New Zealand Giant Weta

22.8.1.1 Course Description and Student Demographics

Course-based research experiences that integrate learning activities emphasizing general principles in biotremology and vibrometry need not be limited to traditional classroom settings. Courses that integrate a robust field study dimension, for example, may provide students with easy access to specimens that could be useful in either instructor-led demonstrations, student-developed research projects, or service learning (Robinette and Noblet 2009). These types of instructional experiences, perhaps hosted residentially at an ecological research station or facilitated during day visits to local nature reserves or outdoor classrooms, often create a teaching–learning environment that leads to much deeper student (and oftentimes educator) engagement with the process of inquiry and knowledge building (Easton and Gilburn 2012; Fägerstam and Blom 2013). In this example, we describe how principles in biotremology were integrated into a study-abroad field course taught in New Zealand, where students conducted course-based undergraduate research (using a CURE model) studying seismic signaling in endemic giant weta (Deinacridae). The upper division undergraduate course offered through Augustana University (SD) and entitled *Explorations in Aotearoa: the biogeography and culture of New Zealand*, was offered each January from 2010 to 2015, with 12–14 life science students traveling with the authors to field sites across New Zealand. The course concluded with students conducting ecological, environmental, or ethological research on Matiu/Somes Island Scientific and Historic Reserve, North Island New Zealand, a 25 ha biosecure island in Wellington Harbor managed by the New Zealand Department of Conservation and owned by the local Te Atiawa Maori tribe (Howard 2016; Howard et al. 2018).

22.8.1.2 Student Learning Outcomes

In addition to providing students enrolled in this course a conceptual framework in New Zealand biogeography (see Gibbs 2006) and indigenous Maori culture (see Berkes 2009), the primary emphasis of the CURE learning activities centered on achieving student learning outcomes (SLOs) associated with principles (*content*) in animal communication and technical (*process*) skills in biotremology. Establishing clear and relevant SLOs that can be measured by appropriate evaluative instruments is considered a critical first step in designing effective learning experiences in any instructional setting or area of study (Felder and Brent 2016). *Content* SLOs for this course included understanding the following: 1) how animals extract information from the environment consistent with the ideas inherent in information theory (Shannon and Weaver 1949), 2) the distinction between the form and function of signals versus cues and how this relates to the sender–receiver dyad (Seyfarth and Cheney 2003; Bradbury and Vehrencamp 2011), and 3) the role of biotic and abiotic elements of the transmission medium in driving the ecology of signaling and the evolution of animal signals (Morton 1975; Wiley and Richards 1978; Krause 1993). Students were encouraged, via a primary literature immersion pedagogical approach, to scaffold (Hogan and Pressley 1997) existing knowledge framed around their understanding of how animals use airborne sound in communication to similar principles associated with substrate-borne signaling, with a focus on mechanistic contrasts in producing and perceiving substrate-borne waves (Markl 1983; Hill 2009) and in the ubiquity of utilization among certain animal groups (Cocroft and Rodriguez 2005; Hill 2008). These general concepts were then assigned to more specific ecological and evolutionary contexts by exploring local examples from the endemic New Zealand fauna. *Process* SLOs in the course focused on three areas of student proficiency: 1) effectively using the scientific method, 2) designing valid experiments in biotremology, and 3) communicating their research results.

To achieve the first process learning objective, students working in small teams gained hands-on experience in utilizing the scientific method by first observing giant weta behavior in the field and then forming an investigative question, creating a testable hypothesis, and identifying the logical predictions of the hypothesis. Students then turned their observations into new knowledge by designing experiments to test their hypotheses using standard substrate-borne vibration test measurement and playback methods, along with acoustic analytical techniques. Students were trained to measure substrate-borne vibration using laser Doppler vibrometry (LDV) and accelerometers; to conduct calibrated playbacks using digital audio workstation software providing an output signal to a portable amplifier-electromagnetic shaker preparation; and to analyze the temporal, spectral, and amplitude statistics of recorded substrate-borne vibration using sound analysis software and techniques summarized by Elias and Mason (2014). Finally, students communicated their findings and engaged in the process of peer review by presenting research results via oral presentations and submitting written reports to peer members for review prior to final submission. All content and process learning activities were conducted at field station facilities at the Matiu/Somes Island study site.

22.8.1.3 Instructional Implementation

Cook Strait giant weta (*Deinacrida rugosa*) are found in moderate abundance at the study site, and represent one of the few lowland ground-dwelling species of this endemic genus of Orthopteran insect (Field 2001). Due to its endangered status and cultural importance to the Maori, a New Zealand Department of Conservation-issued permit (WE-32885-RES to DRH) was required to conduct research with *D. rugosa*, and completed permit application materials were submitted well in advance of the scheduled course dates to ensure that the appropriate permissions were obtained in a timely fashion. We *strongly* recommend that details regarding permissions procurement be investigated and settled during the very early stages of course design when contemplating a biotremology project with students, especially when studying at foreign sites and/or when working with insects of conservation interest. Here, *D. rugosa* was identified as a tractable biotremology research subject for the course due to the authors' preliminary data that identified tremulatory behavior in the species, their relative ease of collection, and stakeholder interest in their communication behavior. Student teams conducting research on substrate-borne signaling in *D. rugosa* opportunistically collected animals at night in appropriate shrub and grassland habitats across the island study site, documented their collection locales using GPS, and placed specimens separately in temporary holding containers with food and water provided *ad libitum* until trials were completed. At the termination of experiments, all animals were released at the original capture location.

Student investigations centered on identifying the social context of seismic signaling in *D. rugosa*, characterizing the spectral and temporal properties of signals, and describing how animals responded to signal playback. To address these questions, the appropriate vibrometry test measurement gear was transported to the field site, including a Polytec PDV-100 LDV (Polytec GmbH, Waldbronn, Germany), microminiature accelerometers (Vibrametrics Model 9002A, 100 mV/g) with battery-operated constant current power supplies (P5000-110; Mistras Group Ltd., Princeton Junction, NJ), Marantz PMD 661 (Marantz America, LLC., Mahwah, N.J.), Tascam DR100 MKII (TEAC Corporation, Montebello, CA) digital audio recorders, and a 20 N electromagnetic shaker (TMS 2004E, The Modal Shop, Cincinnati, OH) driven by a battery-powered 15 W mini-amplifier (DTA-1, Dayton Audio, Springboro, OH) connected to a PC laptop (Lenovo X220, Morrisville, NC), with playback of signals occurring in Adobe Audition ver. 3.0 software (Adobe Systems, San Jose, CA). All trials were captured with standard speed high-definition video using a tripod-mounted Sony CX440 Handycam (Sony Corporation, Tokyo, Japan) for behavioral coding. Students involved in conducting research in biotremology received training onsite in recording substrate-borne vibration using both the LDV and accelerometers, in synthesizing and conditioning signals for playback, in calibrating and monitoring playback signals for experiments, in classic acoustic analysis techniques using either Audacity® or Adobe Audition software, and in relevant biostatistics using JMP (ver. 75; SAS Institute Inc., Cary, NC) or SPSS (ver. 21; IBM Corporation, Armonk, NY) statistical software. Students were involved in designing and constructing appropriate behavioral arenas in which to measure and play back substrate-borne signals. The custom 1.0 m^2 arenas were constructed from 3.75-cm-thick painting canvases enclosed around the perimeter with an attached 15-cm-high plastic strip to prohibit animal escape from the arena, with four 15-cm legs attached at the corners to allow space under the arena for the shaker placement. The taut canvas substrate, similar to that used on a smaller scale by Girard et al. (2011) in studies of Australian peacock spiders, effectively transmitted substrate-borne vibrations produced by both the giant weta and reproduced by the electromagnetic shaker, with low spectral and amplitude distortion. Given the nocturnal behavior of *D. rugosa*, all experiments took place between the hours of 2200 and 0400 under red illumination produced by battery-operated headlamps (Princeton Tec Remix, Trenton, NJ) suspended above the arena and worn by students conducting the experiments.

22.8.1.4 Evaluating Student Learning

Student-collected data showed that *D. rugosa* males produced a low-frequency seismic signal via dorso-ventro tremulation (Fig. 22.3), and that these signals were typically produced in the context of intrasexual contests between males that were courting a female. Of importance to note here is that the term *seismic* refers explicitly to substrate-borne vibration transmitted through the soil. Adhering to the strict technical definition generally yields “teachable moments” in biotremology, as students tend to use the term interchangeably (and inaccurately) in describing other forms of substrate-borne vibrational signals. These data from students have been presented at scientific meetings, described in an education paper focused on the logistics of teaching in a study abroad setting (Howard 2016), and are in preparation by student co-authors for publication in a technical paper on animal communication via seismic signaling. Achievement of content SLOs were evaluated using formative assessment techniques (Angelo and Cross 1993) during small group discussion where students would dissect and argue the predictions of animal communication theory in the context of educator-presented problems. Summative evaluation (Angelo and Cross 1993) of content SLOs occurred via instructor and peer assessment of background information presented during the introduction and discussion components of student oral presentations and written reports on their biotremology research projects. These data were obtained via a grading rubric that asked particular questions about how students integrated key content concepts into the presentation and writing product (see Felder and Brent 2016 on best practices for composing grading rubrics). Formative evaluation of process SLOs, which measured how adept and reliable students were with using the techniques utilized in biotremology research, occurred during training sessions via structured practice exercises with sample WAV files. Students achieved “go/no go” proficiency evaluation of each technique, and progressed at their own rate until technically accomplished in the requisite technique. Summative evaluation of process SLOs occurred via instructor and peer assessment of the methodological description of

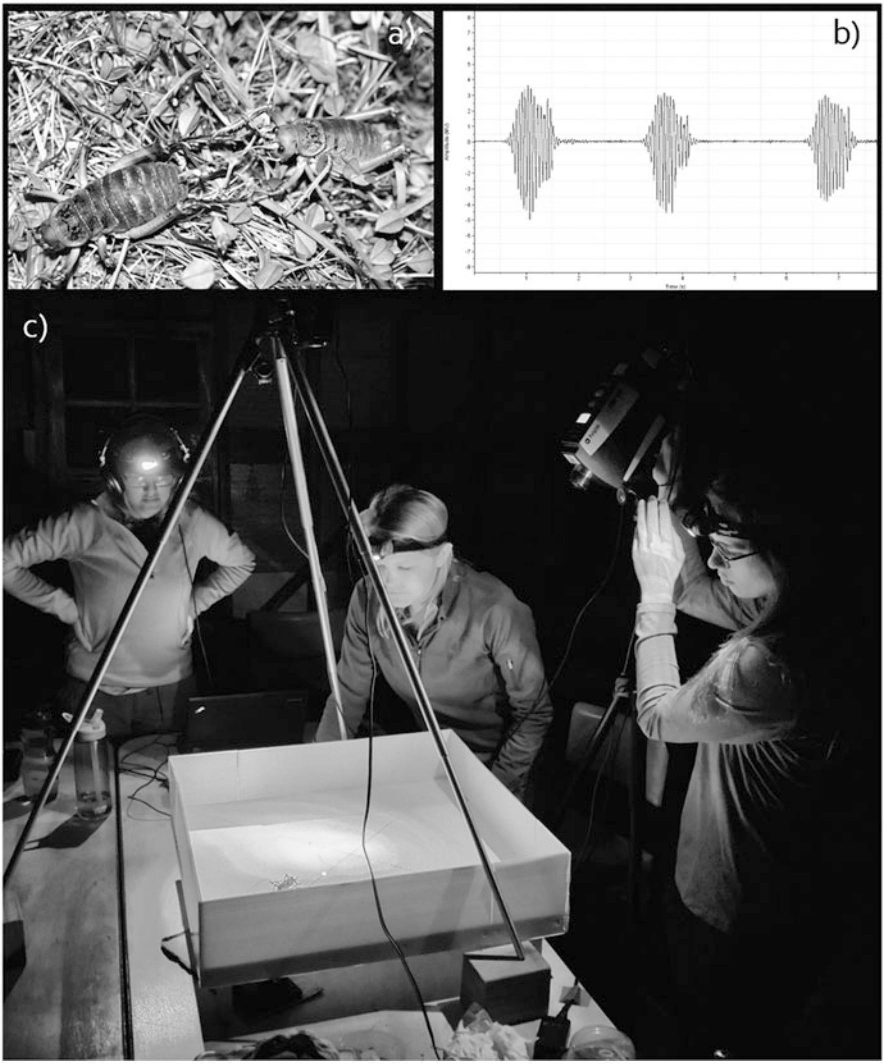

Fig. 22.3 Students enrolled in an upper division undergraduate study abroad course entitled *Explorations in Aotearoa: the biogeography and culture of New Zealand* (**a**) conducted biotremology research on a rare endemic insect, The Cook Strait giant weta (*Deinacrida rugosa*); here the smaller male on the right courts a female. (**b**) Male giant weta produced a low-frequency substrate-borne signal intrasexual contests for mates. (**c**) Students were trained in the use of laser Doppler vibrometry to record signals produced during behavioral trials at Matiu/Somes Island Scientific and Historic Reserve, North Island New Zealand. (Photo and figure credits: the authors)

their research, which was presented during student oral presentations and in written reports, in a question-and-answer session over the presentation. Further evaluation of process SLOs was accomplished through evaluating the raw data produced during the biotremology research projects. A final summative product from the course included the construction of a video that highlighted individual learning experiences that resonated with students; biotremology research with New Zealand giant weta most always surfaced as a course highlight.

22.8.1.5 Pedagogical Practicalities and Alternatives

In evaluating the integration of a biotremology research component into a course, several factors should be considered during initial course planning. If focusing student research experiences on questions requiring the recording of substrate-borne signals, the choice of study system is important. Selecting a species or group of species that readily produce signals in field or lab settings, as opposed to those whose vibratory behavior is rare and/or dependent upon rare conditions, will help sustain student engagement in the research project. On the other hand, studies in substrate-borne communication can afford students an unparalleled opportunity for discovery, given the lack of research coverage across certain taxa. While an endemic *Deinacrida* (Anostostomatidae) species was selected as the focus of study in this course, other local study systems that purportedly produced substrate-borne signals were likewise available, such as ground weta (*Hemiandrus*; Gwynne 2004; Strauß et al. 2017), tree weta (*Hemideina*; McVean and Field 1996), and cave weta (Rhaphidophoridae; Stritih and Čokl 2012), a group similar to North American cave crickets that remain relatively unstudied in New Zealand. Potential study models for use in teaching biotremology range from tiny braconid wasps (Joyce et al. 2008) and pygmy grasshoppers (Kočárek 2010), to jumping (Elias et al. 2003) and orb weaving spiders (Masters and Markl 1981), to giant Madagascar hissing cockroaches (Clark and Moore 1994). For a comprehensive survey of potential study organisms, see Hill (2008). It is important to stress that it is not necessary to journey across the globe to locate animals that produce measurable substrate-born vibrations; there are likely multiple prospective species just outside your classroom window (Cocroft 2001).

While access to appropriate technical gear can impose a limitation to integrating biotremology research into the curriculum, meaningful student learning experiences can be developed with a bit of industrious ingenuity. Owning a portable LDV for recording substrate-borne vibration and piezoelectric actuators or electromagnetic shakers to play back stimuli remains the preferred technical solution in designing teaching demonstrations and problem-based learning activities, but less expensive alternatives exist for those on a more modest budget. For detecting and measuring the temporal and spectral parameters of substrate-borne signals, accelerometers represent an attractive pricing solution. While some models produced for precision test measurement applications can cost over US$1000 per unit with the power supply, the increased integration of accelerometry into consumer electronics has driven down cost and expanded supply options. Piezoelectric materials represent another cost-effective solution to recording substrate-borne vibration, but generally lack the sensitivity of accelerometers. In considering purchases of either, many suppliers will offer educational discounts of 10–25%, on request. Additional cost-saving approaches include purchasing used sensors from discount vendors that refurbish and resell test and measurement equipment, or from online auctions that do the same. In either case, it is strongly recommended that some form of quality guarantee be obtained prior to purchase, with adherence to a *caveat emptor* procurement approach. An attractive low-cost solution for producing substrate-borne playbacks include electromagnetic or piezoelectric speakers, which can be easily modified with a small solid extension (metallic rod or screw) affixed to the piezoelectric material or speaker magnet to transduce the motion that normally produces airborne sound into substrate-borne vibration, instead. The challenge in these modified preps is to design both the speaker modification and the playback signal to eliminate the production of unwanted airborne vibration. Electromagnetic transducers designed to introduce a substrate-borne vibrational component to musical or theatrical presentations (see Lewis et al. (2006) for an example) can also provide an inexpensive alternative to more expensive electromagnetic shakers, and are readily available from online vendors like Parts Express (https://www.parts-express.com/), Sweetwater (https://www.sweetwater.com/), and others. Regardless of the playback solution chosen, it is imperative to assess the actual response of the device when coupled to an amplifier, along with the transfer function of the preparation, to ensure that that the substrate-borne stimulus arrives at the point of the receiver encoding the desired temporal, frequency, and amplitude properties. Cocroft et al. (2014) outline common pitfalls encountered when conducting playbacks, and identify best practices to ensure reliable and repeatable substrate-borne stimulus presentations. These practices are equally as important in a teaching and learning context as they are in the research laboratory, and apply whether studying seismic signaling in giant weta on a wind-swept New Zealand island or in singing pygmy grasshoppers on the sandbar along the small creek that flows through the green space just behind the science building on your campus.

