



Welcome to the 3rd International Biotremology Conference!

The Organizing and Scientific Committees welcome each of you, joining us either live in Piran or online from your respective countries around the world, to Biotremology 2022. This year, we should actually welcome you already to the 4th Biotremology Conference, but pandemic forced us to postpone twice the conference originally planned for 2020.

The conference gathered biotremologists from 12 countries, from undergraduate students to emeritus professors. In 41 contributions, we will report on our work on taxa from spiders to birds and among others cover research topics from sexual selection to pest management, examining interactions from mating pairs to communities and ecosystem level and using tools from molecular biology to machine learning. Biotremology is undoubtedly a really exciting research field. We have an advantage to study a communication channel with a long evolutionary history, as well as communication modality that is an evolutionary result of interactions between physical properties of the environment and animal's anatomy, physiology and behaviour. We also have on our side the power of numbers and diversity and we should also remember, that mechanoreceptors able to detect substrate vibrations are ubiquitous and that vibrational information present in the environment is most likely available to all organisms. We are also good at capturing the interest and imagination of general public, as well as attracting researchers to our fold, since we work with charismatic animals, like elephants and jumping spiders. And last but not least, we also have the opportunity to transfer our basic knowledge into application, because our study species are also economically important pests and information extracted from substrate vibrations present in the environment can be used to comprehensively assess and reliably predict ecosystem changes.

I would like to thank all participants, since you are the crucial part of the conference, by giving presentations, sharing your ideas, and asking questions. I'm convinced that with your contributions this will be a very productive and successful meeting and big THANK YOU to all of you for making this conference possible.

On behalf of the Organizing Committee, Meta Virant-Doberlet

Conference Chair

Meta VIRANT-DOBERLET

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List of presentations

Tuesday, 20 September

8:30 – 10:25 Session: Behavior 1 (ch. Meta Virant-Doberlet)

Biotremology: where we are, where do we go – introductory lecture (Meta Virant-Doberlet, Slovenia)

Deciphering the evolutionary patterns of spider songs (and dances) (Eileen Hebets, USA)

Variability of vibratory performance during courtship of a cursorial spider (Morgan Oberweiser, Germany)

Courtship signalling in the Western Black Widow spider (Araneae: Theridiidae) (Andrew Mason, Canada)

11:00 - 12:50

Session: Behavior & interspecific interactions

(ch. Hannah ter Hofstede)

The effect of band-passed noise on the vibrational communication and searching behaviour of *N. viridula* males (Rok Janža, Slovenia)

Spontaneous emission of vibrations by the planthopper *Scolypopa australis*: does the »ballerina« sing as well? (Sabina Avosani, Italy)

Vibrational duetting and signal production *in Aprhodes makarovi* leafhoppers (Anka Kuhelj, Slovenia)

Leafhopper males compensate for unclear directional cues in vibration-mediated mate localization (Jernej Polajnar, Slovenia)

Exploring the role of vibrational cues in a parasitoid-host interaction (Caterina Zippari, Italy)

Influence of vibrational cues on G1 *Ganaspis* cf. *brasiliensis* host searching behaviour (Lorenzo Fellin, Italy)

14:20 – 16:10 Session: Behavior 2 (ch. Wolfgang Kirchner)

Back to the roots: vibrational communication in cave planthoppers (Hemiptera: Fulgoromorpha) (Hannelore Hoch, Germany)

Vibrational communication in the bark beetle *Ips typographus* (Julian Kampschulte, Germany)

Testing alternative hypotheses for the origin of vibrational signaling in lebinthine crickets (Hannah ter Hofstede, USA)

Birds feel the vibes: the role of vibrations in songbird courtship communication (Nao Ota, Germany)

Cicadatra persica use tymbal sounds and wing clicking during the courtship song (Matija Gogala, Slovenia)

A study of multimodal communication using multiple approaches: Uncovering signal functions in a neotropical katydid (Jennifer Hamel, USA)



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Tuesday 20 September (cont.)

16:40 - 17:30

Session: Behavior & miscellaneous

(ch. Nataša Stritih-Peljhan)

The post-diapause vibrational behaviour of the brown marmorated stink bug *Halyomorpha halys* (Stål) adults at different temperatures (Jalal Fouani, Italy)

Developmental environment shifts choice of feeding environment, signaling environment and signal properties in the treehopper *Entylia carinata* (Kasey Fowler-Finn, USA)

An open-source tool for conducting high-fidelity vibrational playbacks (Alana Evora, USA)

Wednesday, 21 September

8:30 – 10:30 Session: Behavior & social insects (ch. Rachele Nieri) Stinkbug love story (Andrej Čokl, Slovenia)

Tremolo dancing with multimodal signals in jewel bugs (Hiromi Mukai, Japan)

The important role of parental vibrational signaling during brood care in the burying beetle Nicrophorus vespilloides (Taina Conrad, Germany)

Sex and caste effects on the sensitivity of the sense of vibrations in honeybees (*Apis mellifera*) (Sarah Chehaimi, Germany)

A comparative analysis on vibrational signals in burying beetles (Caterina Rughetti, Germany)

11:00 – 12:50 Session: Behavior & ecology (ch. Eileen Hebets) Vibroscape variability within hay meadow habitat (Behare Rexhepi, Slovenia)

Active space of substrate-borne signals in a hay-meadow habitat (Juan José Lopez Díez, Slovenia)

In search for information in the hidden world of vibroscape (Rok Šturm, Slovenia)

Who's shaking? On using machine learning to detect vibrational signals in laser vibrometry recordings (Matija Marolt, Slovenia)

Vibratory communication of the Russian-leather beetle – a field study (Manfred Hartbauer, Austria)

Comparing airborne and substrate-borne signaling investment across pseudophylline katydids (Ciara Kernan, USA)

The role of amplitude in a multimodal insect duet (Mia Phillips, USA)

Wednesday, 21 September (cont.)

