Animal Signals and Communication 8

Peggy S. M. Hill · Valerio Mazzoni ·
Nataša Stritih-Peljhan ·
Meta Virant-Doberlet ·
Andreas Wessel *Editors*

Biotremology: Physiology, Ecology, and Evolution

Springer

Animal Signals and Communication

Volume 8

Series Editors

This book series provides a wide coverage of animal communication research including signal production and perception, development, behavioural mechanisms, signal function, population effects and the evolution of communication systems. It includes intra- and inter-specific communication, addresses communication in all taxa including humans and covers signals of all sensory modalities - visual, acoustic, chemical, tactile and electrical. Each volume summarises our current understanding of signals and communication in a particular context, this may be in a single taxonomic group or as a topic of current interest across a wide range of taxa. The series is aimed at scientists, university teachers and graduate students.

Peggy S. M. Hill • Valerio Mazzoni •
Nataša Stritih-Peljhan • Meta Virant-Doberlet •
Andreas Wessel
Editors

Biotremology: Physiology, Ecology, and Evolution

Springer

Editors
Peggy S. M. Hill
Department of Biological Science
University of Tulsa
Tulsa, OK, USA

Valerio Mazzoni
Research and Innovation Centre, Fondazione Edmund Mach
San Michele all'Adige, Trento, Italy

Nataša Stritih-Peljhan
Department of Organisms and Ecosystems Research
National Institute of Biology (NIB)
Ljubljana, Slovenia

Meta Virant-Doberlet
Department of Organisms and Ecosystems Research
National Institute of Biology
Ljubljana, Slovenia

Andreas Wessel
Center for Integrative Biodiversity Discovery
Museum für Naturkunde - Leibniz Institute for Research on Evolution and Biodiversity
Berlin, Germany

ISSN 2197-7305 ISSN 2197-7313 (electronic)
Animal Signals and Communication
ISBN 978-3-030-97418-3 ISBN 978-3-030-97419-0 (eBook)
https://doi.org/10.1007/978-3-030-97419-0

This Springer imprint is published by the registered company Springer Nature Switzerland AG
The registered company address is: Gewerbestrasse 11, 6330 Cham, Switzerland

To Matija Gogala,
A pioneer in studying vibrational communication, and the founder of the Slovenian School of Biotremology.

Contents

Part VI Applied Biotremology

Part I
Studying Vibrational Behavior: Ideas, Concepts and History

Chapter 1
Quo Vadis, Biotremology?

Peggy S. M. Hill, Valerio Mazzoni, Nataša Stritih-Peljhan, Meta Virant-Doberlet, and Andreas Wessel

Abstract Since our first collaborative book in 2014, which also included the first suggestion for a name for our new scientific discipline of biotremology, our focus has shifted from studying vibrational communication in a few groups of arthropods, to studying vibrational behavior (so that cues could be included) and now to a focus on physiology, ecology, and evolution. During this time, our scope has dramatically increased, but so have the numbers of publications on biotremology, as have the numbers of biotremologists of all ages, representing all continents on the Earth except for Antarctica. Our range of taxa has also expanded to encompass nematodes to mammals and birds. In this first chapter, our international editorial team, which represents Italy, Slovenia, Germany, and the USA, has taken on the role of writers to introduce each of the other 22 chapters in a preview of what the reader will find within the book. We also have collaborated to address the question in our chapter's title, "Quo vadis, biotremology?" Where are we going with this scientific discipline, and where would we aspire to go, if we had unlimited funding and unlimited years to our lives?

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

V. Mazzoni
Department of Sustainable Ecosystems and Bioresources, Research and Innovation Center, Fondazione Edmund Mach, San Michele all'Adige, Italy

N. Stritih-Peljhan · M. Virant-Doberlet
Department of Organisms and Ecosystems Research, National Institute of Biology, Ljubljana, Slovenia

A. Wessel
Museum of Natural History Berlin, Leibniz Institute for Evolution and Biodiversity Science at Humboldt University Berlin, Berlin, Germany

P. S. M. Hill et al. (eds.), *Biotremology: Physiology, Ecology, and Evolution*, Animal Signals and Communication 8, https://doi.org/10.1007/978-3-030-97419-0_1

1.1 Introduction

"Quo vadis, biotremology?" Authors in our growing research alliance in biotremology continue to ask this question of where we think we are going as a discipline in the short-term, as well as what we hope to explore as a community as we face a more distant future full of promise. As in our two previous volumes, we provide a figure that reveals the growth in the use of the term *biotremology* in publications, based on a Google Scholar search (Fig. 1.1). From being found in one publication in 2014 (not recognized by Google Scholar), growth in the use of the term biotremology increased rather linearly until early in 2018, when there was a clear inflection point with a change in slope of the line. In spring 2018, the slope of the line was similar, but the number of results for the use of the term increased measurably, until in November 2019 there was a leap in numbers due to the

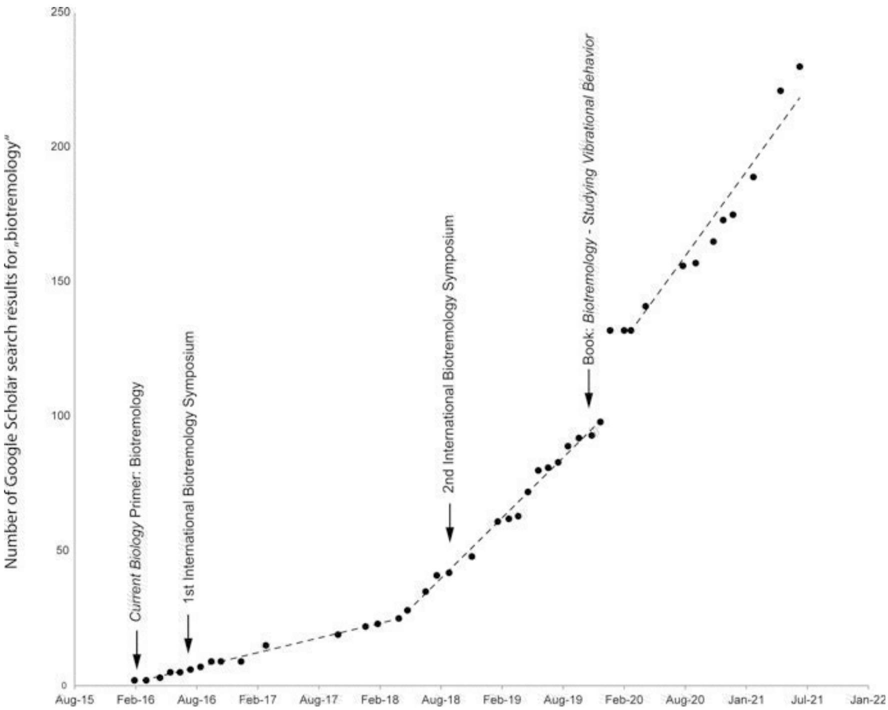

Fig. 1.1 Results of Google Scholar searches for the term *biotremology*, over the period from December 2015 to July 2021. The search results reflect the actual numbers for a full search on a certain day, and did not use the "custom range"-function for a retroactive limitation of search time periods. 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, April 2018 to November 2019, and December 2019 to July 2021, respectively. For each of these three time periods, the increase in search results is highly significantly linear