22.8.2 Case Study #2: Female Preference for Multimodal Signals; Testing the Importance of the Substrate-Borne Component of an Airborne Sexual Signal in Crickets

22.8.2.1 Course Description and Student Demographics

Research investigating the ecological contexts and evolutionary explanations for why animals employ multimodal signals has captured the attention of behaviorists for more than a decade (Partan and Marler 1999; Candolin 2003; Bro-Jørgensen 2010). University students studying animal behavior are likewise drawn to the topic due to the often-charismatic displays produced by senders that engage multiple sensory channels of a receiver (see Girard et al. 2011). In this example of integrating biotremology into the classroom, students enrolled in an upper division undergraduate Animal Communication course at the University of New Hampshire conducted project-based research across a variety of relevant topics, with some student research groups (consisting of 3–4 classmates) from the class of 24 choosing to study whether substrate-borne vibrations produced by stridulating male crickets may be under assessment by females responding to the airborne sexual signal. Substrate-borne information is known to function as an important channel of information in female choice decisions in other arthropods (Stratton and Uetz 1983; Hebets and Uetz 1999; Elias et al. 2003), and after observing cricket reproductive behavior in the laboratory, students hypothesized that female Orthopterans might likewise extract information about a suitor from the substrate. Students selected female mole crickets (*Gryllotalpa major*) as their model system since males are known to call from subsurface burrows, producing a robust substrate-borne artifact of the intense airborne signal (Walker and Figg 1990; Hill and Shadley 2001). Students enrolled in the class had access to the rare insects that had been recently collected from a tallgrass prairie field site in Oklahoma for use in another research project.

22.8.2.2 Student Learning Outcomes

The primary SLOs associated with the course were accomplished through a hybrid instructional platform consisting of a combination of traditional teaching techniques and more active learning strategies. As there was not a formal laboratory section for the course, students attended instructor-led lectures one day per week, explored the primary literature through student-led presentations and follow-up discussion of designated publications during another meeting day, and then worked on technical training or research implementation on the third meeting day of each week, plus a 1-h recitation period. *Content* SLOs specifically related to biotremology in this course included understanding the following: 1) the signaler–receiver paradigm of animal communication (Endler 1992), 2) the physiological and environmental constraints to signal production, propagation and reception (Forrest 1994), and 3) the form and function of multimodal signals (Higham and Hebets 2013). These core principles were embedded in the aforementioned educator-provided lectures and extracted from the primary literature explored each week in the course. For students selecting a research project focused on the question of female cricket use of substrate-borne information in mate choice, developing a working understanding of the predictions of the multiple messages vs. redundancy explanations for the function of multimodal signals was a critical dimension of the content learning objectives. Similar to other case studies treated here, the core *Process* SLOs in the course focused on four key areas of student proficiency, with the third tied specifically to the research project testing female preference for a substrate-borne component in male cricket song. These four areas included the following: 1) understanding and articulating the key structural elements and findings from a published scientific study, 2) effectively using the scientific method to answer a causal question, 3) designing playback experiments in bioacoustics and biotremology, and 4) communicating research results to a peer community. Student training in the first process SLO was accomplished through weekly examination of the design structure and findings of animal communication literature; training in the second process SLO was accomplished through immersion in the hypothetico-deductive method via the development and implementation of a student-designed short-term research project. The third process proficiency involved hands-on training and practice in conducting airborne and substrate-borne playbacks in a laboratory setting (Hopp et al. 2012; Cocroft et al. 2014). Students were trained in how to construct synthetic signals with particular spectral and temporal characteristics, how to calibrate both airborne and substrate-borne stimuli, how to extract animal path data via image-based animal tracking software packages, and how to provide relevant animal care and handling during trials. Students gained expertise in data analysis appropriate to the questions being asked using R statistical software (R Core Team 2013), and then communicated their research findings via a digital research poster presented in a mini-symposium at the conclusion of the course to gain hands-on practice in the fourth process SLO.

22.8.2.3 Instructional Implementation

The student lab groups who proposed a project with a biotremology dimension completed the course benchmarks of formalizing their research question and structuring their experimental design associated with the study during the first three weeks of the course. Individuals then received training in animal handling using a proxy species first (*Acheta domesticus*) to gain proficiency in conducting preference trials with insects. This step was included in the training regimen to increase success with the larger and more handling-sensitive study species and to increase the comfort level of students unfamiliar with handling insects. During the period when students were conducting the research trials, female prairie mole crickets were kept in individual containers of moistened peat moss, and provided food (dried cat kibble) and water *ad libitum*, with care provided by the student research teams. Given that male prairie mole crickets signal at dusk, and females were kept in seasonally relevant 13:11 light–dark cycle, students ran trials after-hours in a large audiometric booth (Eckel Industries 3.1 m × 2.4 m × 2.4 m) under red light illumination. Students used a 1.0 m × 1.0 m arena with 15.0 cm upright PVC wall and a floor constructed from light-colored and acoustically transparent material stretched taut over a wooden arena frame, with 15.0 cm corner legs to provide space for an electromagnetic shaker beneath the floor (Fig. 22.4). The behavioral arena was constructed to reduce unwanted interference between airborne signals and the arena floor, and to transmit substrate-borne playbacks with minimal distortion.

To test the hypothesis that females might gain useful information from the substrate, students learned to construct synthetic signals to represent a standard form of the male prairie mole cricket 2.0 kHz airborne calling song. Speakers (Orb Audio Mod1) were positioned at opposite sides of the arena in cutouts in the PVC

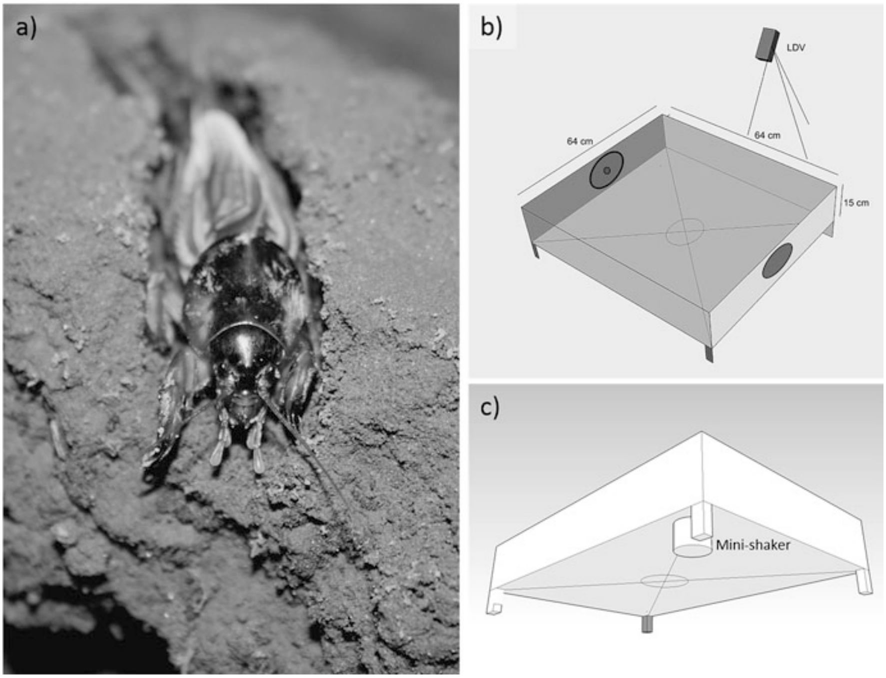

Fig. 22.4 Students enrolled in an upper division undergraduate Animal Communication course at the University of New Hampshire conducted project-based research studying whether substrate-borne vibrations produced by stridulating male prairie mole crickets, *Gryllotalpa major* (**a**) may be under assessment by females responding to the airborne sexual signal. Students constructed a behavioral arena (**b**) that allowed them to conduct playbacks to females that included both airborne and substrate-borne signal components (**c**). Students found that test subjects preferred multimodal signals, and that they exhibited shorter paths when responding to signals with a substrate-borne component. (Photo and figure credits: the authors)

wall, and calibrated to 80 dB SPL (B&K 2550 LT sound pressure meter) at the center point of the arena where females were released. Control trials thus presented females with two identical signals with non-overlapping chirps, and, as predicted, female response was random. In experimental choice trials with multimodal signal presentation, students introduced a substrate-borne signal that was temporally synchronized to the airborne signal into a randomized side of the playback arena. The substrate-borne component was generated by an electromagnetic mini-shaker (TMS 2004E, The Modal Shop, Cincinnati, OH) coupled to the arena floor, with the mini-shaker contact point positioned directly in front of the focal speaker. The substrate-borne stimulus was calibrated using a Polytec PDV-100 LDV to produce a signal just measurably above the noise floor at the center release point of the arena; students measured and monitored the LDV output during playbacks on an oscilloscope (Tektronix TDS2024C). Airborne and substrate-borne signals were played back from a PC workstation (Lenovo M910) that was coupled to an external sound card (Scarlett 18i20 USB 2.0 Audio Interface) and an amplifier (ART SLA-4) that drove the speakers and mini-shaker prep. Digital trial videos were collected via a Logitech C920 webcam positioned above the arena and connected to the PC workstation. During the course, students were trained in the use of Ethovision (Noldus Information Technology, Wageningen, The Netherlands) to track animal movement, and used the software in this experiment to quantify animal path metrics, using these data to test their predictions.

22.8.2.4 Evaluating Student Learning

Students engaged in biotremology research found that test subjects preferred multimodal signals, and that they exhibited shorter paths when responding to signals with a substrate-borne component. This led to the conclusion that female prairie mole crickets may use substrate-borne information as a signal localization or distance estimation cue that complements the information in the airborne signal produced by males. These findings provided summative evidence of proficiency in three of the four process SLOs. Formative evaluation of process skills occurred via student-led question-and-answer sessions during review of literature, and via formal feedback on the research proposal draft submitted prior to initiating the research project. Student proficiency in synthesizing literature was assessed formatively through evaluation of the weekly writing prompt, a two-page written summary of that week's scientific paper, using a writing rubric provided to students at the outset of the course. Additionally, instructor and peer review of formal student presentations of these weekly papers contributed to the formative evaluation of fluency in the literature. Summative evaluation of proficiency in critically evaluating the primary literature occurred by the inclusion on exams of short answer questions drawn from a published short communication (i.e., *note*) that was appended to each course exam as supplementary reading material. Course content SLOs were evaluated using formative assessment techniques during lecture, such as 2-min essays that students composed individually, or mid-lecture thought questions that students addressed in small groups. Summative assessment of content knowledge was accomplished using traditional exams scheduled approximately every 4 weeks of the course, which included student-crafted questions over the scientific papers reviewed in class. A final summative product from the course included the construction of a digital scientific poster that students presented during a scheduled mini-symposium open to students and faculty from across departments. Attendees were encouraged to submit brief critiques on the presentations in the form of five-question Likert-scale survey instruments, which, along with a more formal and extensive instructor assessment, served as the evaluative instrument for the assignment.

22.8.2.5 Pedagogical Practicalities and Alternatives

Disentangling the function of a substrate-borne component in a multimodal signal is an ambitious task for undergraduate students to undertake in the few weeks available to design and conduct a project-based research experience during a standard semester-long (15 weeks) course. In this example, students were able to show preference for the more complex signal, but did not have sufficient time to conduct the required follow-up series of tests to discriminate between the predictions of the redundancy and multiple messages hypotheses. However, a student research group from a subsequent year's course leveraged the previous students' findings to examine if the addition of the substrate-borne component improved performance in noisy conditions, testing whether the substrate-borne element of the signal acted as a redundancy for the airborne information. As it turned out, it did not, but students were able to compare their results to those of published studies where females were shown to actively assess some element of male proximity or condition through the substrate-borne component of a display (de Luca and Morris 1998; Elias et al. 2010; ter Hofstede et al. 2015). In this example of bringing biotremology into the classroom, students used a rather unique study system to address their question, but instructors need not depend upon such rarities. In most green spaces around campus, several viable alternatives likely exist. Female katydids (bushcrickets) of several species are known to pay attention to some form of substrate-borne vibration produced by a calling male (Keuper et al. 1985) and could serve as tractable models for a classroom research project. Similarly, but more difficult to handle than larger orthopterans, jumping spider females have well-documented engagement with male substrate-borne song elements, and representatives of this speciose group can likely be found near campus, if one looks closely. If a course is offered during a time of year when field collecting is not feasible, male house crickets (*Acheta domesticus*) and Madagascar hissing cockroaches (*Gromphadorhina portentosa*) likely produce substrate-borne artifacts of their airborne signals, and both species are readily available year-round (with certain considerations to shipping in very cold weather). Both are also easily kept as classroom cultures, offering students ready-made study subjects for a variety of projects including those examining sensory system response to vibration using simple electrophysiology rigs such as those offered by Backyard Brains (https://backyardbrains.com/).

As noted in the New Zealand giant weta case study, there are technical alternatives to purchasing an expensive Doppler laser vibrometer system to calibrate substrate-borne playback signals. Polytec (Polytec GmbH, Waldbronn, Germany; info@polytec.com) currently offers a portable LDV equipment loan program to qualified college/university instructors who develop curricular activities that require the use of this technology. Moreover, accelerometers work fine, and, in fact, are easily attached to the underside of an arena for constant monitoring during trials, without the fuss of having a tripod obstructing one side of the arena, and signals can be reasonably generated using a modified speaker. Airborne and substrate-borne vibrational signals can be recorded, synthesized, and played back using free software such as Audacity (http://www.audacityteam.org/), Ravenlite (http://

www.birds.cornell.edu/brp/raven/RavenOverview.html), or packages in R statistical software (R Core Team 2013), such as Seewave (http://rug.mnhn.fr/seewave/) or WarbleR (https://cran.r-project.org/web/packages/warbleR/index.html). Another technical factor to consider when conducting playback experiments requiring more than two channels of output, as described above, is that a multichannel sound card is required. An aftermarket sound card can be purchased and installed permanently into a desktop computer, or standalone alternatives can be connected to either a desktop or laptop computer via USB or Firewire ports. Sound cards generally require the installation of proprietary drivers, which allow the cards to interface with the playback software enabling it to load and playback (and record) multiple channels of sound at the same time. Of course, one could get around this two-channel limitation inherent in most computer systems by simply integrating a no-choice, rather than two-choice, experimental design in student projects.

22.8.3 Case Study #3: Come on Feel the Noise; Testing the Effects of Substrate-Borne Vibrational Disturbance on Animal Daily Activity Patterns

22.8.3.1 Course Description and Student Demographics

Students enrolled in courses that emphasize ethological principles often look for ways to connect theory to practice in the context of current problems in conservation biology (for a review of the field of conservation behavior, see Blumstein and Fernández-Juricic (2010). Noise effects on terrestrial and aquatic wildlife are widely documented (Kight and Swaddle 2011; Popper and Hawkins 2012; Francis and Barber 2013; Shannon et al. 2016), and are often considered one of the critical dimensions driving human-induced rapid environmental change (HIREC; for a review, see Wong and Candolin 2015).