14:20 - 16:10

Session: Behavior, ecology & morphology

(ch. Taina Conrad)

Vibrations in multimodal interactions in insects (Alenka Žunič Kosi, Slovenia)

A multicomponent acousto-vibratory courtship described for the first time in a model cricket species (Nataša Stritih Peljhan, Slovenia)

The subgenual organ complex in stick insects: Functional morphology and its implications for vibration detection (Johannes Strauß, Germany)

Morphological coupling of mechanosensory organs in stick insects (Johannes Strauß, Germany)

Exploring the role of plant heterogeneity on the transmission of insect vibrational signals (Rowan McGinley, USA)

Characterization of substrate-borne vibrational communication of Bagrada hilaris (Marica Scala, Italy)

16:40 – 18:20 Session: Behavior 4 (ch. Andrew Mason)

Unpredictable vibratory environments affect prey capture and web structure of the funnel-weaving spider Agelenopsis pennsylvanica (Brandi Pessman, USA)

Does male vibratory courtship influence female predatory behaviour in the cursorial spider, *Pisaura mirabilis*? (Stefan ter Haar, Netherlands)

Rethinking communication and sexual selection in spiders (Damian Elias, USA)

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8:30 - 10:30

Thursday, 22 September

Session: Applied biotremology 1

(ch. Takuma Takanashi)

Applied biotremology towards the future (Valerio Mazzoni, Italy)

Five years of vibrational mating disruption in the vineyard (Imane Akassou, Italy)

Substrate-borne vibrations reduced the infestation of the tobacco whitefly Bemisia tabaci (Hemiptera, Aleyrodidae): an experimental assessment in tomatoes, Solanum lycopersicum (Haruki Tatsuta, Japan)

Substrate-borne vibrational signals and stridulatory organs for sexual communication in leafminer, Liriomyza sativae (Diptera: Agromyzidae) (Qikai Zhang, China)

11:00 - 13:10

Session: Applied biotremology 2

(ch. Valerio Mazzoni)

Exploitation of vibration sensing for pest management in whiteflies (Takuma Takanashi, Japan)

Not just mating: The unexpected side-effects of the disturbance noise on the flight activity and oviposition behavior of leafhoppers (Rachele Nieri, Italy)

Vibrational monitoring of invasive hoppers in the apple agroecosystem (Giovanni Dalmaso, Italy)

Vibrational disruption approaches for interfering with vector-borne plant pathogens transmission (Valentina Zaffaroni-Caorsi, Italy)

Potential use of acoustic communication for pear psylla IPM (Dowen Jocson, USA)

Potential of biotremology for monitoring and control of stink bugs: a ******* Brazilian experience (Raul Alberto Laumann, Brazil)

How to teach biotremology in experimental home lab classes under Covid-19 lockdown conditions (Wolfgang Kirchner, Germany)

Legend:

keynote





Biotremology: where we are, where we go?

Virant-Doberlet, Meta*

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The increased awareness that substrate vibrations are an ancient and widespread form of animal communication, as well as that vibration receptors are ubiquitous in organisms, lead to the establishment of biotremology as discipline of study of vibrational behaviour. Following official recognition, the scope of biotremological studies increased enormously. However, we should keep in mind that biotremology is still an emerging discipline, which will become as strong and recognized by wider research community as well by funding bodies, as much effort we will put into representing this discipline as a whole. We need to develop common biotremology concepts or even paradigm, as well as establish a sense of biotremology community.

As biotremologists, we have reached the stage, where we can start building the big picture about the vibratory world around us and recognizing the challenges that animals relying on vibrational signalling are facing in their environment. We have great opportunity for many ground-breaking studies in close collaboration with researchers from many different fields. Taking into account the enormous diversity of organisms using vibrational information, research in biotremology offers numerous opportunities to unravel mechanisms that are central to our understanding not only behaviour, but also the world around us in general.

Deciphering the Evolutionary Patterns of Spider Songs (and Dances)

Hebets, Eileen*

University of Nebraska-Lincoln, Lincoln, NE, USA *Presenting author, email: <u>ehebets2@unl.edu</u>

In North America, the wolf spider genus *Schizocosa* includes more than 23 described species, each with unique secondary sexual traits, male courtship songs, and sometimes elaborate courtship dances. Despite being the subject of many past comparative studies, only recently have new molecular tools allowed *Schizocosa* research to be placed in a rigorous phylogenetic framework. Using anchored hybrid enrichment, we generated a large data set that recovered a well-supported phylogeny demonstrating that New World *Schizocosa* are not monophyletic, and that multiple prior model species are not genetically distinct. Analyses of morphological traits associated with courtship signaling indicate multiple gains and losses of ornamentation, with losses often coincident with high divergence between closely related species.

We focused on two syntopic sister-species with divergent ornamentation -S. *bilineata* and *S*. *crassipalpata* - to directly test if they have diverged in their reliance on modality-specific signaling. In support of modality-specific divergence, we found diet-dependent vibratory signaling in *S*. *crassipalpata* and diet-dependent visual signaling (brush area) in *S*. *bilineata*. We also found that the vibratory signaling environment was crucial for mating success in *S*. *crassipalpata*, while the light and vibratory signaling environment interacted to influence mating success in *S*. *bilineata*. Vibratory signaling in *S*. *bilineata* was only important in the absence of light.

We have also quantified the transmission efficacy of substrate-borne vibratory signals as well as substrate-specific mating success for multiple *Schizocosa* species. Generally, mating success is highest on each species' natural substrate. In *S. retrorsa*, this high mating success is despite low transmission efficacy. These data allow us to generate hypotheses regarding the role of substrate type and associated microhabitat on the evolution and function of vibratory courtship signaling across *Schizocosa*.

Variability of vibratory performance during courtship of a cursorial spider

Oberweiser, Morgan^{*}; Eberhard, Monika

University of Greifswald, Greifswald, Germany *Presenting author, email: morgan.oberweiser@uni-greifswald.de

Arachnids are especially responsive to vibrations of all types, even cursorial spiders which perceive signals through diverse environmental substrates rather than a stationary web. One such species is the Nursery Web Spider, Pisaura mirabilis. This species employs several reproductive tactics which make it especially valuable for study. It is one of only a handful of taxa in which males offer females a nuptial gift during the reproductive process, typically consisting of a prey item wrapped in silk. The male's courtship also includes visual, chemical, and most notably, vibrational signals. Courtship vibrations consist of short, low-frequency pulses repeated at equal intervals, and honestly advertise the male's condition. My project explores the functional role of vibratory communication within the complicated framework of *P. mirabilis* reproduction. I evaluated the vibratory performance of 150 male spiders by collecting repeated recordings and analyzing the pulse train associated with the courtship. Based on the pulse rate and consistency of pulse interval, two temporal variables shown to influence female choice in *P. mirabilis*, I assessed the variability of vibrational performance within the sample and categorized males as either "high-signaling" or "low-signaling." Female spiders were then mated sequentially with males of both good and poor courtship performance, and their behaviors indicating preference were recorded. These were assessed to determine the effect of male vibratory performance on the pre-mating choice of female spiders. The newly-developed methods and results from this study will additionally inform future work on the full reproductive consequences (paternity of mixed broods) of male vibratory performance in *P. mirabilis*, as well as the role of vibration within the multimodal courtship signal of these spiders.