publication of the second volume. In this third free-standing book of chapters on biotremology for the Springer series, *Animal Signals and Communication* (see Cocroft et al. 2014a; Hill et al. 2019), this need to define and make adjustments as we go is evident in our shift away from the 2014 focus on research in the field of animal communication, but almost exclusively arthropod communication. By 2019, we were expanding our collective vision at a great rate after having found a name (Endler 2014) and established biotremology as a broad discipline with boundaries that extend beyond the study of communication in animals to encompass the study of vibrational behavior of all types (Hill and Wessel 2016).

The change in focus was rapid once we faced the realization of at least two facts, which could not be ignored. First, the receiving mechanisms that detect animal signals also detect incidental cues. These bits of information are transduced and transmitted through the nervous system in the same way and, as far as we currently know based on limited publications, may be perceived in the same region of the nervous system. Further, mechanical waveforms that carry information in both signals and cues cannot be fully understood without knowing more about all mechanical waveforms and the physical world where these waveforms also propagate. Substrates filter and change mechanical waves in ways that must be reversed in order to produce functional playback signals, for example. We also know that energy carried in mechanical waveforms is transferred at a boundary between media (such as the soil and air, or water and air) and may propagate through the second medium in a different waveform, as is likely at junctions of spider web threads. We know that most all communication signals and cues that pass between living things are carried as boundary waves (Rayleigh waves in the Earth and bending waves in plants). However, there are many other types of mechanical waves on this planet that are not known at this time to be involved in sound communication or used for vibrational signals and cues. Are they involved in vibrational behavior in ways yet to be imagined and documented? This caused us to broaden our interest in mechanical waves, generally. We then had to consider that other lifeforms, and their interactions that fell outside the animal communication paradigm, as well as the physical environment, could be studied using many of the concepts and tools already in use for studying communication. Yet, as we look to the future to expand our understanding of the scope and depth of biotremology, we are also increasingly aware of how ancient, broadly represented and diverse the interactions studied within biotremology actually are. Therefore, we continue our commitment to ground our current and future investigations in the findings of the pioneers of our past, and even to a world (and beyond) that we now know existed more than 230 million years ago when there were no human scholars, and there was no science, but biotremological interactions were already taking place (Hoch et al. 2006). Thus, we find ourselves as a discipline and a community that embrace work focused on the distant past and the distant future, while we also examine questions at any of the levels of biological organization, from cells to the biosphere. Further, we do this at the pure, practical, and applied levels. The core terminology required to anchor this diversity has to be both durable and flexible, and so we also attempt to adapt new language elements and stabilize others as the discipline evolves, while maintaining cohesion of our shared principles.

As in the two previous Springer books from our biotremology community, we use the structure of the part/section topics to present a portfolio, of sorts, that reflect the scope of research areas that belong under the umbrella of the discipline of biotremology. Most of the topics remain the same through the three volumes, even though the chapters themselves have very different contents; however, after 2014, we added a section on Applied Biotremology. In this third book we changed the section in the previous two books that dealt with detection and orientation to a new section on Vibrational Behavior in Less Explored Contexts. This first chapter serves as an introduction by the Editors to the book, as a whole, as well as to Part I: Studying Vibrational Behavior: Ideas, concepts, and history. We continue our short tradition of including a translation of an important and classic historical text that is only poorly known to the broader biotremology community (see Chap. 2). Here the work of Karl H. C. Jordan on sound production in two families of true bugs is showcased as an early study of both airborne and substrate-borne signal components. In translating from the original German the text from two papers that most directly impacted research in biotremology, Hoch and Wessel also give our community an opportunity to honor, for the first time, the work of Helga Slowioczek. The findings published in these translated passages of Jordan's two papers were taken from Slowioczek's unpublished diploma thesis on work supervised by Jordan. As was conventional at the time, Slowioczek was not included as co-author on either paper, thus this chapter honors her as a pioneer in biotremology for arguably the first time.

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

This part topic has been included in all three of the Springer biotremology books written by our research community. With this section we hope to present something of the research being conducted at the extremes of our discipline, or work that has moved beyond what is known about a group of living things in a way that explores newly identified interactions in vibrational behavior.

The endemic weta of New Zealand (Orthoptera: Anostostomatidae) are not well-known to most biologists, unless the scientists have experience with the New Zealand fauna or perhaps are entomologists with a particular interest in the Orthoptera. Yet, this unique group offers us a gold mine of information that can be used in comparative studies that would, among other things, help to resolve phylogenetic relationships in the Orthoptera. However, their importance to biotremology exceeds even this valuable contribution. For example, the giant weta of the Deinacridinae were the largest animals ever confirmed to produce substrate-borne vibrational signals through tremulation. Strauß and Howard (see Chap. 3) provide us with a primer, introducing the weta and the diversity of their vibrational behavior.

Within this group, mechanisms for production of substrate-borne vibrations via drumming, stridulation and tremulation are all found, and in at least one group multiple examples of organs used in stridulation are also known.

In behavioral ecology studies, so many investigations are grounded in cost-benefit analyses of a functional behavior, especially in exploring sexual selection of a trait/behavior. Energetic costs are often estimated in the absence of data without any physiological testing, or assumed to be greater or lesser in comparative studies. Only a handful of academic publications actually address the issue of energetic costs in biotremology based on the classic respiratory studies that have been conducted from a wide representation of animal life. Kuhelj and Virant-Doberlet (see Chap. 4) report on their work with a model organism, the leafhopper *Aphrodes makarovi*, one of only four species of arthropods for which energetic costs have been studied. Their very careful case study can be used as a standard for future studies in other organisms that use vibrational signals exclusively in mating behavior, or as part of a multimodal system that also includes acoustic components.

The Hawai'ian Islands serve as a laboratory for radiation and evolutionary dynamics of so many species of living things, and this is also true of the planthoppers of Hemipteran Fulgoromorpha. Indeed, before pioneering investigations in the early 1990s, no information was available on behavior of any Hawai'ian planthoppers. Ashe and colleagues (see Chap. 5) summarize the current state of knowledge of vibrational signals of a large number of species of Cixiidae and Delphacidae that were recorded in Hawai'i between 1989 and 1998. Signals are characterized and other details of morphology and natural history are documented. Photographs and graphical representations of the signals are included, and recordings are available from the VibroLibrary at the Museum fur Naturkinde in Berlin.