For this reason, research on noise effects often captures the attention of undergraduate bioscience students. While most studies have traditionally focused on the influence of airborne or water-borne noise on animal behavior and life history, researchers have only recently begun examining how substrate-borne vibrational disturbance impacts animal decision-making and behavioral ecology (Warkentin 2005; Mazzoni et al. 2009; McNett et al. 2010). In this case study, students enrolled in an undergraduate Research Methods in Animal Behavior (RMAB) course offered in the Department of Biological Sciences at the University of New Hampshire recognized this knowledge gap while exploring the noise literature early in the course. As part of their required independent research experience, students chose to conduct an investigation that integrated techniques from biotremology into an experimental design that compared the effects of substrate-borne noise on animal daily activity patterns to both those produced by airborne noise alone, and by multimodal noise (airborne and substrate-borne vibration combined). Given that the course had a technical training focus, enrollment in the course was limited to sixteen students, with each working as a member of a paired team during course technical training practicums and while conducting research to address their chosen animal behavior study question.

22.8.3.2 Student Learning Outcomes

The RMAB course described here was designed to provide students with hands-on experience with modern methods for studying animal behavior both in the field and in the laboratory; thus, all SLOs focused on process skill proficiency. Supervised animal behavior research experiences complemented a sequence of targeted technical training sessions, the goals of which were to provide students with practical expertise in modern ethological methods. Skills training included techniques for appropriate experimental design in animal behavior research, image-based animal movement tracking, sensor-based measurement of activity patterns and circadian rhythms, animal color signal analysis, acoustic recording and playback techniques, advanced sound analysis, capture/marking methods, neuroethological techniques, remote sensing methods for animal behavior, and behavioral statistics in *R* statistical software (R Core Team 2013). Because the course took a "learn by doing" approach to animal behavior research, student research teams advanced their relevant methodological proficiencies in the context of a project-based investigation of their own design. For example, students conducting research on how substrate-borne vibrational disturbance influences animal behavior were required to demonstrate skills in (1) generating playback signals in Adobe Audition software, (2) conducting calibrated airborne sound and substrate-borne vibration playbacks, (3) using automated animal activity monitors, and (4) using packages in *R* statistical software (R Core Team 2013) and ImageJ (Schneider et al. 2012) software that facilitated analysis of animal activity data. Relevant content background for the questions that informed student research was accessed by immersion in the primary literature, with weekly student-led paper discussions incorporated into the training curriculum, and additional project-related readings assigned to each research team, as appropriate. Thus, fluency in synthesizing and presenting the findings of primary literature were an important process SLOs incorporated into the technical training goals of the course.

22.8.3.3 Instructional Implementation

The student research team choosing to study substrate-borne vibrational disturbance effects on animal behavior selected a study subject that was easy to handle and maintain in long-term activity trials, readily available from an existing laboratory culture, and one whose sensory system putatively makes the question of both airborne and substrate-borne noise biologically relevant: the Madagascar hissing cockroach, *Gromphadorhina portentosa* (Florentine 1968; Nelson 1979; Shaw 1994). During the early stages of the course after which students had identified their respective research questions and were actively developing the experimental design framework for their research projects, 32 *G. portentosa* adults (16 of each sex) from an existing laboratory culture were removed to set up two sex-segregated aquaria from which to draw individuals for playback experiments. Prior to and between trial periods, animals were provided food (a mixture of ground rabbit food and cat kibble) and water *ad libitum*.

Students tested whether Madagascar hissing cockroach daily activity patterns were influenced by different forms of noise, and thus needed to establish a protocol for reliably measuring individual time budgets in control conditions. They did so using a custom locomotor activity monitor (Trikinetics Inc. Waltham, MA USA) that measured animal activity using nine consolidated infrared beams reading binary beam interference status at the midpoint of a 5.0 cm diameter × 25 cm glass tube. Data were simultaneously taken from 32 tubes containing individual subjects. Activity data were logged in real time using Trikinetics DAMSystem3 software, and consolidated into 60-min bins using Trikinetics FileScan software prior to data exploration and analysis with ShinyR-Dam software (https://karolcichewicz.shinyapps.io/shinyr-dam/). Students ran control trials ($N = 32$) in an audiometric booth (Eckel Industries, Cambridge, MA) with a 14:10 light:dark cycle and room temperature set to 23 °C. Animals were placed into the locomotor activity monitor tubes for seven days, and provided food and water *ad libitum* during trials. Mean daily activity data were extracted from days 3–7 of the trials, after a 48-h acclimation period. Instruction in the use of the locomotor activity monitors and associated software was included in a course training module, but students conducting the noise assays were required to master additional data analysis techniques to address their particular research question. Students documented peak activity in *G. portentosa* during the first 4 h of the dark period, with no sex-based differences in activity budgets. The "cockroach team," as they were subsequently known, then synthesized airborne and substrate-borne playback stimuli for experimental noise trials with Adobe Audition software and conducted trials using a repeated measures design (as with controls, $N = 32$, evenly mixed sex ratio). Airborne stimuli were 10 s white noise pulses presented every 20 s during the 4-h peak activity period (2000–2400 h); substrate-borne noise followed the same presentation, but pulses were synthesized from 10 s brown noise exemplars with an FFT filter applied to concentrate energy between 10 and 300 Hz. During noise experiments, trial tube ends were covered with acoustically transparent material and airborne sound pressure levels were calibrated at the midpoint of each of the 32 tubes using a B&K 2550 LT sound pressure meter with the microphone attached to a 3.0 m extension cable. Airborne noise was played back through a speaker (Orb Audio Mod1) at 95 ± 1.5 dB SPL, alone or in combination with substrate-borne stimuli, using the multitrack player in Adobe Audition, which was connected to a sound card (Scarlett 18i20 USB 2.0 Audio Interface) and 100 watt/channel amplifier (ART SLA-4). Substrate-borne noise was delivered to all 32 test tubes by attaching the locomotor activity monitor via clamps to a customized wooden base connected to an electromagnetic transducer (BST-1 Bass Shaker, Dayton Audio Springboro, OH). Using skills developed during course training modules, the students recorded the substrate-borne stimulus at four points on the base, and at eight points on the locomotor activity tubes using a Polytec PDV-100 LDV connected to a Tascam DR 100 MK3 digital recorder (TEAC Corporation, Montebello, CA). They then used a custom script in Matlab (ver. 2016b; The MathWorks, Inc., Natick, MA) to correct for the inherent distortion resulting from the transfer function of the preparation, and calibrated the intensity of the substrate-borne vibration to 15 ± 1.3 mm/s. Using the LDV connected to an oscilloscope (Tektronix TDS2024C), students then compared mean daily activity patterns between control, airborne noise, substrate-borne noise, and multimodal noise treatments to address their primary research question.

22.8.3.4 Evaluating Student Learning

Students found that daily activity patterns in Madagascar hissing cockroaches differed between noise treatments and control, with the most dramatic change occurring when substrate-borne vibration was added to the airborne noise to create a multimodal noise source. Both male and female *G. portentosa* adults shifted their activity to periods of the night in which noise was absent, and increased activity during the light periods. The students were able to demonstrate that, even with the addition of noise during just a small fraction of the day, animal time budgets were disrupted, and that this effect was most profound in the context of multichannel noise that included a substrate-borne component.

Formative evaluation of student technical skills development occurred during training sessions via guided practice scenarios with discrete proficiency benchmarks. Student mastery of the benchmarks had to be demonstrated prior to completing the module. Summative evaluation of skills attainment occurred during instructor supervision of research projects, into which students integrated more advanced applications of the techniques learned during the targeted technical training sessions. Student grasp of the primary literature was evaluated through assessment of written summaries submitted by students each week, and in the depth of knowledge demonstrated during student-led paper presentations. Both assessments were conducted using a standardized writing rubric provided to students at the outset of the course. Students gained insights into how the rubrics would be applied to their own learning products by engaging in peer-review exercises in which they utilized the rubrics to evaluate their classmates writing submissions during the early weeks of the course.

22.8.3.5 Pedagogical Practicalities and Tractable Alternatives

Students conducting studies on noise effects are required to consider their results in the context of the life history of their chosen study system. In this case study, Madagascar hissing cockroaches provided an unambiguous model due to their obligate nocturnal behavior and exploitation of acoustic and substrate-borne information. As noted previously, the species is easy to rear, and a culture can easily be maintained in the classroom or laboratory for use in a variety of student projects. An extension to the noise project outlined above could include identifying sensory thresholds for both sound and substrate-borne vibration, using extracellular electrophysiology techniques. While this could be accomplished using a research grade electrophysiology rig, if available, alternative equipment for a teaching lab environment, such as the small amplifiers available through Backyard Brains (https://backyardbrains.com/) could provide a low-cost solution to introducing students to the physiological dimensions of biotremology. Animal systems that are generally available at low cost from science supply retailers, or those readily collected in greenspaces on university campuses, could also work in similar noise experiments; house (*Acheta domesticus*) or field crickets (*Gryllus* spp.) are likely tractable alternatives, as is *Drosophila melanogaster*, given the importance of substrate-borne vibration in the courtship repertoire of fruit flies (Fabre et al. 2012). A plethora of true bug (Hemiptera) species that produce substrate-borne signals, including some easily plucked as pests from local gardens (Ota and Čokl 1991; Miranda 2006; Polajnar et al. 2016), present another opportunity for studying substrate-borne noise effects, as do Lepidoptera larvae (Castellanos and Barbosa 2006), frogs (Narins 1990), terrestrial crabs (Salmon et al. 1977), and even benthic marine or freshwater invertebrates, if one is creative in designing experimental solutions to conducting playbacks in an aquatic setting (Roberts et al. 2016).

Integrating acoustic noise into animal behavior experiments is often perceived as a simple task. In some respects, this is true, but providing instruction to novice learners on the importance of proper signal conditioning, measuring transfer functions, and correcting for spectral distortion in noise presentations should be included as key student learning outcomes aligned with technical best practices. This is especially true when integrating substrate-borne vibration into noise experiments, where some form of signal distortion is almost always to be expected. Generating substrate-borne noise can be accomplished using a variety of low-cost methods (for examples see Hill and Shadley 1997; Pruitt et al. 2013), but it is important to integrate a technical solution for recording the playback at the point where the recipient organism will be positioned, to conduct spectral analysis to evaluate response of the substrate to the stimulus input, and then to apply a correction to the input signal to achieve the desired presentation. This is often done using custom scripts in Matlab or through a more manual approach using equalizer control functions in the playback software. Controlling ambient environmental noise can pose a challenge to studies like those described above, especially when including substrate-borne stimuli. Building vibration can produce an unacceptably high noise floor in some spaces, especially in older buildings or those located near high traffic areas. While vibration isolation tables remain the ideal solution, there are a variety of low-cost vibration reduction products designed for industrial applications that can affect measurable improvements, and even just relocating student experiments to an unused basement space can produce unexpectedly positive results.

22.9 Conclusion

Bringing biotremology into a lecture or laboratory teaching environment using active learning strategies can add a new and exciting dimension of scholarship for both the instructor and students. Engaging learners in the parameters that constrain and facilitate the use of substrate-borne signals or cues in animal systems can serve as stand-alone student learning outcomes as well as important gateway concepts to more advanced principles in the physical and biological sciences. While the broad aim may be to develop critical thinking or technical skills attainment through discovery, students will also come to appreciate how biotremology represents an elegant expression of "science as a way of knowing." Further, designing courses around active engagement in critical thinking, problem solving, discovery, and in scientific inquiry provide the most effective learning environment for students, the most satisfying teaching and research experiences for educators, and ultimately contribute to an education of enduring worth.

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Chapter 23
Call for the Establishment of a VibroLibrary at the Animal Sound Archive Berlin

Karl-Heinz Frommolt, Hannelore Hoch, and Andreas Wessel

Abstract The Animal Sound Archive (Tierstimmenarchiv) of the Museum of Natural History Berlin (Museum für Naturkunde Berlin) is one of the oldest and largest collections of animal sounds worldwide. It was founded in 1951 by Günter Tembrock and comprises now more than 18,000 hours of audio material. During the last decades, the animal sound archive has been transferred from a collection of analogue tape recordings toward a completely digital collection. Recordings can be shared for scientific and educational purposes using the web-based infrastructure. The biotremology community is invited to use the infrastructure of the Animal Sound Archive to establish a VibroLibrary.

23.1 History and Structure of the Animal Sound Archive (Tierstimmenarchiv) at the Museum of Natural History Berlin

The Animal Sound Archive at the Museum für Naturkunde Berlin (in German: Tierstimmenarchiv) is one of the oldest and largest collections of animal voices in the world. It was founded in 1951 by Günter Tembrock (1918–2011) at the Institute of Zoology of Humboldt University Berlin. In 1995, the collection was transferred to the museum. The aim of the collection was the scientific documentation of animal voices as one expression of animal behavior. In the first years, the work was focused on the vocal behavior of red foxes kept at the Zoological Institute, and other animals in captivity and zoo animals. Based on this material, Tembrock wrote the review papers on acoustic communication of mammals published in R.-G. Busnel's 1963 milestone book "Acoustic behaviour of animals" and T. S. Sebeok's

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"Animal Communication" (Tembrock 1963, 1968). From 1960 onwards, more and more animals were recorded in the wild.

While up to 1990 the majority of the recordings were made by Günter Tembrock, his collaborators and students, in the last decades the collection has been expanded by external collections such as the complete collection of Michael Schubert (author of many published records with bird voices), the comprehensive bioacoustic collections of Erwin Tretzel and Gerhard Thielcke, but also the collection of vibrational signals recorded by Hildegard Strübing, one of the pioneers of biotremology (see Wessel 2014). In recent years, research projects of the Animal Sound Archive are focused on the application of bioacoustic methods for long-term monitoring of vocalizing animals. Soundscape recordings are already a significant part of the collection.

The Animal Sound Archive as a unique research infrastructure has been transferred from a collection of analogue tape recordings toward a completely digital collection. In order to retain high quality, digitalization has been carried out at a sampling rate of 96 kHz and 24 bit resolution. All the older recordings on magnetic tapes are now digitized. Direct access to sound recordings via web interface allows for cooperative comparative research (e.g., Bowling et al. 2017) and has facilitated the publication of selected recordings as audio CD (Dingler and Frommolt 2016). Currently, a significant portion of the recordings are accessible via the website of the archive (www.animalsoundarchive.org), GBIF or Europeana. In the future more and more recordings will be made available and access will be improved. The collection will be developed as a reference system for bioacoustic research in biodiversity research, functional bioacoustics, and bioacoustic pattern recognition. The free access to the recordings allows their use for lectures, exhibitions, and cultural purposes.

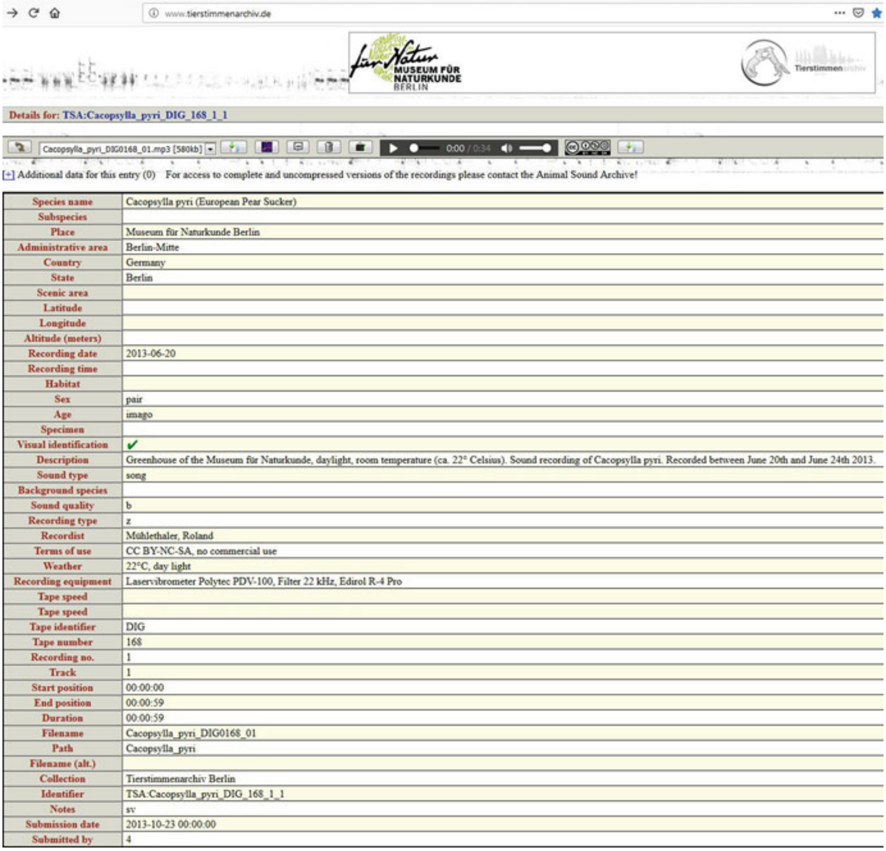
23.2 The Animal Sound Archive as Global Repository

The Animal Sound Archive is open for any scientist working in the field of bioacoustics. We offer the opportunity to store sound recordings used for scientific papers. For example, we reposit sound recordings used for spectrograms published in the Journal of Ornithology. The sound recordings are provided by the Animal Sound Archive under a non-commercial creative commons license (CC BY-NC-SA). The sound files can be directly uploaded by the author of the paper via an entry form. Access to the sound recordings will be given using a separate DOI. Thus the sound recordings of the paper from Jakubowska and Osiejuk (2018, DOI: https://doi.org/10.1007/s10336-018-1607-3) can be accessed by the DOI: https://doi.org/10.7479/0k18-gzxm.