Courtship signalling in the Western Black Widow spider (Araneae: Theridiidae)

Sivalingham, Senthurran; Mason, Andrew*

Dept. Biological Sciences, University of Toronto Scarborough, Toronto ON Canada *Presenting author, email: <u>andrew.mason@utoronto.ca</u>

In web-dwelling spiders, web-borne vibrations are thought to be the primary form of communication during mating interactions. We have examined the structure and function of male vibrational courtship signals in the Western Black Widow (Latrodectus hesperus). In these species, along with other theridiid spiders, males are known to produce multiple vibrational signals during courtship interactions. Our work indicates that, over the course of extended courtship interactions, males transition from unstructured signalling (distinct vibrational components are produced apparently haphazardly) to structured signalling (signal components combined in a consistent temporal pattern). Furthermore, these structured signal bouts (but not individual signal components) are correlated with a measure of mating success for males (latency to copulation). Our study animals were from a population of L. hesperus collected in California, USA. Recent molecular analyses suggest distinct lineages exist within the widely distributed *L. hesperus*. Preliminary work on a more southerly population (also from California) suggests divergent courtship signals in these two populations, consistent with a cryptic species hypothesis.

The effect of band-passed white noise on the vibrational communication and searching ability of *Nezara viridula* L. males

<u>Janža, Rok</u>^{1*}; Polajnar, Jernej¹; Stritih-Peljhan, Nataša¹; Škorjanc, Aleš²; Virant-Doberlet, Meta¹

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Research on sexual communication in the laboratory often does not reflect the conditions in the natural environment, in which organisms are exposed to various sources of noise. In general, noise of any kind reduces the ability to detect signals and distinguish between different signals. Understanding the influence of the spectral and amplitude characteristics of noise and the adaptation of organisms to it is key to placing communication in an ecological context. In Nezara viridula, sexual communication is largely mediated by vibrational signals. In response to the stationary females' calling song, the males produce a courtship song that stimulates the female to keep signalling until the male locates her on the plant. Here we have shown that we can interfere with this behavioural process using continuous bandpassed white noise. We have used different spectral and amplitude vibrational noise combinations to reveal their influence on the male searching and signalling ability. Our results show that for N. viridula, the most problematic component of vibrational noise is the low-frequency noise that covers both the dominant and harmonic frequencies of female signals. Higher amplitudes of noise generally inhibit signalling more than the low amplitudes. The noise that does not spectrally overlap with female signals interferes with the male ability to localize the signal source but does not influence male signalling and searching as much. The activity of vibrational receptors measured in the leg nerve is higher in the presence of low frequency noise; therefore, we assume that the differentiation between signals and noise is worse, and as a result, the behavioural response is hindered. The activity of the receptors is much lower in response to the high frequency noise; but since it still inhibits signal localization, we hypothesise that it influences the timing of action potentials produced by the female signals.

Spontaneous emission of vibrations by the planthopper *Scolypopa australis*: does the »ballerina« sing as well?

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The passionvine hopper, Scolypopa australis (Hemiptera: Ricaniidae), is an Australian polyphagous phloem-feeder that, notwithstanding a graceful "ballerina" gait, is causing severe losses to the kiwifruit industry in New Zealand. If, similar to other auchenorrhynchans, this planthopper communicates using substrate-borne vibrations, a pest control tool based on vibrations could be developed and tested in kiwifruit orchards. To study the emission of vibrations by S. australis, vibrations emitted by virgin females and males singly released on leaves of Griselinia littoralis were recorded with a laser vibrometer. Males were tested from five to 10 days after their emergence as adults, whereas females were tested from 11 to 28 days postemergence. Preliminary tests were conducted with female-male pair trials in order to determine whether individuals exchanged signals to achieve mating. The signal repertoire of S. australis comprises a male calling signal and two female calling signals, whose structure was analysed and compared. Nonetheless, duetting behaviours related to the pair formation process were not observed during our trials, suggesting that there is need of a deeper understanding of the role of vibrational signals in the sexual behaviour of this planthopper. In addition, the influence of factors such as sexual maturity and host preference should be investigated, as well as the potential role of vibrations in aggregation. By disclosing similar information, a new residue-free pest management tool against this pest may be developed in the near future.

Vibrational duetting and signal production in *Aphrodes makarovi* leafhoppers

<u>Kuhelj, Anka^{1*}</u>; Škorjanc, Aleš ²; Vittori, Miloš²; Žnidaršič, Nada^{2;} Hoch, Hannelore³; Wessel, Andreas³; Virant-Doberlet, Meta¹

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Communication between partners is an essential part of reproductive behaviour and as such, it is subjected to sexual selection. Considerable indirect costs are resulting from high energy expenditure during signalling. In the leafhopper *Aphrodes makarovi* (Hemiptera, Cicadellidae) sexual communication is mediated by reciprocal exchange of vibrational signals. We investigated the mechanism of signal production in *A. makarovi* with focus on: (a) structure of the tymbal; (b) tymbal muscles; (c) mechanism of vibrational signal production and (d) energy consumption. *A. makarovi* males are able to perceive the non-overlapped part of the female reply only. Our results suggest that the length of the reply has a great impact on males' searching behaviour, calling effort and consequently on costs of mating. Besides our results show that *A. makarovi* males are able to eavesdrop on male–female duet maintained by the calling male and by doing so they increase their mating success by lowering energetical costs. Females, which mate only once in their lifetime, on the other hand show preferences toward different males.

Leafhopper males compensate for unclear directional cues in vibration-mediated mate localization

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Ambient noise and transmission properties of the substrate pose significant challenges in vibrational signal-mediated mating behavior of arthropods, especially considering the fact that vibrational signal production is energetically demanding. We explored implications of these challenges in the leafhopper Aphrodes makarovi (Hemiptera: Cicadellidae) by exposing males to various kinds of vibrational noise on a natural substrate and challenging them to find the source of the female playback. Contrary to expectations, males exposed to noise were at least as efficient as control males on account of similar searching success with less signaling effort, while playing back male-female duets allowed the males to switch to satellite behavior and locate the target without signaling, as expected. Analysis of signal transmission revealed ambiguous directional cues, which might explain relatively low searching success, but it also indicates the existence of behavioral adaptations to complex vibrational environments. Male searching tactic emphasized speed rather than thorough evaluation of directional cues. Interestingly, this seemed to allow the males to compensate for ambiguous or partially obscured cues because the target was relatively near.

