Animal Signals and Communication 3

Reginald B. Cocroft
Matija Gogala
Peggy S.M. Hill
Andreas Wessel *Editors*

# Studying Vibrational Communication

Springer

# Animal Signals and Communication

Volume 3

*Series editors*

Vincent M. Janik
School of Biology
University of St Andrews
Fife, UK

Peter McGregor
Centre for Applied Zoology
Cornwall College
Newquay, UK

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Editors

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*Editors*
Reginald B. Cocroft
Division of Biological Sciences
University of Missouri-Columbia
Columbia, MO
USA

Matija Gogala
Slovenian Academy of Sciences and Arts
Ljubljana
Slovenia

Peggy S. M. Hill
Faculty of Biological Sciences
University of Tulsa
Tulsa, OK
USA

Andreas Wessel
Museum für Naturkunde, Leibniz-Institut für Evolutions- und Biodiversitätsforschung
Humboldt-Universität zu Berlin
Berlin
Germany

and

Zoologisches Museum
Universität Hamburg
Hamburg
Germany

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*To*
*Hildegard Strübing*
(8 May 1922–18 May 2013)

# Foreword

## The Emerging Field of Tremology

Vibrations and chemicals are the oldest modes of communication and both probably evolved from the original cell–cell mechanical and chemical interactions within early metazoans. In spite of vibrational communication being so widespread (more than 230,000 arthropods species and many vertebrates too), it is probably the least commonly known and least well known of all the sensory modes. This is partially because it is often lumped with auditory communication, with which it is related. It may also be because it is not as familiar to humans as other sensory modes (we only use it in the final stages of mating), and most people may not even think to ask if an animal is using vibrational communication, especially if it is using another form of communication very conspicuously. The possible vibratory communication through perches of night roosting birds is a good example. Scientific social facilitation is another possible reason; the authors of this book represent a significant fraction of people working in the field; other sensory modes are being researched by 1–2 orders of magnitude more people. Perhaps one reason is that there is not a word describing what we do; I suggest the term "tremology" (the study of tremors, vibrations, etc.). This book aims to redress this absurd lack of attention to an absolutely fascinating subject.

Vibratory communication is distinguished from auditory communication in that it is transmitted through solids or the air–water interfaces rather than only through air or water. This may sound like a small and arbitrary difference but it has major consequences for signal design and content. The major difference between vibrations and sounds is that sounds travel long distances through homogeneous media, whereas vibrations generally do not or travel shorter distances before losing their detectability. The distance between any impedance changes in air or water takes place over scales of thousands of wavelengths and hundreds or thousands of meters for sound. In contrast, changes in impedance take place on very small scales in solids, even in less than a wavelength. This means that the effects of the communication environment on the efficacy and evolution of signals are potentially much greater for vibrations compared to sound. In fact, vibratory communication may be the best model system for examining and predicting the effects of the environment on the function and evolution of signals, precisely because environmental effects are so strong.

This book provides an encyclopedic introduction to our current (2014) knowledge of vibratory communication or tremology. It covers the amazing diversity of vibration generating mechanisms, signal forms, receptors, neuroscience of reception, and some signal processing, in a variety of arthropods and vertebrates. Mollusks and "minor" phyla are not covered but this may be more a matter of unasked questions than a lack of vibratory use. Plants are not covered either, but vibrations are known to trigger pollination mechanisms in many taxa, and could possibly be used by vines for climbing cues. The general questions are addressed in various ways with different taxa as examples: What signals are important to the individual of a particular species? How are they generated? How do they impedance match with the environment for efficient transmission? How do environmental properties and environmental heterogeneity affect transmission from sender to receiver and from sender to eavesdropper (such as a rival or predator)? Does this lead to predictions about the form of vibrational signals under specified conditions? What kinds of receptors are used for detecting and gaining information on identification, distance, and direction, and how do they and the brain extract information? Over what range does detection work and is this used to intentionally communicate at shorter distance to conspecifics than to predators or other eavesdroppers? What is the effect of communication networks on the evolution of signal forms and content? And what are the effects of the environment on the evolution of signals?