23.3 Establishment of VibroLibrary as Research Infrastructure for Biotremology

We invite the biotremology community to establish a library of vibratory signals (VibroLibrary) using the framework of the Animal Sound Archive. Several recordings of vibrational signals, e.g., from the ground-breaking studies of H. Strübing, cave-dwelling planthoppers from around the world (see Hoch and Wessel 2006), or recent studies on pest species (see Fig. 23.1) are already represented in the collection.

Recordings for VibroLibrary should be saved in an uncompressed format, but there is no upper limit for file size. Additionally to the data provided via the entry form, the VibroLibrary welcomes detailed metadata, e.g., scans of original protocols as PDF; it is also planned to provide the opportunity for the storage of related video



Details for: TSA:Cacopsylla_pyri_DIG_168_1_1

[+] Additional data for this entry (0) For access to complete and uncompressed versions of the recordings please contact the Animal Sound Archive!

Species name	Cacopsylla pyri (European Pear Sucker)
Subspecies	
Place	Museum für Naturkunde Berlin
Administrative area	Berlin-Mitte
Country	Germany
State	Berlin
Scenic area	
Latitude	
Longitude	
Altitude (meters)	
Recording date	2013-06-20
Recording time	
Habitat	
Sex	pair
Age	imago
Specimen	
Visual identification	✓
Description	Greenhouse of the Museum für Naturkunde, daylight, room temperature (ca. 22° Celsius). Sound recording of Cacopsylla pyri. Recorded between June 20th and June 24th 2013.
Sound type	song
Background species	
Sound quality	b
Recording type	z
Recordist	Mühlethaler, Roland
Terms of use	CC BY-NC-SA, no commercial use
Weather	22°C, day light
Recording equipment	Laservibrometer Polytec PDV-100, Filter 22 kHz, Edirol R-4 Pro
Tape speed	
Tape speed	
Tape identifier	DIG
Tape number	168
Recording no.	1
Track	1
Start position	00:00:00
End position	00:00:59
Duration	00:00:59
Filename	Cacopsylla_pyri_DIG0168_01
Path	Cacopsylla_pyri
Filename (alt.)	
Collection	Tierstimmenarchiv Berlin
Identifier	TSA:Cacopsylla_pyri_DIG_168_1_1
Notes	sv
Submission date	2013-10-23 00:00:00
Submitted by	4

Fig. 23.1 Screenshot of a publicly visible recording entry. This recording can be played in the browser or downloaded free under a common license

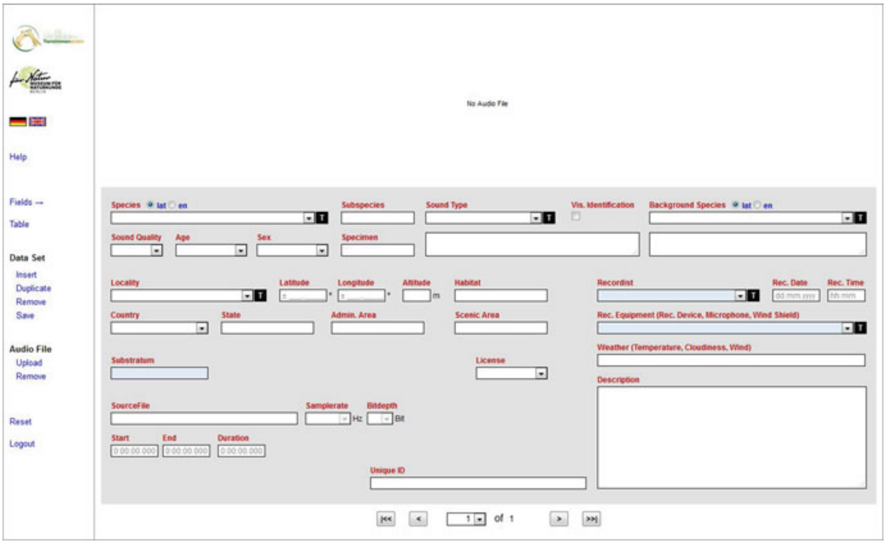


Fig. 23.2 Screenshot of the entry form of the VibroLibrary

files. Also, physical voucher specimens could be deposited in the collections of the museum on agreement with the responsible curator. Each recording gets an individual identifier and can be published with a DOI (see above). The recordings are accessible via www.animalsoundarchive.org or are published with a DOI by default under the Creative Commons license CC BY-NC-SA; however, authors can choose another license (or even that the entries not be publicly visible) while entering the data.

An entry form for a VibroLibrary is already prepared (Fig. 23.2). Large data collections can be filled in by using an Excel template. Please feel free to contact us and join the VibroLibrary!

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Chapter 24
Arachnid Orchestras: Artistic Research in Vibrational Interspecies Communication

Tomás Saraceno, Ally Bisshop, Adrian Krell, and Roland Mühlethaler

Abstract *Arachnid Orchestra. Jam Sessions*, *Cosmic Jive: The Spider Sessions* and the *Cosmic Dust Web Orchestra* are pioneering and visionary projects by artist Tomás Saraceno that fold his long-term research on spider webs into the realm of vibration and sound, to develop playful and experimental systems for interspecies communication. Working at the intersection of art, architecture and science, for these projects Saraceno transformed spider webs into musical instruments that play upon the incredible structural and mechanical properties of spider silk, and also tune into the spider's sophisticated forms of vibrational communication. Exhibited at Saraceno's first solo show in SE-Asia at the NTU Centre for Contemporary Art in Singapore, *Arachnid Orchestra. Jam Sessions* was developed in collaboration with experts from various fields of knowledge—and extends upon Saraceno's earlier bioacoustic projects. With this interdisciplinary team, Saraceno created a musical system for translating the spiders' vibrations into acoustic rhythms: amplifying the spiders' biotremological signals and web pluckings, and making these substrate-borne vibrations audible to humans. During the exhibition, musicians and sonic artists were invited to attune and respond to the spiders' vibrational signals through the multispecies instruments that Saraceno created via three live performances (jam sessions), creating a collective and immersive interspecific orchestral composition. The exhibition space was thus transformed into an interactive sound and visual installation: a process-driven laboratory for experimentation that pushed the boundaries of interspecies communication. During the First International Symposium on Biotremology in San Michele all'Adige, sonic excerpts from *Arachnid Orchestra. Jam Sessions* were played to a scientific audience.

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24.1 Introduction

Since 2006, Tomás Saraceno has been working with and researching spiders and their webs. Beginning with questions about the structural, functional and architectural properties of the web, Saraceno's inventive research and experimentation led the artist to establish a dedicated Spider/Web Research Group within his expansive studio premises in Rummelsburg, Berlin.

24.1.1 Spider/Web Research Group

Studio Tomás Saraceno's Spider/Web Research Group is dedicated to the hosting, interdisciplinary research and development of projects and artworks about spiders and their webs (Fig. 24.1), and attracting prominent researchers from around the world for collaborative projects. Situated in-studio—and thus placing the scientific research activities in close proximity with the artistic and architectural production teams—the Spider/Web Research Group hosts a range of spider genera and species from diverse geographic origins, averaging hundreds of juvenile and adult spiders at any one time. It also hosts the world's largest collection of spider webs that Saraceno has gathered over years of careful curation, and which grows in concert

Fig. 24.1 Tomás Saraceno, *Spider Salon* set up, 2016. Spider/Web Research Group, Studio Tomás Saraceno, Berlin. Photo by Studio Tomás Saraceno, 2016. Courtesy the artist

with his efforts to research spider web architecture and spider silk preservation and conservation methods.

Saraceno's research into the webbed world of the spider arose with what appeared, at first glance, to be a relatively simple question:

> Is it possible to recreate a precise three-dimensional model of a spider's web?

From this initial question, Saraceno began a conversation with arachnologist Peter Jäger (Senckenberg Research Institute and Natural History Museum, Frankfurt am Main, Germany) to explore the possibility of creating a 3D scan of a natural spider web, and using these data to reconstruct a large-scale model of the web for an art exhibition. On Jäger's suggestion, Saraceno focused on the web of a black widow spider [*Latrodectus mactans* (Fabricius, 1775)]—chosen because of the relative availability of this spider, and also for the large, complex 3D web that it weaves.

Early efforts to create a 3D scan of this web using existing scanning methods proved unsuccessful—as the unique properties of spider silk (the fineness and reflective qualities of the threads) made it unsuitable for capture by conventional approaches. As the experiments progressed, the collaborative dialogue also grew, enrolling the expertise of Samuel Zschokke (University of Basel) in web construction and evolution, and Christof Wulff (Technische Universität (TU) Darmstadt, Germany) in photogrammetric capture techniques. After exploring a number of different methods that proved inadequate to the task, Saraceno proposed the use of a sheet laser to illuminate and scan complex spider/webs. The successful technical development of this technique was then realised in collaboration with researchers at the TU's Photogrammetric Institute.

From a 2-year collaborative research effort to address this question, Saraceno pioneered the *Spider Web Scan* technique: a scientific method combining laser supported tomography with photogrammetric analysis, to allow the 3D-scanning of a spider web.[1] This technique has since been developed and refined in cooperation with a number of other scientific institutions. The first successful deployment of this technique was in 2009, with the scanning of the complex, 3D web of the black widow spider.

The next step in this process was to develop a computational methodology capable of extracting digital data from the spider web scans. Working with his studio team, Saraceno developed the *Spider Web Digitization* method—which allowed 3D information about the *Latrodectus mactans* web to be assembled from 110 pairs of stereoscopic slides of the web captured by the scanning process (Figs. 24.2 and 24.3). Structural 'gaps' in the scanned images—areas of the webs where the stereoscopic photos were unable to capture the detail of the silk thread structure—were reconstructed after an analysis of the total web architecture. Through a process

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[1] Originally developed specifically for this artistic project, this technique is now used by scientific collaborators at MIT (Department of Civil and Environmental Engineering), and at the Max Planck Institute for Ornithology, Konstanz.

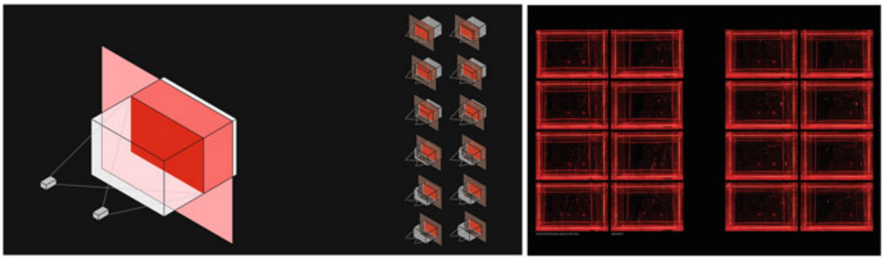

Fig. 24.2 Spider Web Scan technique (laser-supported tomography, following an idea by Tomás Saraceno) developed by Studio Tomás Saraceno in collaboration with the Photogrammetric Institute at TU-Darmstadt. 3D scanning of the complex *Latrodectus mactans* (black widow) web. Left: Original experimental setup including stereoscopic cameras and sheet laser; Right: Stereoscopic scanning images of sections of the black widow web. Extracts from Arrhenius and Saraceno, 2011. © Tomás Saraceno

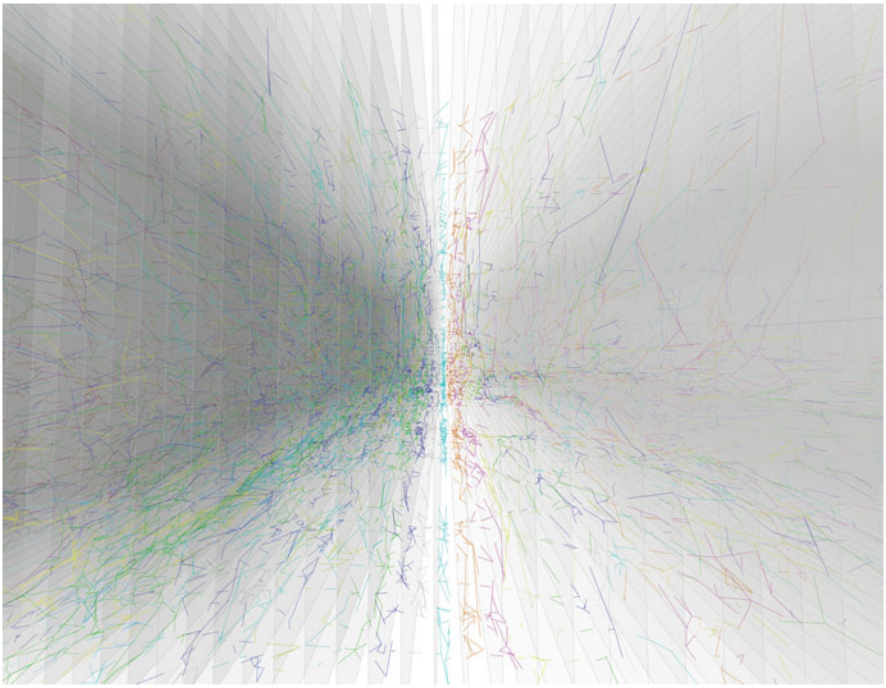

Fig. 24.3 Tomás Saraceno: *14 Billions (Working Title)*, 2010. 110 pairs of stereoscopic-photogrammetric pictures of the complex *Latrodectus mactans* (black widow) spider web, in preparation for the installation of the 17:1 reconstructed web. Photo by Studio Tomás Saraceno, 2010. Extracts from Arrhenius and Saraceno, 2011. © Tomás Saraceno

called *orthographic projection* these data were compressed into two dimensions, creating a map of intersecting black lines—with each line and each point assigned a unique number.

The final stage of this intensive research process was the development of an analogue method for reconstructing a physical, large-scale 3D-model of the web, based on the 3D scanning and digital data. To this end, Saraceno and his studio team developed the *Spider Web Reconstruction* method, which was realised and refined during the construction of a 17:1 scale installation of the *Latrodectus mactans* spider web, realised for the art installation *14 Billions (Working Title)* at Bonniers Konsthall, Stockholm in 2010 (Arrhenius and Saraceno 2011). The final reconstructed web included 36.4 km of nylon thread in a complex knotted structure that included 6593 junctions, and measuring 8 m × 7 m × 5 m in size (Figs. 24.4 and 24.5).

This project charts the beginning of Saraceno's foray into the complex vibrational world of spiders and their webs. It is also a concrete example of how an innovative approach to collecting data can become an artwork, and how multidisciplinary research can generate novel and unexpected outcomes and scientific innovations. From this initial project, the beginnings of an arachnid research endeavour and a unique and multidisciplinary collaborative research network began.