We found evidence of alterations of mitochondrial structure in males with high signaling effort that likely indicate early damaging processes at the cellular level in tymbal muscle, but no relation between biochemical markers of oxidative stress and signaling effort.

We conclude that the configurational diversity of medium as a factor in vibrationmediated mate localization merits further research.

Exploring the role of vibrational cues in a parasitoid-host interaction

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The green peach aphid, *Myzus persicae* Sulzer (Aphididae, Hemiptera), is a major agricultural pest worldwide, and an efficient vector of several plant viruses, whose control still majorly relies on pesticides. However, the need to reduce pesticide use, given their side effects on non-target organisms and human health, and their inefficacy for containing the spread of aphid-borne viruses, call for research on alternative tools for pest control, such as biological control. *Aphidius colemani* Viereck (Braconidae, Hymenoptera) is a parasitoid that is commonly used as a biological control agent of *M. persicae*, but little is known about the behavioral interaction with its host.

The potentiality of Biotremology for pest control has already been highlighted by several studies. However, the role of substrate-borne vibrations in inter- and intra-specific communication in some insect *taxa*, including aphids and parasitoids, has never been addressed, and further studies may pave the way for the sustainable control of species currently representing major threats for food safety and security.

Therefore, the aim of this study is to characterize the role of substrate-borne vibrations in: i) the inter-specific interactions between *M. persicae* and its parasitoid *A. colemani*; ii) the intra-specific communication between an "attacked" aphid and its conspecifics. Thereafter, the impact of previously recorded vibrational cues or signals on the aphid feeding behavior will be assessed using the Electrical Penetration Graph (EPG) technique, with a particular focus on the patterns conducive to viruses acquisition and inoculation.

Two are the major outcomes expected from the present study: i) insights into the role of substrate-borne vibrations in aphid intra-specific communication and parasitoid foraging behavior; ii) a proof of concept of the applicability of semiophysicals as an alternative to pesticides for aphids and aphid-borne viruses control.

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Influence of vibrational cues on G1 *Ganaspis* cf. *brasiliensis* host searching behaviour

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The larval parasitoid *G1 Ganaspis cf. brasiliensis* (Hymenoptera: Figitidae) has been selected as the best candidate to release for classical biocontrol programs of spotted-wing drosophila (SWD). The parasitoid shows high specificity and prefers to attack 1st and 2nd instar host larvae within freshly infested fruits. While long- and medium-range host location heavily rely on chemical stimuli, the detection of the host in its microhabitat is likely mediated by the vibrations produced by the larvae inside the fruit pulp. We identified and described a variety of vibrational cues emitted by SWD larvae of different age and at different infestation densities, and create an artificial signal that could be reproduced into uninfested fruit. We performed bioassays to investigate whether *G. brasiliensis* uses mechanical cues to discriminate between suitable and unsuitable host patches. The wasp reactions were analyzed considering the time spent foraging on the fruit and the number of ovipositor insertions. We discuss our findings in relation to the parasitoid's behavioural ecology.

Back to the roots: vibrational communication in cave planthoppers (Hemiptera: Fulgoromorpha)

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How do blind and flightless insects locate and recognize potential mating partners in the vast expansion of permanently dark caves? This question marked the origin of our research – now spanning more than 3 decades - on obligately cavernicolous planthoppers from Hawaii, Australia and the Canary Islands.

Much of what we know about vibrational communication in obligately cavernicolous planthoppers comes from studies on the blind, unpigmented and flightless *Oliarus polyphemus* from lava tubes on Hawaii. Investigating populations from lava tubes of Mauna Loa, Kilauea, and Hualalai volcanoes on the Island of Hawaii revealed that

- cave planthoppers maintain the communication system of their surfaceliving relatives: they communicate by substrate-borne vibrations
- populations from different lava tubes differ significantly in their signal patterns, indicating that *O. polyphemus* is in fact a complex of closely related species, with its evolution apparently closely linked with the geologic dynamics on active shield volcanoes
- the planthoppers'vibrational signals are transmitted via living roots of the indigenous tree *Metrosideros polymorpha*, a pioneer plant on young basaltic lava flows, which dangle freely into the caves or grow along rock surface.

While our research has largely been taxon-based, I strongly encourage studies on vibrational communication in an ecological context. Recent advances in soil biology and exploration of the soil sound- and vibroscape from an artist's perspective suggest that roots may also play a significant role in the communication of soil-dwelling organisms, and it is conceivable that even surface dwelling planthoppers and other insects communicate via this "underground information superhighway", as signals may not only travel between neighbouring plants, but across larger-scale root networks, and over much longer distances than was previously presumed.

Vibrational communication in the bark beetle Ips typographus

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Due to global warming, the european spruce bark beetle *Ips typographus* (L.) has become the most important causative agent of forest damage throughout Europe in recent years. Vibro-acoustic communication has been studied in several bark beetle species. Stridulatory signals are emitted in the context of mating, search for mates, mate choice, and competition with conspecifics. In the European spruce bark beetle, *Ips typographus*, two different acoustic enissions signals have been previously recorded with microphones, transmission, perception and biological function have not been studied so far.

We therefore recorded vibrational signals emitted by the beetles. They do not stridulate, but produce two types of vibrational signals, single clicks and longer trains of vibrations produced by scraping with their mandibles across the substrate.

Playback experiments revealed that the beetles respond behaviourally to both types of vibrational signals. Artificial vibrations of 4000 Hz resembling the scraping sounds attract female beetles and increase their probability of entering an artificial borehole.

Artificial clicking sounds are repellent. In a y-maze the beetles prefer the silent side when artificial clicks are played back as vibrations of one side of the Y-maze whereas scraping vibrations are attractive.

We conclude that although there are no stridulatory signals like in several other species of bark beetles vibrations play a role in the communication system of the European spruce bark beetle *lps typographus*.

Testing alternative hypotheses for the origin of vibrational signaling in lebinthine crickets.