1.3 Practical Issues in Studying Vibrational Behavior

This section has been a mainstay of all three of our research community's Springer volumes on biotremology. In it we attempt to showcase some technical or theoretical issues specific to working within the science of biotremology. In this section we address three topics that have not been covered in previous volumes and, additionally, are not widely covered in other biotremology literature: noise in the vibrational channel, development of equipment to solve a problem in playback stimulus delivery, and a comparison of current and historical research methods for sending and receiving substrate-borne vibrational signals or cues.

Human activity represents a considerable source of mechanosensory disturbance in the environment, which acts through both airborne and substrate-borne channels. While its acoustic influence on animal communities has received considerable research attention, the interference of anthropogenic noise on animal behavior via the vibrational channel remained largely unstudied. In the review of Roberts and Howard (see Chap. 6) the state-of-the art in the study of vibrational noise is explored by describing noise sources, its impacts on organisms and their strategies for communication in noise, the ways to measure and mitigate anthropogenic noise in the substrates, and suggestions for future studies for this largely understudied area. Twenty-two existing studies, altogether, that deal with vibrational noise in aquatic or terrestrial habitats suggest that much is left to be done to start understanding the actual scope of influences of anthropogenic vibrational noise on the species, population, and ecosystem levels before we will be able to take effective measures in its mitigation and control. In particular need of research are aquatic environments, where the impact of anthropogenic vibration is much less known than in terrestrial ones, starting with an almost unknown sensitivity of aquatic animals to substrate vibrations.

While vibrational signaling through the substrate has been traditionally considered merely a (side) component of acoustic signaling, the development of biotremology facilitated our understanding of the distinction between the acoustic and vibrational communication channels at basically any system level, from signal emission and transmission to detection and neuronal processing. Similarly distinct may be the methodological aspects in studies of these systems, including both signal presentation and recording. Conducting a behavioral playback experiment in a vibrational system is typically much more complex and technically challenging than an experiment including presentation of acoustic stimuli. A review of the more than 20 years of work of Warkentin and coworkers (see Chap. 7) on playback experiments provides an example of highly challenging development of a stimulus delivery system that requires vibrational playback to egg clutches (i.e., embryos), combined with tactile stimuli, in such a way as to mimic conditions occurring in nature during predator attacks. The authors present a step-by-step development of a complex device that enables a high level of control for the simultaneous and independent playback of both modalities, along with a detailed control over their application to individual eggs in a clutch, while maintaining minimal variation across experimental replicates. In addition to stressing differences between studies of vibrational behavior between embryos and adult animals, studies of Warkentin and her group demonstrate how extensive the distinction between approaches and methods in bioacoustics and biotremology studies can be.

Despite considerable progress in biotremology and the increasing recognition of the field among researchers studying animal behavior, an important goal of our community continues to be raising awareness of the vibrational channel as a highly important mode of information exchange among animals. As discussed previously (Cocroft et al. 2014a, b), studying vibrational communication has a large potential for answering behavioral research questions that could not be explained by studying other modalities. Due to the price, however, the specialized research equipment standard for vibration recording and playback is limited mostly to laboratories focused on vibrational communication research, thus precluding the possibility of considering this mode more widely. Nieri and colleagues present the results of tests on the performance of various older, inexpensive alternatives to the specialized equipment used in vibrational recording and playback, in particular in the research of animal interactions through plants (see Chap. 8). Especially for the playback, they demonstrate almost no difference in the performance of the cheap vs. expensive actuators that vary 1000-fold in price, while the use of alternative low-cost sensors is more limited and is suggested to be used in cases where quantitative signal analysis is not required.

1.4 Vibrational Behavior in Less Explored Contexts

The topic of Part IV in this book is new to our portfolio of areas covered in our ever-expanding discipline of biotremology. In this section our chapter authors cover topics not addressed in our two previous Springer books from the biotremology community, whether the chapters be taxon-specific, niche-specific or an introduction to novel research methods.

The lack of an established evolutionary framework is often cited as a weakness of studies in biotremology. We consider that the hundreds of millions of years spent in evolution of vibrational behavior have provided unique challenges to modern researchers in obtaining empirical support from controlled experiments conducted with remnant populations that may, or may not, be representative of the ancestral condition. Conrad presents a review of her sexual selection studies of population divergence and speciation in the red mason bee (see Chap. 9). Of particular interest is the novel solution for modifying the vibrations produced by courting males of the divergent populations in a carefully controlled experimental design.

Ota and Soma review their work on the tap-dancing behavior in the blue-capped cordon bleu finch (see Chap. 10), which is a socially monogamous song bird with multimodal courtship displays. Both males and females of these birds exhibit singing and visual courtship displays. Yet, they also produce a bobbing behavior on their perches that has been described as a sort of tap dance, once high-speed video was viewed at a lower speed so the motion of the feet could be observed. This body of work represents the first and only case describing the presence of substrate-borne vibration in bird multimodal courtship displays. In fact, the previous lack of reports of any sort of vibrational behavior in birds was a major barrier to acceptance of the study of vibrational behavior as a significant component of bioacoustics studies. Thus, this chapter and its findings, after a comprehensive analysis of the substrate-borne component of the multimodal display, represents a portal into a totally new research line in birds, where the realm of biotremology has essentially been ignored/overlooked in the recent past.

Some related, but still distinct, research areas that currently are not incorporated into biotremology are very well developed and have their own research communities and international conferences. Some may continue to exist into the future as distinct entities without external ties to any one related school of thought, while others will find commonalities with biotremology that make joining with this new discipline very attractive. One such research area is that of buzz pollination, which is presented (see Chap. 11) as a potential good fit within biotremology. Buzz pollination represents a type of pollinator-plant mutualism where plants only release their pollen when exposed to vibrations delivered by a bee probing for nectar. The pollen lodges on the hairs covering the bee and can then be deposited on a neighboring plant of the same species as the bee continues to probe for nectar resources. Our current understanding of plant biotremology is still in its infancy, but pioneering studies are being completed that show the plant as more than just a substrate for animal interactions. Inclusion of the study of buzz pollination as a component of biotremology, much as the study of vibration-induced rapid hatching has been (see Chap. 7), will make currently unknown questions available for exploration, or perhaps older, resolved questions can be revisited with fresh eyes.