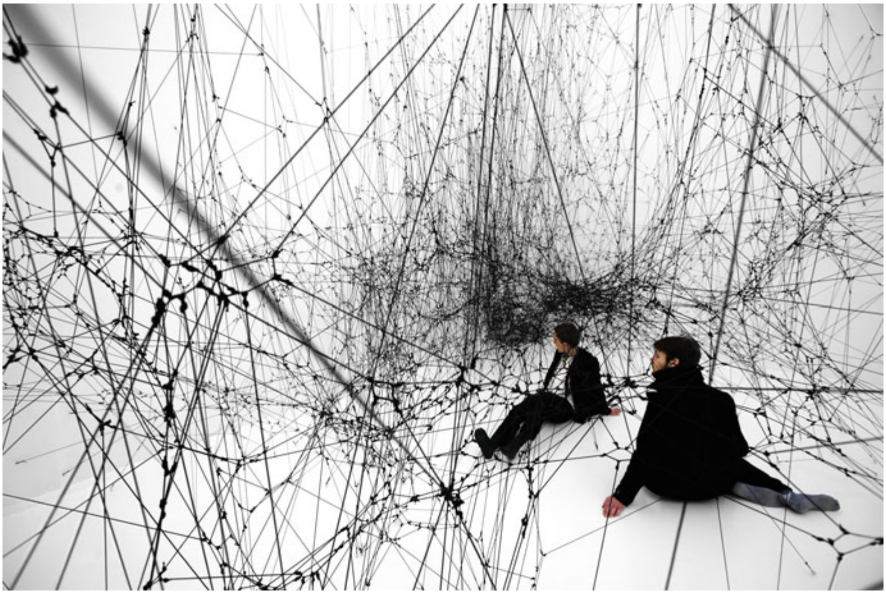

Fig. 24.4 Tomás Saraceno*: 14 Billions (Working Title), 2010*. Installation view of a reconstructed complex *Latrodectus mactans* web, scale 17:1, Bonniers Konsthall, Stockholm: Curated by Sara Arrhenius. Photo by Studio Tomás Saraceno, 2010. Courtesy the artist; Andersen's, Copenhagen: Ruth Benzacar, Buenos Aires; Tanya Bonakdar Gallery, New York/Los Angeles; Pinksummer contemporary art, Genoa; Esther Schipper, Berlin

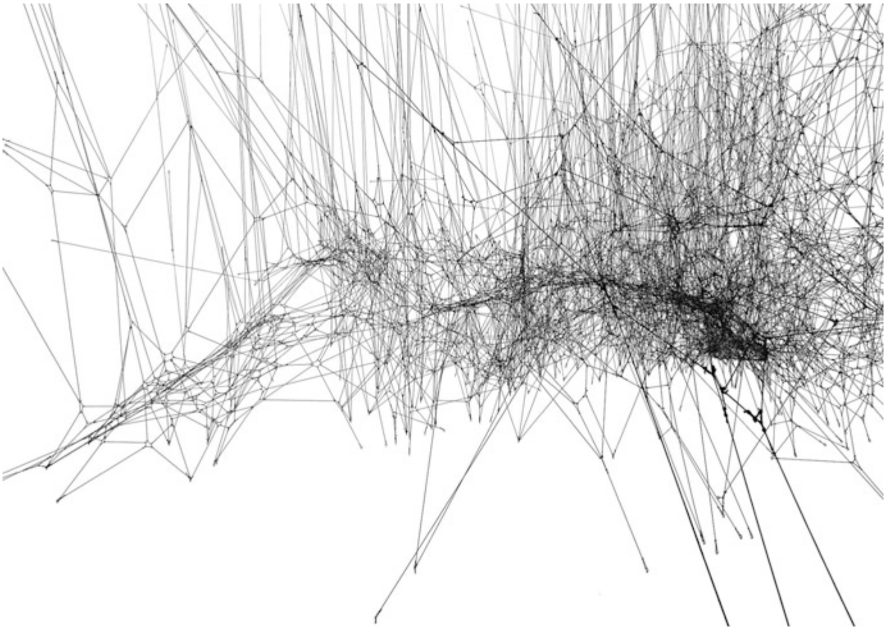

Fig. 24.5 Tomás Saraceno: *14 Billions (Working Title), 2010*. Black cords, elastic rope, hooks, scale: 17:1 *Latrodectus mactans* web. Installation view, Bonniers Konsthall, Stockholm: Curated by Sara Arrhenius. Photo by Studio Tomás Saraceno, 2010. Courtesy the artist; Andersen's, Copenhagen; Ruth Benzacar, Buenos Aires; Tanya Bonakdar Gallery, New York/Los Angeles; Pinksummer contemporary art, Genoa; Esther Schipper, Berlin

The Spider/Web Research Group has since built a strong and extensive network of scientific collaborators across the globe—the *Interspecific Network*—with whom Saraceno pursues his unique arachnid research program.

With the support of this network, the hybrid artistic-scientific research and experimentation of the Spider/Web Research Group has generated technical inventions, artworks and insights across a number of strands of scientific research, including the following:

- Material science, and the emerging field of *biomateriomics*
- Animal social and collective behaviour and
- Bioacoustics and biotremology, respectively

24.1.2 Material Science and Biomateriomics

This strand of research describes an approach to studying the properties and mechanics of spider silk, including longevity, integrity, and possible applications in architectural, structural and even acoustic design (Buehler and Saraceno 2017).

A key research partnership in this area is with Markus Buehler at the MIT Department of Civil and Environmental Engineering (CEE).[2] The focus of the collaborative research between MIT and the Spider/Web Research Group is in optimising Saraceno's web-scanning process, and using this method to collect data on the materiality of the web for possible future application in art, architecture and structural design (Su et al. 2018).

Additional research projects in material science include collaborations with Martín Ramírez (Museo Argentino de Ciencias Naturales) to generate SEM images of spider silk; Ansgar Greshake (Museum für Naturkunde Berlin) to analyse the chemical and optical properties of spider web samples and meteorite dust using an Electron Probe Microanalyzer; and Jonas Wolff (Macquarie University, Sydney) to study spider web attachment points.

24.1.3 Animal Social and Collective Behaviour

Another strand of research pursued by Saraceno's Spider/Web Research Group is in understanding the relationship between material structure/architecture and 'social' or collective behaviour in spiders. While sociality is rare in spiders [of the ca. 47,500 known spider species, fewer than 25 species exhibit social behaviour (Lubin and Bilde 2007)],[3] spiders' collective behaviour can have fascinating material and architectural implications, from the construction of gigantic communal spider webs, to the phenomenon of mass aerial dispersal by 'ballooning' of social *Stegodyphus* spiders (Marshall 1898; Wickler 1973; Schneider et al. 2001).

In the Spider/Web Research Group, this research strand involves collaborative research projects with Iain Couzin, Alex Jordan and Matthew Lutz (Department of Collective Behaviour, Max Planck Institute for Ornithology, Konstanz) in combining Saraceno's 3D web-scanning technique with tracking of the spider's' movements, to better understand how spiders build their webs, and the relationship of collective behaviours to web architectures. The Spider/Web Research Group also has ongoing dialogues with Yael Lubin (Ben-Gurion University, Israel) and Jutta Schneider (University of Hamburg) on social and semi-social behaviours in spiders, including spider ballooning behaviour. Future research in this area will

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[2] A team of researchers and students at MIT have been using Saraceno's scanning system to experimentally investigate the deformation mechanism of spider webs, applying different loads (e.g. point, wind, stretch and combination) to the webs and analysing the stresses on individual fibres. This analysis will assist in understanding how the location of each fibre impacts upon the load, and the overall architecture of the web (Buehler and Saraceno 2017).

[3] Sociality in spiders takes a number of forms. 'Social' spiders are considered as those forming 'family-group territories' and building communal webs, where colony members cooperate in raising their young and foraging for food. Around 60 spider species are considered 'colonial'—living in aggregations, but foraging and raising their young alone (Lubin and Bilde 2007).

explore the relationship between sociality and vibrational signalling, including signal propagation in colonial webs and other social spider architectures.

24.1.4 Bioacoustics

The Spider/Web Research Group's research into bioacoustics—and more specifically, biotremology (see Hill and Wessel 2016)—extends Saraceno's interest in exploring the possibilities for interspecific communication, and our capacity to communicate with our nonhuman kin through attuning to and producing vibrational signals. This strand of research is led by in-house Spider/Web Research Group researcher Roland Mühlethaler, and through collaborations with biotremology experts Hannelore Hoch and Andreas Wessel (Museum of Natural History, Berlin), as well as Peggy Hill (University of Tulsa).

Saraceno's foray into bioacoustic research began when Mühlethaler (then a researcher at the Museum für Naturkunde Berlin) was invited to join visiting colleague Yael Lubin on her tour of the Spider/Web Research Group—at that time located in Saraceno's old studio premises at the Hamburger Bahnhof, Berlin. During this visit, Saraceno was excited to learn about Hoch and Mühlethaler's research into vibrational communication in insects, and invited the researchers to explore and measure the vibrational capacity of his private collection of spider webs. Hoch and Mühlethaler returned to Saraceno's studio with a Laser Doppler Vibrometer (PDV-100), which they then used to measure the vibrational signals that were passing along the threads of a *Nephila* sp. web (see Fig. 24.6). From this first visit, a mutual collaboration and interest in spider vibrational communication was born, which led to Mühlethaler eventually taking up a position within Saraceno's Spider/Web Research Group, heading up the bioacoustic experimental research program.

24.2 Transcoding *Umwelten:* Possibilities for Interspecific Communication

Much of Saraceno's biotremological research is linked to ideas of cross-species attunement and communication—and the possibility of gaining some insight into the unique sensory world of the spider. In the early twentieth century, the biologist Jakob von Uexküll proposed that the universe consists of an infinite number of perceptual worlds, or *Umwelten*, that are unique to individual species (Uexküll 1934). These unique perceptual worlds are reciprocally noncommunicating and 'unknowable': we cannot know the *Umwelt* of the spider, nor can the spider know the *Umwelt* of the fly that it seeks to ensnare in its web. Nonetheless, these *Umwelten* are all linked, 'as if in a gigantic musical score' (Agamben 2004: 40). Even without knowing it, we are *in tune* with the perceptual worlds of other species.

Fig. 24.6 Spider sound recording sessions of *Nephila kenianensis* playing its hybrid instrument. Thanks to: Prof Hannelore Hoch, Dr Roland Mühlethaler, Museum für Naturkunde, Hemiptera Research Group, Leibniz-Institut für Evolutions und Biodeiversitätsforschung, Humboldt Universität, Berlin. Photo by Studio Tomás Saraceno, 2014. Courtesy the artist

Uexküll uses the example of the spider web to illustrate this paradoxical coincidence of both 'reciprocal blindness' (Agamben 2004: 42) and musical unity. Without being able to see the *Umwelt* of the fly, the web that the spider weaves is already '*fly-like*': the distance between the threads are mapped in accordance with the size of the fly's body, the tensioning of these threads are tuned according to the impact force of the fly's body in the web, even the very size of these threads references the visual capacity of the fly, to whom these threads are invisible. The unique perceptual world of the spider thus expresses a harmonic relationship with the world of the fly, and the site for this harmonic expression is the spider's web.

This idea of the musical score that unifies us across our noncommunicating perceptual worlds is at the core of Saraceno's attempts to initiate acoustic dialogues across the species boundaries of the spider and the human. His biotremological research begins with the understanding of the spider web as a musical instrument—an architecture for acoustic transmission of the vibrational (biotremological) signals specific to the *Umwelt* of the spider, but which is also a potential site for a kind of paradoxical attunement across species, which perhaps allows the spider and the human to transcode each other's signals, and to create a musical passage between unknowable perceptual worlds.

The idea of 'playfulness' underscores these experiments in interspecific (spider-human) communication—where 'play' is understood as a dynamic complex of interactions that open up the possibilities of affective sympathy between and across different species (Massumi 2014). This idea of play also picks up on the idea of the spider webs as instruments that can be *played*—by the spider as it produces signals, or by humans by harnessing the ‘musical’ properties of the web. What Saraceno’s acoustic experiments with the webs propose is not a direct translation of the spider’s signals, but a means of generating a kind of resonant or acoustic sympathy between humans and arachnids.

24.2.1 Hybrid Webs as Multispecies Instruments

One of the most recognisable artistic outputs of Saraceno’s creative research into spiders and webs are his Hybrid Spider Web (HSW) sculptures (Fig. 24.7). These hybrid webs—conceived and realised by Saraceno with the assistance of multitudes of arachnid kin—are built by different spider species from geographically remote

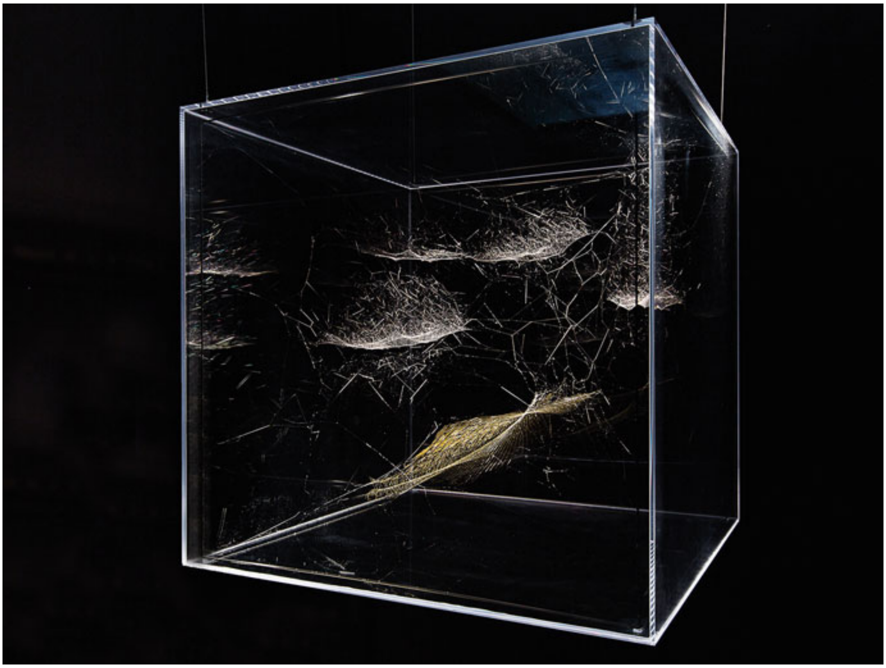

Fig. 24.7 Tomás Saraceno, *Hybrid solitary semi-social musical instrument EGS-zs8-1: built by one* Nephila kenianensis, *one week, and three* Cyrtophora citricola, *three weeks*, 2015. Photo by Studio Tomás Saraceno, 2015. Courtesy the artist

locations, and thus would not be encountered in a 'natural' setting.[4] These webs are constructed in an open frame carbon fibre structure, conceived and designed by Saraceno, which provides attachment points for the webs, and allows for observation of the web-building process and display of the completed hybrid web sculpture (Engelmann 2016, 2019).

Saraceno considers each of these hybrid webs as 'multispecies instruments'—because they are woven by more than one species of spider, but also because of their perceived potential for opening up channels of communication across species barriers, becoming the vehicle and substrate for acoustic (vibrational) dialogues between spiders and humans. Each web is thus figured as a unique musical instrument, whose complex networked architecture performs as an apparatus for communication, cooperation, mediation and sensing.

24.3 Cosmic Jive: The Spider Sessions

Saraceno's first foray into creating a musical interspecific dialogue between spiders and humans was his installation *Cosmic Jive: The Spider Sessions* at the Museo di Arte Contemporanea di Villa Croce, Italy in 2014 (Pezzato 2014). Building upon his collaborative research and experimentation with Roland Mühlethaler and Hannelore Hoch, *Cosmic Jive: The Spider Sessions* allowed audiences to not only encounter Saraceno's unique multispecies Hybrid Spider Web sculptures, but to understand these webs as musical instruments, via a sensorial encounter with their bioacoustic properties.