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Many animals use communication signals to advertise their location to the opposite sex. The origins of these communication signals, however, are often mysterious. To test hypotheses about signal origins, potential precursor structures or behaviors in closely related species are compared to the signal using phylogenetic comparative methods. In most cricket species, males produce calling song with a carrier frequency of 2-8 kHz, and females use phonotaxis to find males. Higher frequency sounds induce startle responses due to their similarity to predator cues. Crickets in the tribe Lebinthini (Eneopterinae) are unusual in that males produce high frequency calling song (>12 kHz), females reply to the calls with vibrational signals, and males search for signaling females. A previous study provided evidence supporting the hypothesis that the female vibrational signal could have evolved from startle responses to the unusually high frequency male calling songs. Alternatively, it has been suggested that these vibrational signals could have evolved from courtship interactions when males and females are in contact. We looked for evidence to support this alternative hypothesis by documenting acoustic and vibrational signaling during courtship in two species from the Gryllinae, sister subfamily to the Eneopterinae. For both Gryllus bimaculatus and Acheta domesticus, males produce both high frequency calls and vibrational signals during courtship, but females did not produce vibrational signals in response to male calls. We are currently testing whether high frequency male courtship calls induce startle in females when detected outside of a courtship context. Although our results do not support the courtship origin of the lebinthine vibrational reply, they also do not refute it. To adequately test this hypothesis, courtship behavior in more cricket species, particularly those in the other tribes in the Eneopterinae more closely related to the Lebinthini, needs to be documented.

Birds feel the vibes: the role of vibrations in songbird courtship communication

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Bird courtship communication studies usually focus on acoustic and visual signals, and less attention has been paid to the signals of other modalities. However, many songbirds are known to perform dance displays to potential mates on a thin perch, which means the vibrations via a perch potentially serve as a communication signal. In this study, we investigated the role of vibrations in the courtship communication of a songbird. Blue-capped cordon-bleus are a socially monogamous songbird, and both males and females perform rapid "tap dance"-like displays with singing, which can produce vibrations via perch. We previously found that vibrational amplitude increases depending on the number of taps in one bobbing. Therefore vibrations can be an efficient signal to convey information about individual motivations and/or physical ability. We expected that vibrations would enhance signal receivers' responses as a redundant signal in addition to visual and acoustic signals. If the prediction is true, cordon-bleus will alter the behaviors during courtship depending on the vibration availability. To test this, we placed male and female cordon-bleus in adjoining aviaries and examined if their courtship displays and the responses varied depending on the efficacy of vibrations. We controlled the vibration availability for signal receivers by connecting or disconnecting between the perches of two aviaries. As a result, signal receivers visited the same perch with display performers more frequently and stayed longer when vibrations were available. On the other hand, the amount of courtship display was not affected by vibration availability. The study provides direct evidence that vibrations produced by cordon-bleu courtship dance displays alter the behavior of signal receivers.

Cicadatra persica use tymbal sounds and wing clicking during the courtship song

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In courtship, the cicadas *Cicadatra persica* and some similar and closely related species use combined sound signals produced singly or a few times by tymbals and a longer series of tremulation signals produced by repeated wing clicks.

The exact mechanism of the tremulation is not known in detail, but it is produced during the wing flapping. From the recorded high-speed video images, it appears that, contrary to some other authors, the inner edge of the clavus remains in place during the wing flapping. Therefore, it cannot be involved in vibration production.

To find out how and why they combine these signals, we recorded the song as airborne sound and tremulation as an acceleration or velocity parameter.

The amplitude of both signals is similar in acceleration. A comparison of both signals suggests that the cicadas use these signals to make sure they have been recognized by sexual partners.

A study of multimodal communication using multiple approaches: Uncovering signal functions in a neotropical katydid

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Animals use mating signals in various modalities to locate, assess, and compete for mates. Male and female neotropical katydids (*Docidocercus gigliotosi*) duet using substrate-borne vibrational signals (tremulations), and males also produce airborne stridulatory signals (calls). To investigate the functions of calls and tremulations during inter- and intrasexual interactions, we quantified behaviors of males and females using two approaches: we first conducted *in situ* behavioral observations and then tested receiver responses to signals with playback experiments.

During field observations, we described the behavior of isolated males and females, as well as male - female and male - male katydid pairs on their host plants. We found that males tremulated regardless of whether a female was present, but males increased their tremulation rates in the presence of females. In contrast, females only tremulated in response to signaling males. We also found that male and female *D. gigliotosi* performed tremulation duets prior to mating.

To test signal functions, we played calls and tremulations to males and females and recorded receiver responses. Overall, males tremulated more than females, and females walked farther than males. In response to opposite sex tremulations, both sexes tremulated more during conspecific than heterospecific signals. Females tremulated more during conspecific male calls and tremulations than during silence or heterospecific signals, and some females located signal sources. Males tremulated more in response to conspecific male calls than to male tremulations.

We conclude that some shared function exists between the two signal types. Both sexes distinguish between calls and tremulations from different species, and males appear to increase their signaling when competing for mates. Our findings enhance understanding about how multimodal signaling mediates mating behavior for this species.

The post-diapause vibrational behaviour of the brown marmorated stink bug *Halyomorpha halys* (Stål) adults at different temperatures

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Substrate-borne vibrational communication is common within pentatomids. Although several works exist on the vibrational communication of Halyomorpha halys, its vibrational behaviour post winter diapause has not been investigated. In this study, we recorded overwintered adults of H. halys at three different temperatures using two laser doppler vibrometers. These were 10°C, 18°C, and 24°C, which respectively coincided with inactivity, breaking of diapause, and peak of mating activity. The aim was to assess the calling dynamics of overwintered H. halys and their adaptation capacity to copulation inhibition. The insects were sexed into cages and were recorded separately or joined with a cage of the opposite sex. The recordings were of 10 minutes each. They took place every 2-3 days until the death of the insects and all treatments were recorded within the same day in a randomised order. We calculated the total time spent on signalling and walking per replica. The males predominantly emitted MS1 signals throughout the four months of recordings. The females exclusively emitted FS2 signals when joined with the opposite sex cage the first two months of recordings. Interestingly, they also started FS2 signalling when recorded separately, after two months. No signalling was recorded at 10°C. At 24°C, the signalling latency time was of 24 hours compared to 23 days at 18°C. The short latency time at 24°C was met with a higher female death rate occurring at early stages of recording. However, higher death rates occurred within the last weeks of recording at 18°C. Walking activity was significantly higher in joined cages at 18°C and 24°C, suggesting the increased searching behaviour of insects to better locate the signal source of the opposing sex. Although further observations are needed, it appears that overwintered H. halys could adapt to different conditions whereas low temperatures maintain the diapause which is characterized by no signalling activity.