Nematodes are so abundant on our planet that we have difficulty even estimating how many there are. Most of the interactions known between and among nematodes and other lifeforms have been assumed to be due to chemical stimuli. In 2004, Torr and colleagues challenged and refuted this conventional wisdom with a well-controlled experiment that found parasitic nematodes responded to host-generated vibrations in the soil that allowed them to locate and infect the host (Torr et al. 2004). Yet, most research today still holds to the convention that interactions are chemical. Sugi (see Chap. 12) provides our biotremology community with its first ever chapter on nematodes as he reviews mechanosensory behavior in *Caenorhabditis elegans*, the model organism that is arguably the best-studied nematode of all. Of particular interest is the ability of this nematode, though it has not been described in others, to acquire memories of mechanical stimuli and then modify their mechanosensory behavior based on these experiences, even though any fitness benefits are still untested in the wild.

Lastly in this section on less explored contexts, Stritih-Peljhan and colleagues use an interesting case study approach to compare and contrast the lives of cave-dwelling insects from two distinct orders: the Cixiidae (planthoppers) of the Hemiptera and the Rhaphidophoridae (cave crickets, cave weta, or camel crickets) of the Orthoptera (see Chap. 13). Authors Stritih-Peljhan and Strauß are Orthoptera experts and focus on caves in Slovenia, while Wessel and Hoch are Hemiptera experts and focus on caves in Hawai'i. Cave environments are highly interesting to study due to their strong influence on organisms, including sensory systems and behavior. Yet, they are among the least studied in all fields, including biotremology. Thus, this chapter provides new and provocative insight into the adaptation to life in caves, and particularly the dependence on substrate as it explores the issue of the evolution of vibrational behavior of cave-dwelling species and solutions found from these two insect orders.

1.5 Vibrational Behavior in Some Well-Studied Taxa

This part topic has also been an important part of all the biotremology books published by our research community with Springer. The description of well-studied taxa may surprise some readers new to the biotremology literature. We refer to taxa in which substrate-borne vibrational behavior has been studied over decades, or perhaps a smaller group has been extensively studied with respect to diverse concepts in biotremology. In this volume we also include taxa that are well-studied, in general, but in which vibrational behavior has gained little attention by way of empirically supported vibrational behavior studies. In each case, however, these studies may or may not be well-known outside the biotremology community. Thus, our chapters are reviews and updates of the literature on a variety of taxa of special importance to our science. These include two vertebrate groups (snakes and the Israeli molerat), three groups of social insects (honey bees, ants and social wasps) and caterpillars (larval Lepidoptera).

Han and Young (see Chap. 14) provide us with an extensive review of the literature on detection of and sensitivity to mechanical waveforms in snakes as they present the current state of our knowledge of snake biotremology. Even though snakes are rather well-known throughout the environments where they are found on the planet, our knowledge of ophidian biotremology is shallow to nonexistent across taxa. Strong evidence exists that snakes are able to detect and respond to substrate-borne vibrations, and in some taxa, i.e., rattlesnakes, we can record and measure vibrations induced by the snake's behavior, as well as the incoming vibrations detected by the snake, and characterize them. Yet, something as basic as the pathway from detection of the signal until it projects onto one or more regions of the brain is still very much a black box. Even more challenging for the non-specialist reader is the blending in the literature of descriptions of hearing and vibration sensitivity, much of which is anecdotal and based on natural history observations. In many cases it is not at all clear that the evidence of *hearing* is referring to the pathway we typically reference when we speak of airborne sound waves setting up tympanic membrane vibrations and eventually leading to projection onto some auditory-specific area of the brain. Snakes do not have external ears and so are considered deaf with respect to classic hearing patterns known from other vertebrate classes. Yet the literature includes information on pathways from detection to perception that are bone-conducted, lung-conducted and somatic receptor pathway-conducted. In newer biotremology literature we have used "extra-tympanic" to refer to pathways carrying bone-conducted information from the substrate to a series of bones that eventually lead to the inner ear, i.e., the quadrate bone to columella path. Yet, is this information perceived in the brain as sound or vibration, or does it even matter? Is there some unnamed aggregate class that includes both? There is clearly much yet to be learned. This review chapter is a major contribution to sorting out what is known through scientific study about how snakes are able to use mechanical waves (including pressure/sound waves) to interpret and respond to their environment. The authors have included reviews of the physiological and anatomical bases that support what we would call vibrational behavior in snakes, as well as suggestions on the likely most fertile research investigations that remain to tempt us to know more.

Nevo reviews his 70 years of research, conducted across disciplines, on the Israeli molerat genus, *Spalax* (see Chap. 15). Few stories, especially in vertebrate animals, are as complete as that of *Spalax*, and here we are able to read this story in the words of the single person who spent his entire career in pursuit of understanding the totality of the *Spalax* system. Nevo's pioneering work is broad-ranging and innovative, and the references list for this chapter provides a rich treasure trove of investigations that will be of interest to most biotremologists, regardless of their specialty. In addition, Nevo integrates and showcases the work of his many students from these decades of field and laboratory work. Furthermore, he encourages us to engage in comparative studies of sound and vibration parameters across Israeli species, while expanding to comparative studies of the species in the Near East and North Africa, as well as to use new tools from genomics and transcriptomics to analyze the evolution of communication in these fascinating animals.

Honey bees are considered to be a model animal study system, and communication in the western honey bee has been investigated intensively for over 100 years. Yet, the well-known dance language still is not fully understood at this time within the honey bee communication system. We know that honey bees use multiple sensory modalities in communication: chemical, visual, tactile, acoustic and vibrational. The chemical and vibrational modalities are considered to be the oldest forms of communication, and even though chemical communication has received much more attention, the acoustic component of mechanical vibrations in honey bees was known and described more than 400 years ago. Kirchner, Hager and Krausa make a first and much-needed review of the terminology used in studying honey bee vibrational behavior (see Chap. 16), even if these terms were first used to describe airborne sounds. Further, they examine the current state-of-the-art findings with respect to each of these terms to simplify, standardize, and align the honey bee communication terminology with the biotremology framework for vibrational communication mechanisms. After this review and detailed analysis, Kirchner and colleagues were able to assign the vibrational behavior of honey bees to the categories of either tremulatory or drumming behavior, both of which can be produced without specialized morphological adaptations. All factual information on vibrational behavior in bumblebees and stingless bees, as well as the Asian species of *Apis*, support the strong conclusion that vibrational behavior is ancestral in bees. However, so little has been investigated systematically, even in western honey bees, that only the stop signal and queen tooting and quacking can be classified as true vibrational communication signals at this time.