Cosmic Jive: The Spider Sessions uses the vibratory signals of the spider as its core acoustic motif: the vibrations produced in the web as the spider plucks, tunes and repairs the web; the tremors produced by impact events in the web—from trapped prey, wind, or other mechanical interventions; the tremulations produced as the spider sends conspecific signals to potential mates. Being substrate-borne, these biotremological signals are usually inaudible to human ears.[5] However, there exists the possibility to amplify these vibrations, making sonorous the 'unknowable'

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[4] There are documented examples of a hybrid webs in 'nature' that were built in an abandoned mammal burrow in South Africa and incorporated the webs of coexisting spiders from *Agelena*, *Euprosthenops* and *Smeringopus* species (Heidger 1988). However, these spider species live in a close geographical proximity to one another—at the level of niche specificity. Saraceno's Hybrid Spider Web sculptures bring together webs spun from geographically distant spiders, for instance, incorporating webs from *Nephila senegalensis* (sub-Saharan Africa, from Senegal and Yemen to South Africa) and *Psechrus jageri* (Thailand, Laos) species, or *Nephila edulis* (Australia) orb webs in co-compositional structures with webs woven by *Larinioides sclopetarius* (Europe, North America and Asia).

[5] In other vibratory spider signals, such as those produced by stridulation, or when a spider drums on a surface such as a dry leaf, a portion of the signal is airborne, and thus potentially audible to humans without technical amplification (Lahee 1904).

signals and movements that are specific to the spider's *Umwelt*, and thus opening up the possibilities for a playful interspecific conversation.

This installation featured a series of Hybrid Spider Webs produced by three different spider species with different levels of sociality: *Cyrtophora citricola* and *Cyrtophora moluccensis* species (semi-solitary, colony-dwelling spiders producing horizontal 'tent' web architectures) and an unidentified *Nephila* species from Kenya (often named *N.* '*kenianensis*'; solitary spiders spinning a classic 'orb' web structure). The first of these multispecies instrument webs was titled *Work in Progress: Hybrid-web Instrument Centaurus A, constructed by the solitary Nephila kenianensis for three weeks, with Live performance by the quintet of semi-social Cyrtophora citricola.* This web was begun by a *Nephila* spider, and elaborated and remodelled by five *Cyrtophora* spiders over the course of the exhibition. The second Hybrid Spider Web, titled *Hybrid semi-social musical instrument NGC 2976* (see Fig. 24.8) was built by two successive groups of *Cyrtophora* species. For the first three weeks, the web was constructed by *Cyrtophora citricola* spiders, after which the web was rotated 180° on its *Z*-axis to invert the force of gravity active in the architecture of the web. The rotated web was then completed over four weeks by *Cyrtophora moluccensis* spiders.

To focus attention on the musicality of these hybrid structures, visitors entering the installation space encounter a soundscape of acoustic recordings of the substrate-borne vibrations encountered in and through these webs: the left channel emitting vibrations produced by *Cyrtophora* spiders composing with a *Nephila* web, the right channel broadcasting the signals of a *Nephila* spider composing with a *Cyrtophora* web. These recordings were made using a Laser Doppler Vibrometer, as well as piezoelectric and other sensors for amplifying these subtle web vibrational signals.

24.4 Arachnid Orchestra: Jam Sessions

Extending the cross-disciplinary experimentation of *Cosmic Jive*, Saraceno's next major project in interspecific communication was the *Arachnid Orchestra. Jam Session*s in 2015 (Bauer and Rujoiu 2017; see Fig. 24.9). For this project, Saraceno and his studio team drew inspiration from the acoustic properties of the web—and the different signalling behaviours of the spiders themselves—to create a series of musical instruments for playfully communicating with spiders: for both listening to the substrate-borne vibrations they produce, and playing vibrational signals back into the web, in response.

The instruments created for the Arachnid Orchestra incorporate special sensory devices—transducers, piezoelectric pickups and laser Doppler vibrometers to capture, translate and give voice to these subtle vibrations, as they travel along the threads of the web, or across a percussive surface (Fig. 24.10). These instruments were conceived and arranged with reference to the sections of a classical orchestra, including instruments from the string, percussion and wind families. These instru-

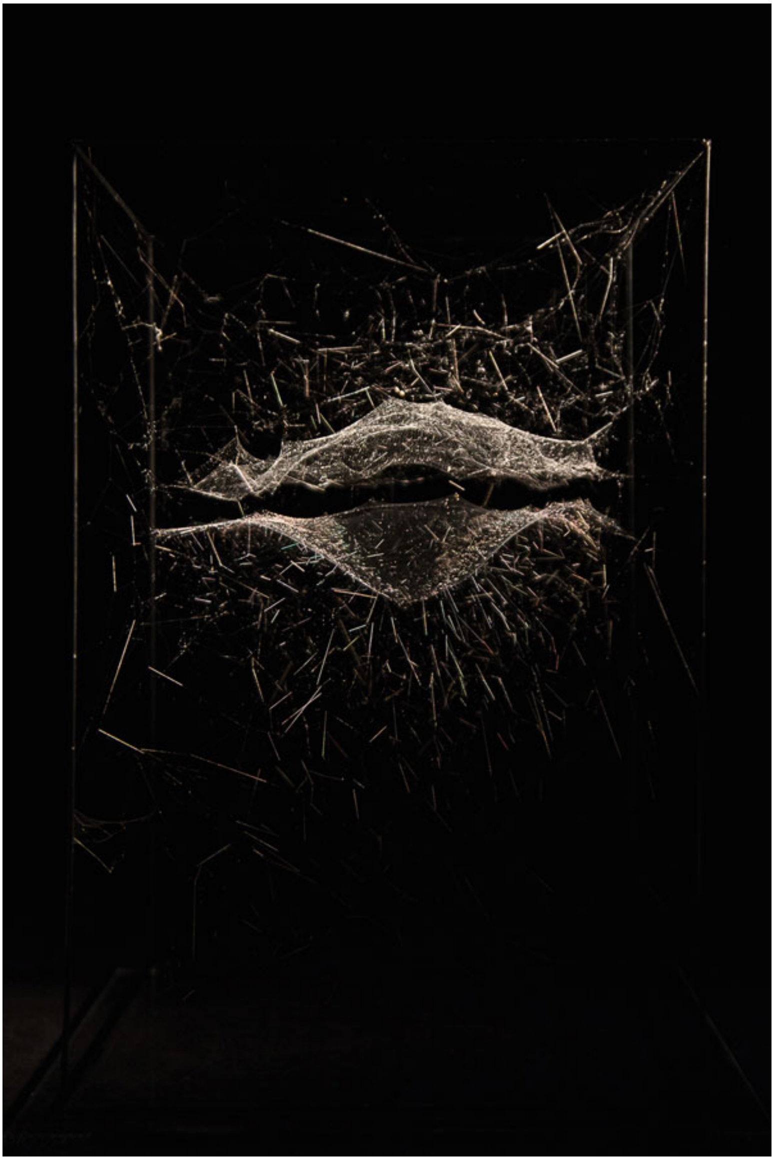

Fig. 24.8 Tomás Saraceno, *Hybrid semi-social musical instrument NGC 2976: built by* Cyrtophora citricola-*3 weeks—(tidally locked)* + Cyrtophora moluccensis-*4 weeks (turned 180° on Z axis) rehearsing towards ISS, 2014.* Spidersilk, carbon fibre, metal, glass, light 150W. Installation view, "Cosmic Jive: the Spider Sessions", Museo di Villa Croce, Genoa, Italy: Curated by Ilaria Bonacossa and Luca Cerizza. Photo by Studio Tomás Saraceno, 2014. Courtesy the artist; Andersen's, Copenhagen; Ruth Benzacar, Buenos Aires; Tanya Bonakdar Gallery, New York/Los Angeles; Pinksummer contemporary art, Genoa; Esther Schipper, Berlin

Fig. 24.9 Tomás Saraceno, *Arachnid Orchestra. Jam Sessions*, 2015. Installation view, NTU Centre for Contemporary Art, Singapore: Curated by Ute Meta Bauer with Anca Rujoiu. Photo by Ruey Loon, 2015. Courtesy the artist; Andersen's, Copenhagen; Ruth Benzacar, Buenos Aires; Tanya Bonakdar Gallery, New York/Los Angeles; Pinksummer contemporary art, Genoa; Esther Schipper, Berlin

ments are also envisioned as recording devices for capturing different bioacoustic signals, thus offering the potential for creating a comprehensive bioacoustic (or biotremological) archive.

A key part of this project was the *Jam Sessions* that were performed in the exhibition space (Fig. 24.11). These were interspecific encounters between spiders and invited musicians and performers, as mediated by the instruments that Saraceno created from the spider's webs and silk. In these experimental and improvised musical dialogues, the human performers *compose-with* the spider and the web, in playful attempts to find a harmonic attunement through a reciprocal process of creating and listening to vibrations together. A sonic exhibition record of these musical interspecific conversations is available on the NTU CCA Soundcloud site (accessible at https://soundcloud.com/ntuccasingapore/sets/arachnid-orchestra-jam).

24.4.1 String Instrument Section

We might most easily recognise the spider web as a *string* instrument—the plucking of every thread voicing a different note, according to its size, tension, material composition and position in the web. The string section of the Arachnid Orchestra

Fig. 24.10 Tomás Saraceno, *Arachnid Orchestra. Jam Sessions*, 2015. Installation view, NTU Centre for Contemporary Art, Singapore: Curated by Ute Meta Bauer with Anca Rujoiu. Detail of the customised piezo microphone used to pick up and amplify web vibrations. Photo by Studio Tomás Saraceno, 2015. Courtesy the artist; Andersen's, Copenhagen; Ruth Benzacar, Buenos Aires; Tanya Bonakdar Gallery, New York/Los Angeles; Pinksummer contemporary art, Genoa; Esther Schipper, Berlin

Fig. 24.11 Brian O'Reilly, *Jam Session #1: Arachnid Improvisations*, 2015 as part of "Arachnid Orchestra. Jam Sessions", NTU Centre for Contemporary Art, Singapore: Curated by Ute Meta Bauer with Anca Rujoiu. Photo by Studio Tomás Saraceno, 2015. Courtesy the artist

carries forward the musical possibility of spider web threads as strings of a musical instrument, using a Doppler Laser Vibrometer and customised, highly sensitive pick-up microphones (piezo elements) to capture and articulate web vibrations—produced by the spider as it tunes, adjusts or plucks the web. The sensitive laser vibrometers were directed toward small reflectors attached to the main lines of the spider webs—the radial threads of the orb web that are most efficient at transmitting longitudinal vibrations. Thin piezo elements were also connected to the radial threads, in order to pick-up the substrate-borne vibrations produced by the spider's movements. As the piezo effect is reversible, these devices also allowed us to play vibrations back into the web, via small, needle-based transducers, which carried back into the web the vibrations produced in orchestrated *Jam Sessions* with human performers. What resulted is a musical dialogue with the spider that evolves in real-time, a live, interspecific 'conversation'.

24.4.2 Percussive Instrument Section

Spiders also produce vibrational signals by drumming, an image which Saraceno and his team fed forward into the concept of a percussive section of the Arachnid Orchestra (see Fig. 24.12). The main elements of these percussive instruments were circular membranes in various sizes, to which sensitive contact microphones were attached. 'Drumming spiders' were then placed upon these membranes—Lycosidae and *Heteropoda davidbowie* spiders that use their pedipalps, legs or body to drum and produce conspecific vibrational signals (both in mating rituals, and to mark and defend territory; Rovner 1980). The percussive instruments used devices to amplify these drumming signals: piezoelectric elements that were attached to the membrane, or laser vibrometers pointing at either the drumming membrane, or the drumming spider itself.

Fig. 24.12 Tomás Saraceno, *Drum-set M33, NGC 598 for a vibrational ensemble*, 2015. Installation views, "Arachnid Orchestra. Jam Sessions", NTU Centre for Contemporary Art, Singapore: Curated by Ute Meta Bauer with Anca Rujoiu. Left: Laser vibrometer, membrane, piezo elements, amplifier. Right: Video recording of Lycosidae spiders playing the drum instrument. Photos by Studio Tomás Saraceno, 2015. Courtesy the artist

24.4.3 Wind Instrument Section

The more speculative element of the Arachnid Orchestra was the wind section, represented by an ‘Aeolian Instrument’ (see Fig. 24.13). This instrument was inspired by certain spiders’ ability to travel long distances through the air, via ‘ballooning’ or ‘kiting’ behaviour. Ballooning or kiting is a method of aerial dispersal by which spiders use updrafts (thermal currents or vertical wind-velocity gradients) to travel long distances and colonise new areas—sometimes in response to local natural pressures, such as floods (Duffey 1998). Typically, young spiders (spiderlings) will climb to an elevated location, perform a ‘tiptoeing’ behaviour (raising themselves up on the tips of their eight tarsi) and release gossamer silk into the air, until the silk, wind and air/thermal currents have generated enough drag and lift for the spiders to become airborne, transforming their gossamer threads into aerial balloons or kites. In particular, this instrument was inspired by the ballooning behaviour of the larger, social *Stegodyphus* species, capable of achieving aerial lift by releasing multiple gossamer strands in mass dispersal events (Wickler 1973).

An Aeolian harp—from which this instrument draws its name—produces harmonic frequencies solely through the motion of wind across its strings. Sound

Fig. 24.13 Tomás Saraceno, *Aeolic instrument for a Lighter-than-Air Ensemble*, 2015. Air stream, spider silk, carbon fibre poles, webcam, video tracking (in collaboration with Odysseus Klissouras); Installation view, “Arachnid Orchestra. Jam Sessions”, NTU Centre for Contemporary Art, Singapore: Curated by Ute Meta Bauer with Anca Rujoiu. Photo by CCA Singapore, 2015. Courtesy the artist; Andersen’s, Copenhagen; Ruth Benzacar, Buenos Aires; Tanya Bonakdar Gallery, New York/Los Angeles; Pinksummer contemporary art, Genoa; Esther Schipper, Berlin

theorist Doug Kahn draws from this image of the Aeolian harp to describe what he calls *aelectrosonic* sounds: sounds produced by ‘nature’, and parsed through natural or man-made instruments such that they are understood as music by human ears—for example, the musical sound of wind through telegraph poles (Kahn and Macauley 2014). Saraceno’s Aeolian Instrument draws on these twinned histories of spiders ballooning on threads buoyed by the wind, and of those same wind drafts and air currents as being capable of transforming the spider threads into a musical instrument that allows us to hear arachnid or aelectrosonic vibrations as music. This instrument also draws technical inspiration from the early electronic *theremin* instruments, which use proximity sensors and aerial gestures to generate musical sounds. The Aeolian Instrument developed by Saraceno and his studio team optically captures the dynamic and continuous movements of floating threads of spider silk from *Nephila* species, transforming these movements into fluctuating sound frequencies.

24.5 The Cosmic Dust Spider Web Orchestra

Saraceno’s next large-scale artistic experiment in the musicality of the spider web—and its potential to open vibrational channels of interspecific communication—was the *Cosmic Dust Spider Web Orchestra* (Fig. 24.14), exhibited at the Museo de Arte Moderno, Buenos Aires (MAMBA) in 2017 in his solo exhibition, ‘How to Entangle the Universe in a Spider Web’ (Ball 2017).

This instrument takes the form of a large-scale, responsive acoustic installation enrolling a suite of human and nonhuman agents: a spider resting within a complex web, a moving field of aerial dust particles, and a series of customised acoustic devices and sonification systems able to pick-up, transmit and transcode this interplay between human, dust and arachnid.