Developmental environment shifts choice of feeding environment, signaling environment and signal properties in the treehopper *Entylia carinata*

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Developmental environment can affect the expression of a range of ecological and mating-related traits, with important consequences for adult habitat use and patterns of mating. Here, we studied the treehopper Entylia carinata to test whether the plant species on which an individual develops affects where it prefers to feed, where it prefers to sexually signal, and the dominant frequency of male vibrational signals. Entylia carinata naturally occurs on three plant species in our focal population and exhibits population genomic structure according to the plant species on which individuals feed. We reared juveniles collected from two of the plant species in a 2x2 design in the greenhouse. We then tested adult preference for the location of feeding and sexual signaling, and quantified variation in male sexual signals. We found no costs of switching plant species in terms of survival, maturation or adult weight. However, we found shifts in maturation time across plant species, and adults preferred to feed and sexually signal on the plant species on which they developed. Furthermore, males that developed on different plant species showed different dominant signal frequencies. Together, our results suggest that developmental plasticity could be involved in multiple mechanisms generating assortative mating by developmental environment, and could contribute to population genomic structure.

An open-source tool for conducting high-fidelity vibrational playbacks

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A playback experiment with substrate-borne stimuli is a simple and effective way to answer an array of questions about vibrationally-sensitive organisms. One challenge associated with such experiments is that the playback stimuli are filtered by both the playback equipment and the substrate. This filtering causes unwanted distortion to the stimulus received by the organism. A common solution to this challenge is to measure filtering by the substrate and compensate for it, such that when the stimulus is played through the experimental substrate, the amplitude spectrum of the recorded stimulus matches that of the original recording.

One convenient tool for measuring and compensating for substrate filtering is a custom-written script in Matlab. Because proprietary software licenses impose economic barriers that can limit access to research, we have developed an analogous approach in Python, an open-source language. Here, we present an outline of the resulting Python script, which has three modules: (a) calculate substrate filtering and compensate for it, (b) calibrate playback amplitude, and (c) play back vibrational stimuli. We demonstrate its functionality, include sample code, and compare its output with that of the existing Matlab tool.

The basic functions provided by this tool are a stepping stone towards increasing access to vibration research. Because it is open-source, we hope the script will be expanded upon by other researchers in the Biotremology community.

Stinkbug love story

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Stinkbugs of the subfamily Pentatominae with about 3300 globally spread solitary species feed and mate in shelter of herbaceous plants. Multimodal communication with chemical, mechanical and visual signals is the essential part of mating behavior running through different phases. Species specific air transmitted male pheromone attracts in the field conspecifics to land on the same plant and there it triggers females to call males by plant-transmitted vibratory signals. Female/male vibrational communication runs through the calling, courtship and copulatory phases by species specific signals emitted by vertical vibration of abdomen and by species non-specific tremulatory, buzzing and percussion signals. Plants take an active and passive role in airborne transmission of pheromones and the amplitude, frequency and temporal characteristics of vibratory signals are significantly changed during transmission through the plant. Stinkbugs tune frequency and temporal parameters of their vibratory signals to mechanical properties of plants and their sensory system is most sensitive in the group characteristic signal narrow frequency range. The underlying neuronal system integrates and filters information arriving from different sensory inputs. High amplitude and species non-specific tremulatory and buzzing signals enable airborne communication contact, precede female calling and characterize the aggression behavior. Currently running studies of the social aspect of stinkbug multimodal communication in imbalanced sexual situation reveal complex intra- and inter-specific interactions between mates on the same plant. The pattern of recently described female rivalry is more complex compared with that described for males. Interspecific communication contact between sympatric species with similar vibratory signal repertoire is currently under investigation. Biorational control of target stinkbug pest species includes knowledge on basic properties of their communication.

Tremolo dancing with multimodal signals in jewel bugs

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Animal elaborate courtship displays often play an important role in sexual communication through multimodal signals' combinational and hierarchical ordering. In species with developed complex communication, the sophisticated ordering of signals may enhance their ability to signal process combinations, making them ideal research models. Calliphara excellens is known as a jewel bug in the Scutelleridae family, owing to its beautiful metallic green coloration. Its males generate complex vibration patterns by oscillating their bodies in small increments on the plant surfaces, and females respond to playbacked male vibrations, indicating that vibratory signals are important in this species' courtship behavior. Furthermore, our detailed observations revealed that the courtship behavior in C. excellens comprises unique behavioral repetitions, which can be classified into at least four phases. In each phase, we found that visual signals comprising movements with their body color, and chemical or tactile signals obtained by touching the male pronotum may be used in combination with vibratory signals. Such repetition of these ordered and ritualized displays in *C. excellens* probably indicates the use of ordered and hierarchical multimodal signals. In this study, we introduce the signals used in courtship communication of *C. excellens*, which have been confirmed in our observation so far, and discuss that clarifying these signals, including their ordering and combination, may provide insights into new aspects of novel signal-use systems in insects.

The important role of parental vibrational signaling during brood care in the burying beetle Nicrophorus vespilloides

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Communication plays a vital part in any form of cooperative behavior for numerous interactions. Apart from odor, acoustic and vibrational signaling is common during various behaviors such as mating, defense, aggregation, and parental care - a prime example of cooperative behavior. One group that exhibits elaborate biparental care are burying beetles of the genus *Nicrophorus*, making them model organisms in behavioral ecology. In this study, we investigated the function of stridulatory signals during brood care in *N. vespilloides*, where parents cooperate in feeding and defending their young. Although their stridulations have been known since Darwin, and both parents stridulate, their specific functions during brood care remain unclear to this day. We first recorded the signals produced by the beetles as well as their behavior during the entire period of biparental care and examined differences between pre- and post-hatching care. Thus, we were able to characterize the signals and find a significant increase in stridulation activity with hatching. Using a uniparental set-up, we were able to show that parents communicate with their larvae through their stridulations. Additionally, through experiments with silenced parents, we were also able to show that a lack of stridulations has a significant impact on offspring fitness, leading to smaller larvae and smaller next-generation adults. This clearly shows that stridulations play a vital role in biparental care. We believe that parents use them to communicate with their young as well as each other in order to improve brood care. This study provides evidence that stridulatory signals play an important role in the social communication of burying beetles, which is particularly important during "family life" after hatching has occurred.