We are told that most all ants communicate essentially through chemicals found in pheromones, but this is not the whole story. Chemical communication is ubiquitous in ants, without argument, but current evidence suggests that vibrational behavior in the form of stridulation. . .where individuals rubbing two body parts against each other produce both acoustic and vibrational mechanical waves. . .can serve to modulate chemical signals and to release other context-specific behaviors. Arguments are made in support of the role of pheromones in ants that vibrational behavior is not at all important in social insects, generally, but especially so in ants. Yet, a long history of empirically supported data reveals that vibrational signals and cues are produced through the mechanisms of drumming, stridulation, and scratching. The literature on stridulation in ants, alone, is almost 150 years old. In Chap. 17 Roces provides a focused review on stridulation in the leaf-cutting ants in the genus *Atta*. He reviews the contributions of Hubert Markl in the 1960s and 1970s, as well as his own pioneering literature, some of it done with Bert Hölldobler, in the 1990s. This is followed by an update of new work from his lab on stridulation by leaf-cutting ants that reveals two unexpected and novel findings. While foraging under natural field conditions, grass-cutting *Atta* use substrate-borne vibrations produced by stridulations in the absence of pheromones for short-range recruitment of helpers. Secondly, while organizing tasks inside the nest, leaf-cutting ants in the genus *Atta* coordinate workers to engage in both digging and waste disposal by attracting them to excavation or unloading sites while stridulating. These contexts were previously unknown and thus represent new knowledge; however, Roces adds that the idea was suggested 120 years ago that stridulation "must be of great service" (see Chap. 17) in maintaining the colony and its excavations. Old ideas, when acted upon, actually can result in new knowledge.

In Chap. 18 Nieri and colleagues review the literature of the three subfamilies of the Vespidae that are considered eusocial wasps (the Stenogastrinae, Polistinae, and Vespinae) to explore the extent of their use of vibrational behavior in a variety of contexts. These wasps have been important in studying the evolution of sociality since the 1940s, in part because of their broad range of social organization. Much as we know a great deal in general about behavior and communication in honey bees and ants, we know a great deal about communication in social wasps. As with ants, chemical communication through the use of pheromones and cuticular hydrocarbons has been studied almost to the exclusion of any other communication modality in social wasps. These wasps exhibit a range of described behaviors that are similar to those that produce substrate-borne vibrations in other animal taxa (tremulations, drumming, and a scraping, which has characteristics similar to stridulation, if one were to consider the substrate to be part of the file and scraper mechanism we see in other arthropods). These described behaviors have also been given many names across wasp species, but few hypotheses have been generated or tested. The wasps even live together as more than one generation in a nest composed of material the adults construct, themselves, and the nest is very well suited structurally to propagate mechanical vibrations throughout. The observed behaviors have led some to conclude that social wasps are a good candidate for the investigation of vibrational behaviors, yet, of the 50 species reported in the literature to perform vibrational behavior, actual vibrations produced by the various behaviors they display have been measured in only four species. Admittedly, social wasps may be a bit more intimidating, even threatening, than a honey bee or an ant. It is yet to be established whether the sting of one wasp is more dangerous to humans than the stings of 10 or more bees, or a hundred ants, but few researchers have chosen to measure the vibrations propagating through the nest material of social wasps. This leaves us with actual functions of these familiar behaviors really not identified for most species of social wasps. Fortunately for us, Nieri and colleagues have sorted out the literature and proposed hypotheses for functions of these myriad observed vibrational behaviors that appear to induce vibrations in a variety of contexts in the lives of social wasps. Our challenge is to use their information to do some data mining.

Biotremology of embryos and/or larvae is a rare focus of current research, whether these young are from vertebrate or invertebrate taxa (but see Chap. 7). Knowledge of this life stage is of primary importance to understanding vibrational behavior in juveniles and adults, but the worlds of individuals in these earliest developmental stages can be vastly different, even if not necessarily less complex, than their succeeding stages. Yack and Yadav (see Chap. 19) review our knowledge of vibratory sensing and communication in caterpillars (larval Lepidoptera), which lags far behind that for adults. Indeed, vibration receptors have not even been identified in any holometabolous insect larvae. So, why would we think that vibrational behavior, or at minimum vibrational sensing, is important in caterpillars, much less required for their survival? These larvae, like most insect eggs, nymphs, and pupae, are obligately substrate-bound. Further, like the social wasps, they exhibit behaviors associated with the ability to detect and discriminate vibration sources, whether these sources are predators, rainfall, other members of their population, or ants with which they maintain a mutualistic relationship. They live in a substrate-bound world and appear to actively respond to and discriminate among diverse bits of information known to propagate through their substrates. Yack and Yadav not only give us the gift of a solid literature review, but they use their own extensive knowledge of larval morphology and physiology to lead us from a primer on vibratory receptors in adults to a discussion of putative receptors in larvae, and where on the body these might be hiding in plain sight, if we find time to look for them.

1.6 Applied Biotremology

Applied biotremology is opening new opportunities in terms of research and innovation for practical applications to agriculture and ecology. Thanks to the enormous potential of multidisciplinary research, many industries, from big multinationals to small startups, are now well connected with the academic world and are supporting the efforts of scientists to find new solutions for manipulation of insect pest behavior through the use of substrate-borne vibrations. At the same time, applied biotremology is attracting experts from many sectors, such as mechanical and electrical engineers, informatics specialists and designers. All this knowledge is converging to create new solutions that result in new devices for field and greenhouse applications, innovative energy supply optimization, and/or algorithms that provide the devices with real-time responses to external conditions.

A wide range of insect pests are being studied in this field, and information on new research on some of them is treated in Part VI of this volume. Behavioral control approaches to control longicorn beetles and stinkbugs are here presented. Compared to other taxa, which are considered as models for biotremology studies, beetles, and Coleopterans in general, have been poorly studied; although, we know that there are species that can detect vibrations via leg chordotonal organs. Takanashi and Nishino (see Chap. 20) review the ability of beetles to sense vibrations, providing a description of the morphology of their femoral chordotonal organs and central projections. Then they discuss how vibrations could be used as a tool of pest control, also presenting a new procedure for vibrational pest management, based on vibration sensitivities in longicorn beetles. Unlike beetles, Pentatomidae have been studied for some decades and now represent model species for research in biotremology. Stinkbugs are important pests for many crops worldwide and many scientists deal with them to find solutions for sustainable control. The massive use of insecticides is no longer an acceptable solution for many governments, which now address funding campaigns toward more environmentally sustainable methods. Laumann et al. (see Chap. 23) explore the available options of behavioral manipulation that derive from the rapidly accumulating knowledge of the mating communication of stinkbugs. Two potential strategies are considered, the first being the contemporary use of vibratory and chemical signals (i.e., pheromones) to attract and trap target pest species, and the other is the transmission through plants of artificial or natural signals to interfere in reproductive behavior (i.e., mating disruption) of the target pest species.