One of the most interesting but also puzzling aspects of vibratory communication is how small arthropods use vibratory communication to find conspecifics and avoid predators and parasitoids when living on plants. The difficulty of finding a vibration source is not just a matter of noise induced by wind, rain, and vibrations from adjacent roads, but also a matter of reverberation. Localization may not be too difficult within a single leaf (as with leaf miners and parasitoids) but it is a difficult and puzzling problem in plant stems. Owing to the complex geometry and small-scale material heterogeneity of branches, the major difference from large homogeneous substrates is that in plants there is no necessary monotonic reduction in amplitude or other signal properties with distance from the signaler. For example, there are significant impedance changes within stems at nodes (denser parts of stems where buds and new branches form), branches, branch tips, and roots and these can result in geometric patterns of both resonance and multiple reflections within the plant. This results in standing waves with wave nodes (zones of very low amplitude at certain frequencies), where the locations of the wave nodes depend on vibration frequency. The consequence is that amplitude may go up and down as an insect or spider walks across the plant toward a signaler. However, not much is known about how often wave reflections and vibration nodes occur; models are needed which include transmission geometry, impedance change geometry, vibration axes, damping and other transmission loss, and transmission efficiency.

The mechanisms of determining location, distance, and direction on plants are largely unknown. Some progress is now being made by modeling various kinds of search and signal reception mechanisms and these show that searches are not simply random trial and error. Given that wave node positions depend on frequency, and different plant species have characteristic architecture (branching geometry), they may provide, on average, a predictable spatial sequence of nodes at different frequencies that might give host specialists clues to distance and direction and, with FM sweeps, the temporal pattern of changing node patterns might also give useful cues. Surprisingly, detailed mapping of spatial distributions of amplitude nodes with frequency over plant architecture is rarely done, and if this were done over the frequency ranges actually used by arthropods, new mechanisms combining frequency and nodal pattern may emerge. We have no idea whether or not there are general geometric nodal patterns generated in plants and how different are different plant species and families, and even the simple (rod) transmission properties are known for very few plant species. All may affect the ability of insects to specialize or generalize on ranges of plant hosts, their ability to detect invertebrate or vertebrate predators or parasitoids, and the ability of predators and parasitoids to find plant-dwelling prey, and the ability to separate useful signals from noise. There is clearly a lot to be done about distance and direction estimation in vibratory signals on plants.

The varying joint use of simultaneous vibratory and auditory signaling mechanisms is discussed at length. One can supplement the other, they can both be used to transmit different signals or both can be used to transmit the same signal content (redundancy) in an effort to reduce noise effects. The conceptual patterns are typical of multimodal signaling in general. However, what is different from other multimodal communication systems is that the two modes can be closely coupled. In many cases the joint use (bimodal signaling) probably coevolved because some sounds produce substrate vibrations, so any species could evolve emphasis on one or the other or both modes. Moreover, in some cases the same mechanisms produce and/or receive both kinds of signals, if so that might provide a constraint to divergence of function and use of the two modes. The transmission properties are so different that both the function (signal design) and purpose (signal content) of simultaneous vibratory and sound signals are often very different. For example, they could be separately used for short and long distance communication, or, due to different ambient noise levels, some may signal yes/no information (as in species and sex recognition) and others provide more detailed signal content (as in mate or territorial assessment).

This book will be valuable to anyone interested in vibratory communication but will also be valuable to anyone interested in the evolution of communication because the environmental effects on communication are covered more thoroughly here than they are in other sensory modes. Historians of Science will also find this a landmark book in the development of a new science because it gives a complete early history of the subject and the field is now just starting to expand rapidly. Perhaps the most valuable part of the book is the host of interesting and important unanswered questions it raises.

John A. Endler
Centre for Integrative Ecology
Deakin University
Waurn Ponds, Australia

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Reginald B. Cocroft
Matija Gogala
Peggy S. M. Hill
Andreas Wessel

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**Animal Signals and Communication 3**
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# Studying Vibrational Communication

This volume explains the key ideas, questions and methods involved in studying the hidden world of vibrational communication in animals. The authors dispel the notion that this form of communication is difficult to study, and show how vibrational signaling is a key to social interactions in species that live in contact with a substrate, whether it be a grassy lawn, a rippling stream, or a tropical forest canopy. This ancient and widespread form of social exchange is also remarkably understudied. A frontier in animal behavior, it offers unparalleled opportunities for discovery and for addressing general questions in communication and social evolution. In addition to reviews of advances made in the study of several animal taxa, this volume also explores topics such as vibrational communication networks, the interaction of acoustic and vibrational communication, the history of the field, the evolution of signal production and reception, and establishing a common vocabulary.

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