Sex and caste effects on the sensitivity of the sense of vibrations in honeybees (*Apis mellifera*)

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In the darkness of their nests, most social insect species communicate relying on chemical and vibrational signals. In honeybees, vibrational signals play a role not only in worker communication, but also in communication among virgin queens in the process of swarming. Whereas the sensitivity of the sense of vibrations has been well studied in worker bees, vibrational sensitivity of queens and males has never been investigated.

We therefore studied the sense of vibrations comparatively in workers, virgin and laying queens and in males. Bees were tested behaviourally for responses to pulses of substrate-born vibrations in arenas placed on vibrational exciters. Vibrational amplitudes were measured using (LDV-calibrated) accelerometers. Stimuli and sham-stimuli were presented in a pseudorandom order. The threshold was defined as the lowest tested amplitude at which significantly more reactions were shown to stimuli than to sham stimuli.

The threshold of responses of isolated worker bees in an arena turned out to be substantially lower than the previously studied threshold of the freezing responses in the hive (see Kirchner et al. 2022). Workers respond to amplitudes down to 500 mm/s². Virgin queens are more sensitive and respond to amplitudes as low as 200 mm/s². The thresholds of laying queens are substantially higher, they respond to minimum amplitudes of 500 mm/s². Males show responses to amplitudes down to 600 mm/s².

We conclude that sex and caste have effects on vibrational sensitivity in honeybees. The high sensitivity of virgin queens indicates that a high sensitivity is crucial to detect the vibrational signals of their sister queens in their competition, at the end of which only one of them inherits the hive and its resources.

A comparative analysis on vibrational signals in burying beetles

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The genus *Nicrophorus* has long been studied for its family life, as both partners take care of their larvae by finding an adequate vertebrate carcass, preparing and burying it, and feeding their larvae. Moreover, different Nicrophorus species differ in their degree of parental care and larval dependency, going from N. orbicollis, whose larvae don't reach dispersal stage without post-hatching parental care, to N. *pustulatus*, which show perfectly facultative parental care. Due to the burying beetle living in small family groups (parents and offspring), they face a high level of inter and intraspecific competition for the carcass, as well as intraspecific competition for mating partners and even intraspecific brood parasites. Consequently, selection favored the evolution of good information transfer and numerous studies have shown complex communication through chemical signals such as cuticular hydrocarbons. However, almost no research has looked into the role of stridulatory signals during brood care and especially how these signals might differ between the different species. Therefore, the present study aims first to account for this lack of investigation of vibrational signals between species. Secondly, considering Nicrophorus convenient variability in family life (aka social complexity), this comparative analysis hopes to provide support to the "social complexity hypothesis", which states that organisms with more complex sociality should have more complex communication. Hence, we assumed that N. orbicollis (the most dependent species) should have the most complex signals. To this end, we have recorded and analyzed vibrational signals of mating pairs of 4 different species during their entire brood care and we were able to show that there are distinct differences between them. However, N. orbicollis has so far not been proven to have a more complex vibrational communication than the other species.

Vibroscape variability within hay meadow habitat

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Vibroscape comprises so far overlooked environmental vibrations originating from different sources; geophysical, biological or anthropogenic. Although vibrational signalling presents one of the oldest and widespread communication modalities, a complexity of the natural vibrational environment remains largely unknown. Animals continuously encounter a vast number of environmental signals and cues, providing them crucial information for survival and reproduction. At the same time, environment reshapes animal signals and communication strategies by its physical properties, affecting both signal transmission and reception. Finally, it indirectly affects interactions with other species that share the same habitat, resulting in interference. Laser vibrometers were used to record vibroscape from replicates of two different plant species on the same meadow. Recorded vibrational signals were assigned vibrational taxonomic unit (VTU) and we compared the abundance (VTUs per time) and richness (different VTUs per time) within and between different plant species and plant positions within the meadow. The recordings were performed during the period of the highest insect activity with several vibrometers in Ljubljansko barje lowland meadow. Simultaneous recordings of hammer sedge (Carex hirta) and hedge bedstraw (Gallium mollugo) plants, growing near each other in different parts of the meadow, showed that the composition and the cumulative duration of vibrational signalling differ, regarding both the host plant species and the spatial position of individual plants. Our result suggests that the abundance and richness of VTUs shows larger differences on C. hirta than on G. *mollugo*. In both plant species, the most common vibrational signals were attributed to the same three leafhopper (Cicadellidae) species, differing in presence/absence of rare signal types. We hypothesize that the differences in the amount and composition of the vibroscape originate in the heterogeneity of meadow plant composition, plant geometry and structure, and the variability of microclimatic conditions within it, enhancing the need for further research to identify the reasons underlying these differences.

Active space of substrate-borne signals in a hay-meadow habitat

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Active space is defined as the distance from the source over which signal amplitude remains above the detection threshold of potential receivers. An important concept well studied in soundscapes, but equally important in vibroscapes. 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. While it is accepted that in grassland on plants the active space is limited to a plant on which the animal is signalling, the information on active space of vibrational signals under field conditions is lacking. In comparison with air-borne sound, a random distribution of plants within the grassland habitat, together with differences in plant geometries and heterogeneity of plant substrates that strongly affect damping and selective frequency filtering, result in unpredictable size and shape of the active space of vibrational signals.

We studied the active space of vibrational signals in a natural hay-meadow habitat. We used five portable laser vibrometers to record vibroscape from an area of increasing size (0.008 m² to 0.21 m²). One laser vibrometer was permanently focused at the central point, while another four were pointed at the corners of increasing area. At each area size, we registered vibroscape for 60 min. We determined the number of vibrational signals recorded simultaneously at more than two positions and the presence unique vibrational signal types.

The results so far show that while the number of recorded signals and unique VSTs increase with the area size, in the recording areas bigger than 0.095 m² (i.e., recording positions separated by 20cm or more), vibrational signals were only rarely recorded at different positions simultaneously.