A third chapter is, then, dedicated to vibrational communication of a worldwide economically important taxon, the Psyllids. Avosani et al. (see Chap. 22) review the current state of knowledge of this group of insects and discuss strategies to create behavioral manipulations to deal with them. Psyllids are considered major threats to world agriculture in that they are vectors of economically relevant plant diseases. Psyllids, as well as stinkbugs, are hitchhikers. This means that they are easily transported through human trade and touristic routes, thus are able to colonize new geographic areas as invasive alien species. In this chapter, an overview of what is known about their mating behavior, as well as the potential options to interfere with their behavior by means of vibrational signals, is given. Psyllid intraspecific communication is mediated by vibrational signals in the form of stridulations; recent studies indicate that biotremology approaches could be used for trapping and/or disrupting their communication, thus providing tools for monitoring and control. Examples are given for several important psyllid pests, including the Asian citrus psyllid, *Diaphorina citri*, and the North American potato psyllid, *Bactericera cockerelli*, for which specific devices have been developed that are described in the chapter.

Finally, the use of principles of biotremology to study subterranean arthropods, with ecological and economic implications, is reviewed by Mankin (see Chap. 21). Despite the many technical restraints that make the study of the community of subterranean arthropod herbivores a hard task to accomplish, advancing technology is getting us closer to finding some solutions. It is clear that these insects can have tremendous impacts on above-ground biota, including crops to which they cause economic damage; therefore, the use of vibro-detecting systems could provide the farmers with new tools for pest control. Researchers continue to look deeper into this topic of using knowledge from applied biotremology to find solutions for more efficient and ecologically safer pest control. In this chapter, Mankin reports on some of the latest developments of new systems of monitoring and control of subterranean Cicadoidean, Ensiferan, Scarabaeoid, and Curculionid species. The discussion also includes other taxa, such as Lepidoptera, social insects, and spiders, with respect to multimodal communication.

1.7 What Is Left to Be Learned?

In the earliest days of biotremology, before the discipline even had a name, many people worked in isolation to study a communication modality that allowed them to access questions about the taxon of most interest to them. Without moving into the unknown world of substrate-borne vibration in search of answers for their species or genera, the observations that led to their questions would simply continue to exist as anomalies. . .behaviors outside what is known and expected in the explanatory theory of the current paradigm. For some groups of arthropods, a great deal of information has been gathered across our traditional and most common biological disciplines, such as physiology, anatomy, behavior, ecology, and even genetics and neuroscience. For others, almost nothing is known about vibrational behavior and the communication modality that defines the behavior. For example, there are no studies about mites, which are important both as parasites and predators, and in the case of insects there is still a lot to learn about aphids, thrips, and many other groups of general interest that we expect to make extensive use of vibrational signals and cues.

Other than in some mammals and anuran amphibians, we know very little about the breadth and depth of vibrational behavior in vertebrates, which has unfortunately led some experts in animal communication to suggest that biotremology has little to offer to increase understanding of anomalous behavior in vertebrates. If the modality is so ancient and wide-spread as biotremologists claim, it surely would have been recognized in vertebrates before now, would it not? Yet, when vibrational behavior has been explored in mammals, amphibians, and reptiles, mysteries have been solved, and whole new worlds of questions are opened to the curious. Recent work reported on biotremology in birds (see Chap. 10) illustrates this trend very well, but there still remains much to be learned. It is to be expected that vibrational behavior plays a major role in many multimodal displays where it has been previously ignored.

In the recent past with its focused growth of the biotremology community, we have identified a number of areas where initial research efforts have yielded quick success that, in turn, has stimulated interest and growth, even for applicative purposes. In other areas, even when identified and promoted, progress has been slow. However, biotremology is a brilliant example of how basic research can turn, in a relatively short time, into applied research. The next step is to provide this discipline with the proper nomenclature and terminology in order to place biotremology beside chemical ecology, as a sister discipline to reinforce sustainable pest control. In fact, biologically speaking, vibrational signals for mating communication are not that different from pheromones and for this reason we predict a fruitful future of their use in application. Indeed, in the field of applied biotremology there is really much to do and we are seeing only the tip of the iceberg at this stage. The impressively fast progress in technology associated with cost reductions has led to feasible practical solutions that only a few years ago were considered impossible.

As our community was coalescing from isolated groups, we urged others to extend beyond their achievements to put students to work on unexplored peripheral areas to build on the framework already established by the pioneers. For example, we asked if a particular discovery of vibrational behavior in a species could be explored in the most closely related taxa, or within the original species but in new and different contexts. If the research focus had been on behavior and communication, could others be recruited to work on physiology, neuroscience, community interactions, genetics or even comparative studies? In search of an evolutionary framework for biotremology, especially when considering that such an ancient and widely employed communication modality might be basal for all animals, what tools of modern biological research might be employed by scientists who would never have considered research in animal communication? In a genus such as *Spalax*, which is well-studied in Israel but known across the Near East and North Africa, Nevo (see Chap. 15) has suggested using the tools of genomics and transcriptomics to synthesize a fuller picture of evolution of communication among this range of molerat species. One such paper (Su et al. 2021) became available online in May 2021 that reports on a putative abdominal vibration-related gene from transcriptome analyses in the brown planthopper (*Nilaparvata lugens*). Yet, even though dramatic advances have been made across the research areas under study in biotremology, so much is still to be learned.

In this volume, we have two strong chapters on the biotremology of specific embryos and larvae (see Chaps. 7, 19). Yet, most of our research laboratories working in biotremology have focused on adult animals (but see Endo et al. 2019). Progression of the field now allows those whose primary home disciplines are not biotremology to identify a wealth of research questions that can be answered based on their own expertise, and the research techniques used in biotremology are being demystified, as well as becoming more widely accessible.

One extremely fertile area for research is our understanding of *perception*, or how animals become aware of external vibrational stimuli, or interpret them, within the brain. Almost nothing is known of perception and very little has been done across taxa on distinguishing neural pathways once the receiver organs have been located and described. To improve our understanding of the perception of vibratory signals and cues, i.e., to find out which parameters are important for their detection, recognition, categorization, etc., we need to increase our study efforts also in behavioral physiology to explore these parameters, along with deciphering the underlying sensory neural pathways and processing mechanisms. These pathways and mechanisms have only been studied for a limited number of species, predominantly insects, but even here progress has been much slower than for other sensory modalities. Even further, the actual receiver organs for vibrational stimuli have not been identified in many taxa. One aspect that has remained completely untouched, but would be particularly interesting to explore in insects, is the neural mechanisms of noise reduction and selective attention, which may be considered especially relevant in the plant signaling environment. To fill the gap in our understanding of vibration perception, we not only need to increase interest in neurobiology among biotremologists. Since these topics are not as readily accessible for studies as is behavior, for example, it would be of great benefit to our field of study to (re)increase interest in this sensory modality among bioacousticians, as well. In Orthoptera, the established invertebrate models of hearing, the auditory and vibratory senses have often been studied together in the past. Given the close interrelation of the two modalities, it would be beneficial for both disciplines if the perception of sound and vibration signals in animals were again studied together in the future.