Fig. 24.14 Tomás Saraceno, *Arachno Concert with Arachne (*Nephila senegalensis*), Cosmic Dust (*Porus Chondrite*) and the Breathing Ensemble, 2016. Nephila senegalensis* silk, carbon frame, light beam, cosmic dust, stellar wind, sonic waves, video camera, loudspeakers, video projector. Installation views, “Tomás Saraceno: Aeroecene”, Esther Schipper, Berlin. Photos by Studio Tomás Saraceno, 2016. Courtesy the artist; Esther Schipper, Berlin

In this installation, a spider (commonly a *Nephila* species) rests within a complex Hybrid Spider Web to which is connected a number of piezo-sensors that register the vibrations produced as the spider plucks and tunes the web. These vibrations are then sonified and transmitted through a central speaker, above which one can see an illuminated beam of moving dust particles—both common (terrestrial) dust and chondrite (cosmic) dust.[6] The speaker vibrates in response to the spider's movements, which feeds back into this responsive system by shifting the trajectories, speeds and configurations of these moving aerial dust particles. As the dust dances, the movements of individual dust particles are detected and followed by a custom-built tracking system, whose design abstracts from systems used to track animal group behaviour.[7] Using this tracking data, the movements of individual dust particles are translated into an enveloping sonic opera via a unique system for sonifying data and spatialising sound, designed by Studio Tomás Saraceno's audio researcher Dominik Hildebrand. This polyphony of sound also feeds back into the spider's web, and thus its sensory system, perhaps influencing the spider's movements (Frings and Frings 1966), and thus affecting the dynamic composition of this acoustic performance. The human visitors to the installation also become compositional agents in this multispecies score. Their movement and breath is envisioned as a 'breathing ensemble' within the *Cosmic Dust Spider Web Orchestra* that influences the trajectories of the dust particles (see Fig. 24.15), thus modulating their sonic presence within the installation. The whole installation thus performs as a responsive acoustic system whose various components interact with and influence one another, creating a polyphonic concert that humans can *hear*, and spiders can *feel*.

The *Cosmic Dust Spider Web Orchestra* extends the idea of more-than-human communication: exploring our capacity not only to listen to the bioacoustic vibrational signals produced by nonhuman entities (spiders), but to attune to the acoustics of the *abiotic* and the *cosmic*, here represented by the mobile particles of cosmic dust that dance around the room. In this way, the possibilities of more-than-human communication widen to include the possibility of a 'cosmic attunement'—an enhanced sensitivity to the greater, cosmic vibrations of which our experience is a part. The spider web, then, is a threshold instrument through which to sense and attune to a universal vibrational polyphony.

The *Cosmic Dust Spider Web Orchestra* occurred in the context of the broader MAMBA exhibition, for which Saraceno and his team worked with Martín Ramírez (Head of Arachnology, Natural Sciences Museum Bernardino Rivadavia-CONICET) to develop 'Quasi-Social Musical Instrument IC 342 built by 7000 *Parawixia bistriata*—six months', an immersive installation featuring the largest

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[6] The 'cosmic dust' in this installation is materially represented by dust particles that Saraceno generated from crushed meteorites (chondrites). True cosmic dust and interplanetary dust particles, while originating in outer space, are also prevalent on Earth; cosmic dust enters our atmosphere at a rate of somewhere between 5 and 270 tonnes per day.

[7] This tracking system was developed in a research collaboration with *Loopbio GmbH* principal John Stowers and Max Hofbauer.

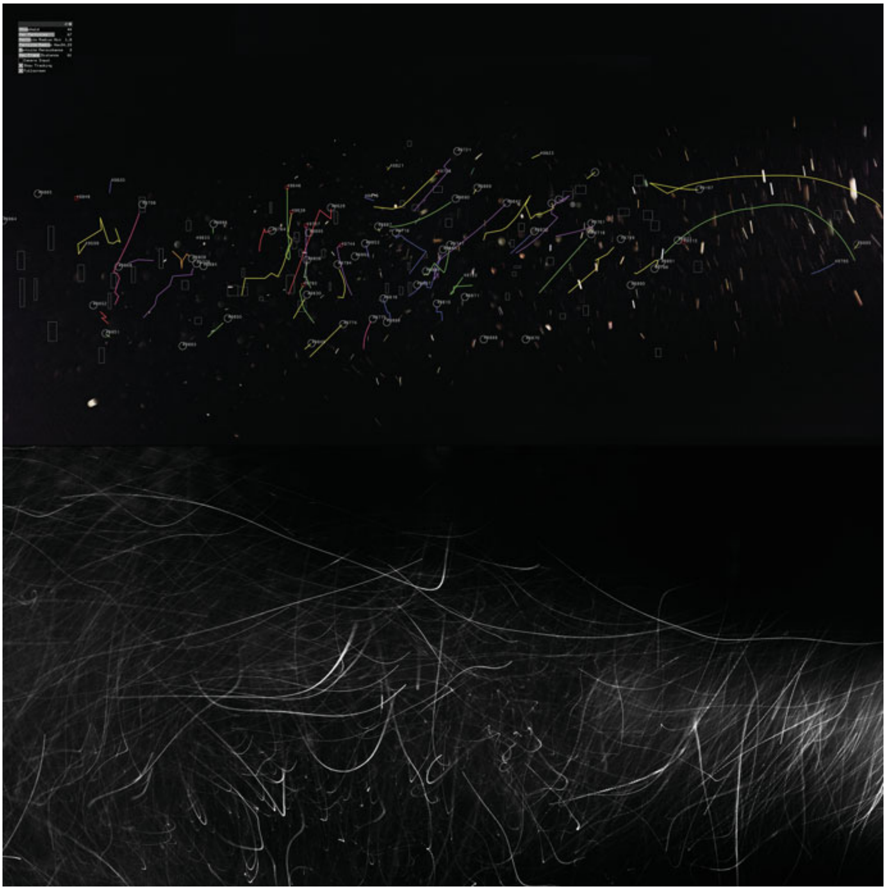

Fig. 24.15 Tomás Saraceno, *Cosmic Dust Spider Web Orchestra*, 2017. Trajectories of cosmic dust particles as they respond to breath and movement, mapped by custom tracking software. Courtesy the artist. © Tomás Saraceno

spider web ever exhibited (Fig. 24.16). Developed over the course of 6 months and involving several field trips to Corrientes y Santiago del Estero in northern Argentina, this installation features the long silk sails and interconnected webs woven by 7000 social territorial *Parawixia bistriata* spiders, whose threads are anchored to and bridging various frames within the architecture of the museum space. The vibrational signals travelling in and through this giant, interconnected web were not amplified, and thus remained inaudible to human ears, but perhaps otherwise perceptible to visitors to the space.[8]

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[8] The vibrational communication channels in social webs are not well understood. *Parawixia* spiders are known to use ‘web bouncing’ to signal to web intruders (Wenseleers et al. 2013), and these bounces might act as perceptible visual indicators of imperceptible biotremological signals.

Fig. 24.16 Tomás Saraceno, *Quasi-Social Musical Instrument IC 342 built by 7000* Parawixia bistriata—*six months*, 2017. Installation view, "Tomás Saraceno: How to Entangle the Universe in a Spider Web", Museo de Arte Moderno de Buenos Aires: Curated by Victoria Noorthoorn. Photo by Studio Tomás Saraceno, 2017. Courtesy the artist; Andersen's, Copenhagen; Ruth Benzacar, Buenos Aires; Tanya Bonakdar Gallery, New York/Los Angeles; Pinksummer contemporary art, Genoa; Esther Schipper, Berlin

24.6 The Spider Salons

In addition to these large-scale artistic projects, Saraceno has created an ongoing platform for staging open experiments in human-arachnid communication, and for engaging a public discourse around the activities of the Spider/Web Research Group, through his *Spider Salon*s. Initiated in 2015 and led by Spider/Web Research Group member Sofia Lemos, the *Spider Salon* program is an ongoing series of performative encounters between various spiders (and their webs) and human interlocutors—be they musicians, biologists, poets, theorists, scientists or philosophers. The format of each *Spider Salon* is open, playful and experimental, often taking the form of *Jam Sessions* in which invited musicians and sound artists perform in concert with the spiders and their webs, transforming the *Spider Salon* into a vibrating laboratory for experimentation.

Salons were an integral part of the research and development of the *Arachnid Orchestra. Jam Sessions*. For example, a Spider Salon held at the Spider/Web Research Group in Rummelsburg in October 2015 was the context for an interspecific interaction between a *Cyrtophora citricola* spider and musician Evan Ziporyn, Kenan Sahin Distinguished Professor of Music and Inaugural Director of the Center for Art, Science and Technology, MIT (Fig. 24.17). The sound recordings produced in this and other encounters were brought together in the *Jam Sessions* album that accompanies the exhibition (Bauer and Rujoiu 2017). The research and salon

Fig. 24.17 *Cyrtophora citricola* duet with Evan Ziporyn. Spider Salon, 28 October 2015, Studio Tomás Saraceno, Berlin. Photo by Studio Tomás Saraceno, 2015. Courtesy the artist

encounters were also presented in an ‘arachnid orchestra’ website produced for this exhibition.

In these encounters, the audience is invited not only to listen and attune to the vibrational cues exchanged between the spider and human performers, but to engage with the philosophical concepts and questions that underpin Saraceno’s spider-related artworks, and the multidisciplinary program of the Spider/Web Research Group. These mediated events between spiders and humans are part of Saraceno’s ambitious attempt to develop an interspecies dialogue; to generate sensory experiences through which to understand our multispecies entanglements.

24.7 Speculations on Future Research

Studio Tomás Saraceno’s Spider/Web Research Group is in a unique position to conduct interdisciplinary research involving spiders and their webs (Saraceno et al. 2010; Saraceno and Jäger 2012). The expertise of its in-house researchers and close collaborative network spans diverse research areas relevant to spider taxonomy and behaviour, web architecture and material analyses, and biotremological communication. The very interdisciplinary nature of the Spider/Web Research Group’s inquiries ensures that the outputs and findings it generates offer insights relevant to discourses from a diverse range of research disciplines, including art and architecture, engineering, sociology, anthropology, cultural theory, posthumanism and cognitive science. These address questions posed in the context of the broader 'nonhuman' research that turn toward understanding the implications and opportunities of multispecies entanglement in our current (Anthropocenic) era.

Future directions for the biotremological research of the Spider/Web Research Group include a study of web-based biotremological signal propagation and attenuation and its relationship to web architecture, which might be better understood through mechanical and functional analyses of web architectures, and through examining the material properties of different types of silk and web fibres. A broader project will investigate this relationship (between signal propagation and web structure) from the perspective of the evolution, differentiation and diversification of web architectures.

The spider web instruments that Saraceno has created are also envisioned as recording devices, capable of generating a repository of biotremological 'sounds' from a range of different spider species and via a range of different web architectures. These include 'solitary' spiders and webs, as well as the webs and signals of social and semi-social spiders in colonial and social web structures. Another of Saraceno's research ambitions is to create an open-access archive of the spider's biotremological signals, to be used as a research resource by artists and scientists alike. In parallel, Saraceno hopes to generate both an electronic (online) archive of 3D spider web scans, and a physical taxonomic archive of spider web architectures, drawn from his collection of spider webs built by spider species sourced from around the globe. In addition to creating an important taxonomic resource, Saraceno's intention is to propose a visual and sonic history that tracks the evolution of spider web architectures in concert with spider morphologies and vibrational signalling properties. These acoustic arachnid projects—including the planned web and biotremological archives—will open a dynamic array of new and exciting experimental possibilities, inspiring new interventions in artistic research, in music and acoustics (performance, composition and recording), and in as yet unimagined scientific ventures arising from a cross-pollination of research practices and concepts between different domains.

Acknowledgments *Cosmic Jive: The Spider Sessions, Arachnid Orchestra. Jam Sessions* and *The Cosmic Dust Spider Web Orchestra* arose from strong and lively collaborations involving Saraceno and his studio team, and numerous arachnid and human collaborators, to whom we would like to express our gratitude. In addition to the team at Studio Tomás Saraceno—particularly Sofia Lemos for leading the Spider Salon program and Dominik Hildebrand for his technical expertise in developing the web sonification devices—we thank the following members of the extended Interspecific Network (in no particular order) for their ongoing contributions, enthusiasm and dialogue: Friedrich G. Barth, Markus Buehler, Hannelore Hoch, Peggy Hill, Peter Jäger, Alex Jordan, Yael Lubin, Matthew Lutz, Zhao Qin, Jutta Schneider, Andreas Wessel, Jonas Wolff, Christof Wulff and Samuel Zschokke. In the development of the *Arachnid Orchestra*, we would like to thank sound engineer Frgmnt Grys, and sound artist Odysseus Klissouras. Thanks to the musicians and writers who jammed with the spiders: Bani Haykal, Joyce Beetuan Koh, Brian Massumi, Brian O'Reilly, Elizabeth Povinelli, David Rothenberg, Etienne Turpin and Evan Ziporyn. We would also like to thank Ute Meta Bauer, Anca Rujoiu, Julie Hyun, Syaheedah Iskandar, Magdalena Magiera, Jegan Vincent de Paul, and Isrudy Shaik at NTU CCA Singapore for their tireless work and assistance in realising the *Arachnid Orchestra. Jam Session*s project. Many thanks also to Claus Andersen, Antonella Berruti, Tanya Bonakdar, Francesca Pennone and to Esther Schipper for their commitment. Of course, none of these works or inspirations would exist without all of the spiders, whose diligent work makes these research projects possible. A huge and warm thanks to all of these arachnid species, particularly *Nephila senegalensis* and *Cyrtophora citricola*.

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Chapter 25
Bioacoustic Music Inspired by Biotremological Research

Matija Gogala and Boštjan Perovšek

Abstract This chapter is not about science. It tells about the natural phenomenon of insect tremulation, bioacoustics in a wider sense, and about sound, art, and music. During the 1st International Symposium on Biotremology, 5–7 July 2016 in San Michele, Italy, as part of the social program, appeared among others Slovenian musician Boštjan Perovšek with a musical performance. The performance entitled, "Bugs, a walrus and a door—Trento 16", was inspired and composed mostly of original recordings of tremulation songs of bugs (Heteroptera), mixed with some underwater sounds of walrus and the recordings of a door creaking at the Vodnik Homestead in Ljubljana. Recordings of the bug tremulation songs originated from the laboratory of Matija Gogala (MG) at the Institute of Biology and Department of Biology, Biotechnical Faculty, University of Ljubljana, and later from the Slovenian Museum of Natural History. This chapter tells about the first meeting between Prof. Gogala and Mr. Perovšek, and by which circumstances the recordings of vibrational songs of bugs have become significant material for the so-called bioacoustic music of Boštjan Perovšek (BP). Explanations about "concrete" and "bioacoustics" music are also added in the chapter.

25.1 Beginnings/Personal Backgrounds

BP I began to get to know music in my childhood by listening to vinyl gramophone disks, and was amazed at the sound combination of instruments and the crackling of the disk underneath the needle. This reminded me of walking in the forest, where branches crack beneath the feet, birds are heard in the treetops, and in the distance

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chirps are heard from the nearby meadow. I found the sound of nature as a mighty orchestra. Many years later, I was impressed with the frog singing and I wanted to make a concert for frogs and ensemble of instruments. Searching for a producer of such a project in 1985, with the help of musicologist Professor Andrej Rijavec, the then head of the musical program at Cankarjev dom in Ljubljana, I met a biologist, Prof. Matija Gogala, who was the first to reveal to me the vibrational songs of bugs. It was an acoustic shock to me . . . as if I were to peep through the sound microscope and find an undiscovered, distant sound world. For some time, I forgot about frogs and took an interest in the orchestra of bugs. Still today, among other sounds of nature and civilization, bugs represent to me an audio source for composing and for electroacoustic live processing at concerts.

MG For me it all began during my high school time and due to my early interest in insects. At the beginning I collected—as many young boys did—butterflies and beetles, but later I decided to direct my attention to the group of true bugs (Heteroptera). I got interested in them especially during my visits to ponds and creeks and I admired the diversity of aquatic and semiaquatic Heteroptera. Very soon I discovered that their terrestrial relatives are also worth observing, studying and collecting. So I found interesting bugs of the family Cydnidae at the forest edges in the early spring. After overwintering they showed many interesting types of behavior like complicated courtship and brood care. Observations of the latter gave some years later the material for my first short scientific paper (Gogala 1959). And the courtship behavior I observed when bringing these cydnid bugs home lead to a suspicion that they probably produce some sounds or vibrations. More about this one can read in the Introduction of my book *On the Trail of Mountain Cicadas* (Gogala 2013a). At the time of my first observation of courtship in these insects, and even some years later at the university, I did not have any possibility to record such signals. However, I read in the literature (Ossianilsson 1949; Leston 1954; Jordan 1958) that a simple method of listening to such signals is through a medical stethoscope. In the 1950s I used this method and discovered an unusual richness of surprising sounds. Only some years later I received from the A. v. Humboldt Foundation my first suitable recording and analyzing apparatus, enabling my research in this topic.