In arthropods, providing information about the direction of the stimulus can be regarded as one of the main tasks of the vibratory system, which most likely underlay escape and prey finding behavior before the use of signals in a social context. The ability to localize the source of vibration had been demonstrated or described for a number of taxa, even when the mechanisms remained unknown, at a time when conventional wisdom held that this was simply not possible. Examples include the pioneering work of Brownell and Farley (1979a, b) with scorpions on sand substrates, Bleckmann and Barth (1984) with a fishing spider on the water surface, Hergenröder and Barth (1983) with a wandering spider, and Salmon and Horch (1972) with ghost crabs. Early investigations with vertebrates were also underway (Hetherington 1985: the bullfrog, Hetherington 1989: the sandswimming lizard). Yet, few species even today, including well-studied ones like the western honey bee (see Chap. 16), have ever been studied for directional vibration sensing. So much information could be gained by investigating relevant directional cues in different species, with potential constraints based on differences due to size or transmission constraints due to characteristics of the substrates on which they vibrate.

Additionally, a great deal could be achieved in advancing the field of biotremology if additional contexts for potential vibrational behavior were investigated in species for which at least one use of vibrational behavior has already been confirmed. Understudied behaviors include typical contexts such as territorial behavior, recruitment of helpers and other social interactions outside mating and parental care, mutualistic or parasitic relationships (especially with ants) and predator detection. Further, examining different developmental stages to investigate vibrational behavior over the lifespan would be very informative, especially in embryos or larvae of taxa already known for vibrational behavior in another life stage. At the same time, we are just now investigating vibrational behavior interactions at the community and ecosystem level, or *vibroscape* (Šturm et al. 2019, 2021). These investigations are revealing to us this previously unexplored world of new vibrational behavior contexts at these levels of organization in natural conditions, with the plethora of signalers, intended and unintended receivers, and noise sources.

References

Bleckmann H, Barth FG (1984) Sensory ecology of a semi-aquatic spider (*Dolomedes triton*). II. The release of predatory behavior by water surface waves. Behav Ecol Sociobiol 14:303–312

Brownell P, Farley RD (1979a) Orientation to vibrations in sand by the nocturnal scorpion *Paruroctonus mesaensis*: mechanisms of target localization. J Comp Physiol A 131:31–38

Brownell P, Farley RD (1979b) Prey-localizing behavior of the nocturnal desert scorpion, *Paruroctonus mesaensis*: orientation to substrate vibrations. Anim Behav 27:185–193

Cocroft R, Gogala M, Hill PSM, Wessel A (2014a) Studying vibrational communication. Springer, Berlin Heidelberg

Cocroft R, Hamel J, Su Q, Gibson J (2014b) Vibrational playback experiments: challenges and solutions. In: Cocroft R, Gogala M, Hill PSM, Wessel A (eds) Studying vibrational communication. Springer, Berlin Heidelberg, pp 249–274

Endler JA (2014) The emerging field of tremology. In: Cocroft R, Gogala M, Hill PSM, Wessel A (eds) Studying vibrational communication. Springer, Berlin Heidelberg, pp vii–x

Endo J, Takanashi T, Mukai H, Numata H (2019) Egg cracking vibration as a cue for stink bug siblings to synchronize hatching. Curr Biol 29(1):143–148

Hergenröder R, Barth HG (1983) The release of attack and escape behavior by vibratory stimuli in a wandering spider (*Cupiennius salei* keys). J Comp Physiol A 152:347–358

Hetherington TE (1985) Role of the opercularis muscle in seismic sensitivity in the bullfrog *Rana catesbeiana*. J Exp Zool 235:27–34

Hetherington TE (1989) Use of vibratory cues for detection of insect prey by the sandswimming lizard *Scincus scincus*. Anim Behav 37:290–297

Hill PSM, Wessel A (2016) PRIMER: Biotremology. Curr Biol 26:R187–R191

Hill PSM, Lakes-Harland R, Mazzoni V, Narins PM, Virant-Doberlet M, Wessel A (2019) Biotremology: studying vibrational behavior. Springer Nature, Switzerland

Hoch H, Deckert J, Wessel A (2006) Vibrational signalling in a Gondwanan relict insect (Hemiptera: Coleorrhyncha: Peloridiidae). Biol Lett 2:222–224

Salmon M, Horch KW (1972) Acoustic signalling and detection by semiterrestrial crabs of the family Ocypodidae. In: Winn HE, Olla BL (eds) Behavior of marine animals, vol 1. Plenum Press, New York, pp 60–96

Šturm R, Polajnar J, Virant-Doberlet M (2019) Practical issues in studying natural vibroscape and biotic noise. In: Hill PSM, Lakes-Harland R, Mazzoni V, Narins PM, Virant-Doberlet M, Wessel A (eds) Biotremology: studying vibrational behavior. Springer Nature, Switzerland, pp 125–148

Šturm R, Rexhepi B, López Díez JJ, Blejec A, Polajnar J, Sueur J, Virant-Doberlet M (2021) Hay meadow vibroscape and interactions within insect vibrational community. iScience 24(9):103070

Su Q, Lv J, Li W-X, Sun J-W, Li S-H, Zhang W-Q (2021) Identification of putative abdominal vibration-related genes through transcriptome analyses in the brown planthopper (*Nilaparvata lugens*). Genomics and Proteomics, Comp Biochem Physiol D. https://doi.org/10.1016/j.cbd.2021.100856

Torr P, Heritage S, Wilson MJ (2004) Vibrations as a novel signal for host location by parasitic nematodes. Int J Parasitol 34:997–999

Chapter 2
Sound Production in True Bugs from the Families Acanthosomatidae and Pentatomidae (1958)

Karl H. C. Jordan, Helga Slowioczek, Hannelore Hoch, and Andreas Wessel

Abstract Representatives of the Heteroptera families Acanthosomatidae and Pentatomidae were studied with respect to their sound production. In the course of these studies, we found that the species studied were capable of producing sound, which could be made audible by means of a modified stethoscope. Sounds were emitted predominantly by males, and, in several species, also by females. Sound characteristics and morphological information suggest that the sounds are not of stridulatory origin, but are produced by a hitherto unknown mechanism, i.e., an oscillating membrane. We hypothesize that the sound-producing organ(s) of the Pentatomidae and the Acanthosomatidae may be a simple precursor of the cicada's drumming organ. Behavioral observations revealed that the sounds certainly play a role in mating behavior, and may also be significant for defense; however, sound

Hannelore Hoch and Andreas Wessel are Translators.

Editorial Note
In 1958, Karl H. C. Jordan (1888–1972, then Zoological Institute, Technical University, Dresden, Germany) published two articles on the biology of the parent bug *Elasmucha grisea* L. (Insecta: Hemiptera: Acanthosomidae) (Jordan 1958a) and on sound emissions in the Hemiptera families Cydnidae, Pentatomidae, and Acanthosomatidae (Jordan 1958b). Both articles are significant contributions to the methodological and behavioral aspects of biotremology, yet have been largely ignored by the international scientific community, as they are both in German. The results published in both papers were findings obtained in the course of a diploma thesis by Jordan's student Helga Slowioczek. As was the custom of the times, Slowioczek was not offered coauthorship for the publications resulting from her work. Her diploma thesis proper has never been published. It is thus also our intention to honor Helga Slowioczek's contribution to biotremology by providing English translations for those text passages that are of direct impact on this field of research. It should be noted that the terminology used in the two publications does not discriminate between air-borne and surface-borne vibrations.

K. H. C. Jordan · H. Slowioczek
Zoological Institute, Technical University, Dresden, Germany

H. Hoch (✉) · A. Wessel
Museum of Natural History Berlin, Leibniz Institute for Evolution and Biodiversity Science at Humboldt University Berlin, Berlin, Germany
e-mail: Hannelore.Hoch@mfn.berlin

P. S. M. Hill et al. (eds.), *Biotremology: Physiology, Ecology, and Evolution*, Animal Signals and Communication 8, https://doi.org/10.1007/978-3-030-97419-0_2

emissions were also observed in situations where the behavioral context remained unresolved. Frequency and amplitude of the sounds emitted were observed to be temperature-dependent.

2.1 Sound Production in the Acanthosomatid *Elasmucha grisea* L. (Jordan 1958a: pp. 393–395)

2.1.1 The Sound Emission of the Imago

Hitherto, there are no reports of sound emissions of *Elasmucha grisea* in the existing literature. I thus encouraged my student Helga Slowioczek to study Pentatomidae with respect to their sound emissions. In the course of her work, she discovered a special mode of sound production that is entirely different from the stridulation that is common in insects, and in particular, Heteroptera.

With the help of a stethoscope as described by Leston (1954), it is possible to detect sound emissions in a number of Pentatomidae. The Institute for Electrical Engineering of the Technical University Dresden enabled us to produce oscillograms. Following multiple amplifications, the sounds were recorded on magnetic tape, and the sounds played from these tapes were made visible by a loop oscillograph.

Among others, *Elasmucha grisea* belongs to those species of which only the male produces sounds, i.e., female sound emissions could not be registered in any case. The “song” of the male lasted for ca. 45 min, while single calls were observed to be of rather long duration and were emitted in irregular intervals. The first sound type, which has a duration of 1.3 s and a fundamental frequency of 67 Hz, increases to 83 Hz. Modulation of amplitude is periodic at the start, and becomes irregular later.

The second sound type has a duration of 1.0 s, and also increases fundamental frequency from 67 Hz to 83 Hz. Impulse frequency of both sounds equals 21 Hz.

In comparison to the pitch of crickets (5000–17,000 Hz), locusts (6000–8000 Hz) and cicadas (7000–8000 Hz), the frequencies of Pentatomid sounds are extraordinarily low, i.e., 2–3 octaves below the standard pitch (440 Hz, oscillations per second).

The (low) pitch right away excludes sound production via a stridulation apparatus; however, it indicates the existence of an oscillating membrane. Although no morphological structures (underlying sound production) could be identified, the behavior of the animals observed during sound emissions hints to sound production being performed in the first two abdominal segments.

Abdominal tergites 1 and 2 are vividly being moved for- and backwards; additionally, rapid up-and-down movements of the whole abdomen are observed simultaneously. It appears as if at the beginning of a sound, the first two tergites move forward, while during the duration of the sound the up-and-down-movements of the whole abdomen are performed, and that towards the end of a sound, the tergites return to their normal position. The stronger the movements, the more intense the sounds. The most plausible conclusion, therefore, is to assume the oscillations of the abdominal integument ["Abdominalwandung"] are responsible for the sounds. A specialized muscular configuration could not be identified; it is thus plausible to assume that normal dorsoventral and longitudinal abdominal muscles trigger the movements during sound production. The sounds of all Pentatomidae studied so far are very soft and not audible to the human ear without amplification. There is no effective resonance body of the kind we know from cicadas. With some reservations, it can be hypothesized that the sound production apparatus for the Pentatomidae is a simple precursor of the tymbal organ ["Trommelorgan"] of cicadas, which show the organ in highest perfection.

In Acanthosomatidae, the mesothorax bears a lamellae-shaped longitudinal carina that touches, laterodistally, a thorn-shaped protrusion for some of its length. It is conceivable that the abdominal movements cause the distal part of the abdominal longitudinal carina to chafe at the thoracal foliate carina—however, there are no teeth or spines of any kind that would bring forth any sound. Sounds produced in this manner would also be stridulatory. It is worth noting that Pentatomidae that do not bear carinae, as described above [in this section] for *Elasmucha*, are capable of producing very similar sounds.

Now the question arises as to the biological significance of sound production. Unfortunately, it was impossible for my student to perform experiments during mating season in spring, but only from the end of September to October. They [the experiments] are yet no less convincing and give proof that sound production is connected to copulation. In an experiment, a pair [of *Elasmucha grisea*] was placed under the stethoscope. The male initiated calling while unfolding his copulation apparatus, and with his antennae vividly moving. The female was grabbed by the male from the side, but did not at first show any interest in mating, but instead tried to get rid of the male by means of abdominal movements. After 45 min of incessant singing [of the male], the female was finally motivated for mating and permitted copulation.

It has been observed repeatedly that Pentatomidae also mate in the autumn, and occasionally even egg batches can be found. I am not aware of any such late oviposition in *Elasmucha*; it is also not reported in the literature. The long period of parental care and the prolonged nymphal development could perhaps barely be completed before the onset of winter, especially since low temperatures would further decelerate developmental rates.

It is also interesting that males (in the absence of females) emit sounds, however, only when they are in contact with other conspecific males. In contrast, males do not react to contact with other species (e.g., *Palomena prasina* L.) by emitting sounds.