In the following years, I heard and recorded many most interesting sounds unlike anything heard or experienced in normal life. I say sounds, because we first used very sensitive microphones in a close range, since we did not know if faint sounds were transmitted to target animals as air-borne sounds or as substrate vibrations. The signals were not easily heard and recorded, due to very low sound levels. During early investigations we used for listening and recording a very sensitive ribbon, a condenser and dynamic microphones at short distance of a few millimeters or a centimeter from the singing bugs. Only later, when we discovered that true bugs (Heteroptera) are using mainly substrate-borne vibratory signals (biotremulation signals) (Gogala et al. 1974; Gogala 2014), we started to use various kinds of contact microphones, other electromagnetic devices (e.g., Strübing and Rollenhagen 1988) and later also laser vibrometers (Gogala 2006). But no matter what technology was used, the signals or songs of this group of insects remained equally unique and surprising.

25.2 Concrete Music

BP In the recent period, the name “bioacoustic music” has been established for the music that has its basic sound origin in natural sounds, mainly of the animal world. Certainly, we can also define it with the somewhat older term “concrete music”, which was introduced by the French composer Pierre Schaeffer (2012). The basic principle of concrete music is the use of recordings of the environment (mostly of nature), which are interconnected in the composing process. The sound modules are created and are combined into sound compositions later in the electroacoustic processing. All this was taken into account when I was acquainted with concrete music at the end of the 1970s and made the first experiments. Significant progress for me, in fact, meant the above-mentioned encounter with the almost inaudible acoustic world of bugs.

MG The fact that the biotremulation signals are not easy to record with microphones made for air-borne sound is well known to all biologists working in the field. And this is also the main reason why such signals, played back through loudspeakers, are not known to most people. Often they appear as very surprising sound patterns and are therefore very suitable for musicians like Boštjan Perovšek (Gogala 2013b).

BP The realization that we are living in the multi-layer sound world from which we hear only a fragment led me to hardly audible sound material. As to that, it was also very important for me to understand better the origin and conditions of the sound formation. Therefore, the cooperation with scientists was a logical decision. To combine various sound layers into compositions is quite different if the musician is aware of combining sounds that could not be heard in nature at the same time, rather than combining those sounds merely according to the principle of liking them. Thus, the aesthetic moment is associated with a rational, scientific one. As an example, let me quote my tripartite composition *Belum* (Perovšek 1995, tracks 8–10) in which the “timetable” of animal sound activity was taken into account. The individual titles of sections define the time occurrence of animal sound activity and at the same time indicate one of the principles of selection of the sound material.

MG The principle of time sharing or a daily timetable of animal sound activity is best evident due to the highest biological diversity in the soundscape of tropical forests as shown in the paper of Gogala and Riede (1995). Stimulated by observations during the MNS (Malaysian Nature Society) Belum expedition in 1994, I myself prepared a compilation of sound mixes in five sequences representing the main sound patterns depending on the day and night time (Belum 1–5: Morning, Before noon, Afternoon, Evening and Midnight) (Gogala 1994). These sound files are also playable on the web (Between Bioacoustics and Music: http://www2.arnes.si/~ljprirodm3/okvir.html). Original recordings were used by Boštjan Perovšek in the bioacoustic composition *Belum* on a CD (Perovšek 1995, tracks 8–10).

It should be mentioned that I published later, due to the repeated initiative of Andrej Rijavec, a paper in the Muzikološki Zbornik (Musicological Annual) (Gogala 1997). Herein I pointed out some characteristics of acoustic and vibratory signals, recorded in the laboratory or in the field, at home or in tropical countries. In this paper, I tried to show that one can find in animal sounds many features typical of music (at least the classical ones): rhythms, tonality, consonances, chorusing and alternation, and more. The examples from my paper are still available on the web at the address given above. This website was mentioned in the BBC Wildlife Magazine as the Website of the month (Blackman 2003).

At that time Boštjan Perovšek had already performed publicly and published some bioacoustic compositions using my recordings. He also helped me with the musical notation of the "drummer bug's" song (*Sehirus luctuosus*) published in this paper. Let us return to the bioacoustic music.

25.3 Bioacoustic Music: Concept, Material Selection, Analysis, and Electroacoustic Processing

BP The creation of bioacoustic music requires an approach differing from that of creating the classically written music in which notation is essential. From a radical viewpoint, music and sound art are supposedly exclusive; sound art, according to some experts, is not music (see Gardner and Voegelin 2016). But I do not share this opinion. I would not discuss the relationship between music that is noted down (if one can read notes, he does not need the performance since he is already experiencing it) and the live music. How much the notes faithfully convey the composer's ideas, with regard to the presentation of the so-called text, mainly the expression, and how faithful a living performance is, would be a question for musicologists. Nye Parry establishes the connection between two notions "music and sound art" in such a way that we can agree that music cannot be separated from sound art and vice versa, it is a question of intertwining coexistence (Parry 2016). The fact is that bioacoustic music uses the principles of concrete and electronic music creation when a composer (a sound artist) has almost absolute control over performance. When creating music the notes are often not written because they are substituted by a soundtrack (audio-recording). Thus, the sound recorder acts as a notepaper on which sounds are recorded, instead of written notes (with all the marks of duration, tempo, expression . . .). The sound recorder acts also as a musical instrument. I myself use the principle of preparing the sound material as modules, miniature sound compositions, which in the processing are combined according to the previous plan. The plan acts as a score that defines the finally recorded song or gives just instructions for the live performance.

When creating bioacoustic compositions the composer/sound artist and the one who selects and makes recordings of the sound material usually work together. I am mostly working with biologists who provide me with various recordings of animal sound activity. The material is scientifically arranged, which helps me in making a selection. It does matter when and how a particular recording is used. Information about recorded specimens and the recording conditions can be compared with the knowledge of instruments that are to be used in musical compositions. Therefore, the sound material arranged from the scientific point of view is extremely important and represents the first step in classification. The further process involves the analysis that has already been made in a scientific laboratory. It is about making the time and spectral analysis of recordings. In combination with a later comparison of sound curves in real-time (when the spectrogram and the sound curves overlap on the timeline), we get an insight into the recorded sound and the comparison with the recordings of morphologically identical specimens, too. This is important for biologists/researchers at the classification, and for the musician to express the differences between the visually identical, but also by the sound different specimens represent in an audio source; we could also say that this is a different instrument within the family (such as strings or wind instruments). At this stage, the first phase of producing a new composition is made. Furthermore, the process involves the classification of material with regard to duration, frequency range, rhythm and tempo, as well as the cuts regarding the extent of everything previously mentioned. In some occasions the recording itself has become a completed sound module (Fig. 25.1) and does not need any additional processing, such as shortening or cutting the frequency range, etc. The only processing is to place it on a timeline. In other cases, however, the original sound recording is adjusted in such a way that a particular

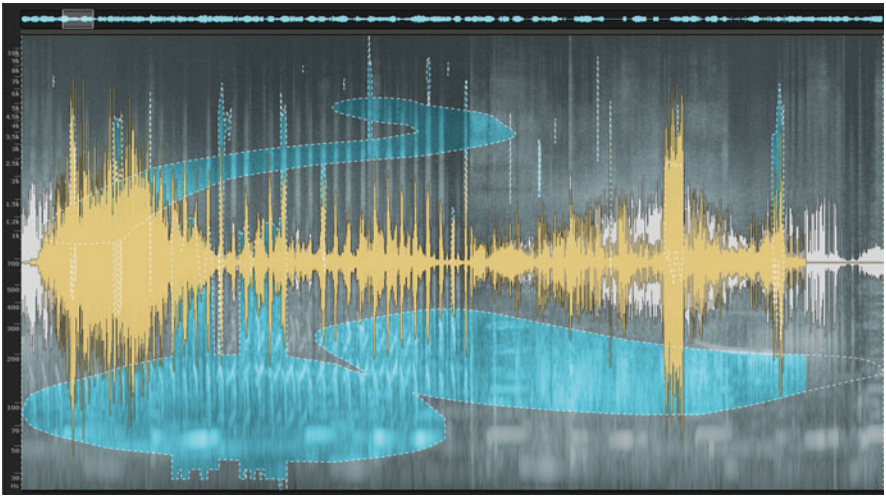

Fig. 25.1 Sound module Bugs WD 01, prepared in iZotope Iris 2

"frequency cake" can be cut out, which has a certain duration, rhythm, and tempo, and it becomes a sound module that is later placed on a timeline.

At the end the obtained modules are interconnected and can be furthermore electroacoustically processed with instruments, such as resounding, repetition, delay, audio loops, premodulation, distortion, sound levelings, compressions .... All this in the end represents the concept/score intended for recorded music or live performance.

The composition "Bugs, a walrus and a door—Trento 16 (live electronics)" was intended for live performance; therefore, some particularities were added in the preparation. Certain modules were pre-processed and did not change during the live performance, while others were provided for electroacoustic live processing. Pure electronic modules were added to the composition, which in their structure resemble the raw or processed modules of animal sound or biotremological activity. The preparation of electronic elements is inspired or powered by the structure of animal sounds or vibration. The result is a song that in some passages causes the listener to doubt whether he is listening to purely electronic or purely concrete music. If the previously recorded composition from 1986 was purely concrete music, realized as a 31-minute, 8-channel composition, consisting of vibratory, biotremological signals of bugs, and the sounds of a door and walrus represent only the sound effect, the 2016 version (Perovšek 2016) was planned as a live performance. Individual sound modules and the electroacoustic live processing are performed on the basis of a time-limited plan/structure. The joining of elements is defined as a performance of sound sets intertwining also on the principle of coincidence and the principle of reactions to intermediary sound results. The final effect is to recall the natural sound environment that is constantly changing. Although the first impression of being in a natural sound environment (particularly for those who do not professionally deal with the monitoring of natural sound environments) is always the very same or at least a similar sound set, possibly depending only on the season, yet a more detailed insight into the structure shows the constant change, addition or even disappearance of individual sounds. Thus, the composition never has the same final form. The only final form is a recording of each individual performance.

25.4 The Bioacoustic Composition "Bugs, a Walrus and a Door—Trento 16"

BP At the end we should describe and comment on the bioacoustic composition, "Bugs, a walrus and a door—Trento 16" from both a musical and biological perspective. The composition is based on the original song, "Bugs, a walrus and a door start dancing", a 31-minute, 8-channel version from 1986, which uses the sound material created by bugs, a walrus and creaking door at the Vodnik Homestead in Ljubljana. Prof. Matija Gogala "equipped" me with a collection of magnetic tapes with various tunes. The tapes consisted of approximately 80 hours of material, from which I took about 20 different length samples—ranging from a few seconds to half a minute. Once they were classified and played to confirm, the sounds of walrus and door were added.

I classified this piece of music as bioacoustic; although, it could easily be considered electroacoustic. However, as I wish to be consistent with the original idea, I insist on this definition. The composition is not called bioacoustic due to the contemporary biotrends, but rather because it is based on the sound material obtained from scientists who investigate animal sounds. This scientific discipline is called bioacoustics. The credits go to the included voluntary live performance in 1986 (by the members of experimental music group SAETA) and involuntary performers (animals)—a result of being consistent in defining the project's starting points and the music itself. The short stereo version of the composition, which can be found on the CD "Boštjan Perovšek—Touchings" (Perovšek 1995, track 7) and on the vinyl LP disk "Bio-Industrial Acoustica (green)" (Perovšek 2013), was also included in the Ars Acoustica 1995–1996 Listening Proposals Programme within the framework of the European Broadcasting Union.

The composition "Bugs, a walrus and door—Trento 16 (live)" (Available from: https://bostjanperovsek.bandcamp.com/album/bugs-a-walrus-and-a-door-trento-16-live-electronics) is a special version based on the 31-minute original version. It can be realized as a 15–20 minute long quadrophonic or stereo version, in which original samples are mixed in a new way and in new combinations. This version also includes a new soloist: a bug *Legnotus limbosus*. The first performance took place during the 1st International Symposium on Biotremology in July 2016, hosted by Fondazione Edmund Mach, San Michele all'Adige, Italy.

MG For the interested biologists, the insect species that contributed with their tremulation signals to this composition, together with the corresponding publications if any, are herein listed:

Heteroptera:

Cydnidae:
Sehirus luctuosus (Fig. 25.2, Gogala 1978, 1997)
Tritomegas bicolor (Fig. 25.2, Gogala 1970, 2006; Gogala and Hočevar 1990)
Legnotus limbosus (Figs. 25.2 and 25.3, unpublished data)
Macroscytus brunneus (Fig. 25.2, Gogala 1978)
Reduviidae, Phymatinae:
Phymata crassipes (Fig. 25.2, Gogala and Čokl 1983; Gogala et al. 1984; Gogala 2006).

Songs of the listed species are described in the above-cited publications with the exception of *Legnotus limbosus*.

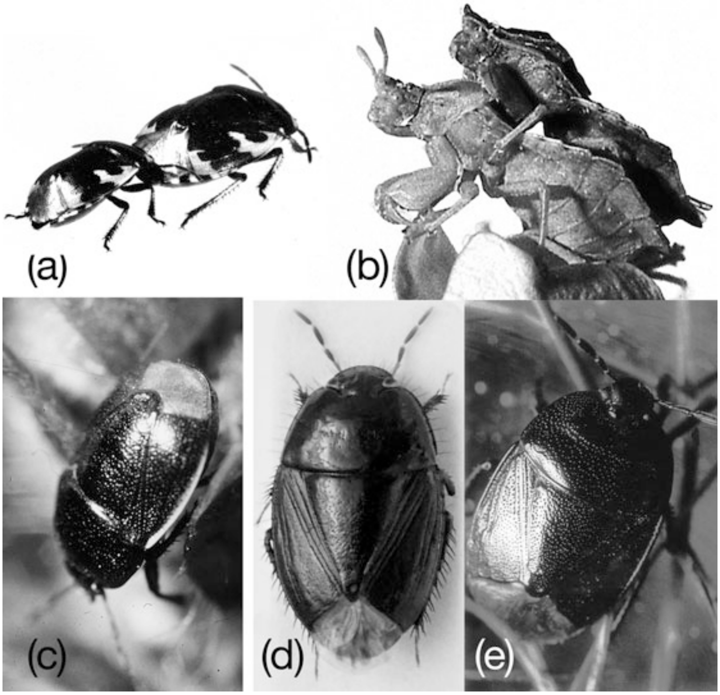

Fig. 25.2 Bug performers: (**a**) *Tritomegas bicolor* pair during courtship, (**b**) *Phymata crassipes* male sitting on the female during courtship, below males of (**c**) *Legnotus limbosus*, (**d**) *Macroscytus brunneus,* (**e**) *Sehirus luctuosus*

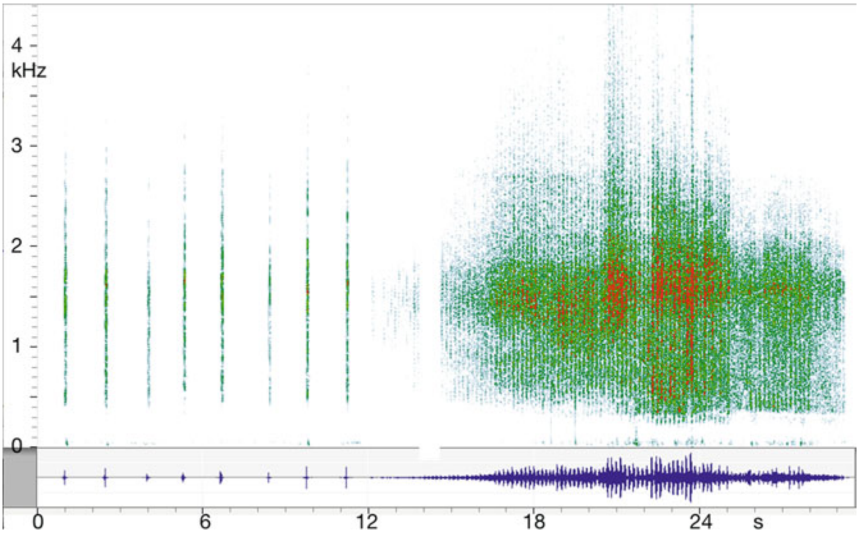

Fig. 25.3 Sonagram. Selection of the vibrational song of *Legnotus limbosus*

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Systematic Family and Species Index

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