In search for information in the hidden world of vibroscape

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Vibroscape is an overlooked world of vibrations occurring in an environment. It has a great potential to extract information about processes taking place on different organization levels (from individuals to community). Substrate vibrations provide information crucial to the reproduction and survival of most animals, especially arthropods, which are essential to ecosystem functioning. Recordings of viboscape from natural environments can hold information that can't be obtained in the laboratory experiments and can be used in diversity assessments and help us to better understand ecological processes. This concept can give us frames of ecotremology studies.

Our case study in the meadow habitat in Slovenia shows possibilities to utilize above mentioned extraction of information from vibroscape recordings. On the one hand it shows seasonal and diurnal changes, and on the other hand interactions of vibrational community members. Highest vibrational activity was observed during the day in the beginning of July. Members of vibrational community avoid overlapping their signals in short time frames.

In an environment that is rapidly changing due to human activities, climate change, and invasive species, this hidden vibratory world is also likely to change in hitherto unknown ways, with potentially crucial effects on arthropod communities. Thus, vibroscape could be utilized as an indicator of large-scale ecological processes and ecosystem dynamics, analogous to soundscape. We would like to encourage researchers in the fields of ecoacoustics and biotremology to incorporate ecotremology into their own studies.

Who's shaking? On using machine learning to detect vibrational signals in laser vibrometry recordings

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The study of vibroscapes involves the analysis of vibroscape recordings, which are gathered in the field for example with laser vibrometry. However, their study is time consuming, as the vibrational signals of different species must first be manually annotated in the recordings.

Our goal is to simplify and speed up annotations by using modern machine learning methods. We analyze vibrational signals of insects living in hay meadows. Altogether, over 100 hours of recordings were analyzed and signals belonging to different species annotated. The vibrational signals are grouped into four distinct vibrational signal types: pulse, train, harmonic and complex, and we develop methods for automatic detection of vibrational signals in the recordings and their classification into the four signal types.

We base our detection and classification models on deep neural networks, which are the preferred choice for pattern recognition tasks in image and audio processing, including bioacoustics. Specifically, we chose to use the Jasper architecture, which is an end-to-end convolutional neural acoustic model. The model was chosen due to its simplicity and a small number of trainable parameters (approx. 300,000 in our models).

The models were trained on a dataset containing four second long vibroscape snippets, where each snippet contained either a vibrational signal or background noise. They were trained to recognize the presence of a vibrational signal in the recording (either any signal, or signal of a particular type). We measured the accuracy of the models on a validation set using standard classification measures of precision, recall and F1. Currently, the best models yield the F1 score of 0.89 for detecting the presence of a vibrational signal, 0.87 for detecting complex, 0.85 for pulse, 0.83 for train and 0.7 for harmonic vibrational signals.

Vibratory communication of the Russian-leather beetle – a field study

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The Russian-leather beetle *Osmoderma eremita* (Scopoli, 1763) is a cryptic species, spending most of its life in the trunk hollows of old trees. Although the sunlight is absent, adult beetles and their larvae have a seasonal rhythm regarding sexuality and pupation. In this study, vibratory signals were recorded from inhabited trees using a laser doppler vibrometer. We found a higher rate of vibratory events during nighttime. Furthermore, we analyzed which factors (day time and ambient temperature) correlate with the vibratory activity. With the help of linear modelling approach, we were able to show that day time is the main factor that correlates with the frequency of vibratory events. Since vibratory tree-data contain signals between 160 Hz and 1150 Hz, we conclude that this beetle species and/or their larvae use low-frequent vibratory signals for intraspecific communication. Our study revealed that vibratory signals recorded from trees indicate the presence of this endangered beetle species.

Comparing airborne and substrate-borne signaling investment across pseudophylline katydids

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Animals often signal in multiple sensory modalities to attract mates, but the level of signaling investment in each modality can differ dramatically between individuals and across species. When functionally overlapping signals are produced in different modalities, their relative use can be influenced by many different factors, including differences in receiver preferences, signal active space, energetic costs, and predation risk. Characterizing differences in total signal investment across time can shed light on these factors, but requires long focal recordings and time- and computing-intensive processing. Neotropical pseudophylline katydids produce mate advertisement signals as airborne sound and substrate-borne vibration. Airborne calls, produced via stridulation, are extremely short, highfrequency, and longer-range signals. Conversely, substrate-borne calls produced via abdominal tremulation are longer, low-frequency, relatively more energetically costly, and shorter-range signals. To examine patterns of stridulation and tremulation across species and test hypotheses about the drivers of signal use in each modality, we recorded focal individuals from twelve pseudophylline species for 24 hours with microphones and accelerometers. We assessed patterns of signaling investment in stridulation and tremulation across individuals and species. We also examined correlations between signaling effort, morphology, and species relative abundance. Species varied widely in their total amount of signaling in each modality, with greater within-species variation for tremulation signaling effort than for stridulation. There was a positive relationship between the total amount of sound and total amount of vibration across species, suggesting that these katydid species are either "high-signaling" or "low-signaling," rather than exhibiting an investment trade-off between different types of functionally similar signals.

The role of amplitude in a multimodal insect duet

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Vibrational signals are used by many species for finding a mate, and the physical properties of these signals are hypothesized to assist with mate recognition and localization. Crickets within the tribe Lebinthini achieve pair formation through a vibro-acoustic duet; males produce a high-frequency airborne calling song which elicits a vibrational reply in females. These behaviors repeat iteratively as calling males search their surroundings to find stationary females. Based on this sequence of events, we hypothesize that female vibrational signals provide information that facilitates male search effort. Here, we test whether male search behavior is altered by the presence of female vibrational replies on a plant. We found that walking and calling increased significantly when their songs were followed by female vibrations. Next, we assessed how signal variation during this duet might convey information that helps male crickets find responsive females. Preliminary observations showed that the amplitude of the female vibration varied with the amplitude of male song. Using an experimental approach, we found a positive relationship between male song amplitude and female reply amplitude. We hypothesize that this "amplitude mirroring" behavior is adaptive and improves the ability of males to locate receptive mates. Given the differences in attenuation during transmission of airborne sound vs. substrate-borne vibration, amplitude mirroring may allow females to reflect distance information back to a calling male. We propose an experimental design to test whether amplitude mirroring improves pair formation in these crickets.

The role of vibrations in multimodal interactions

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Many animals communicate via multiple sensory modalities. Signals from different modalities may provide functionally similar information, or different signals may provide functionally different messages. Thus, multimodality can improve signal detection, the amount of information transmitted, and receiver performance. Research on multimodal communication in insects has increased in recent years, and it has been shown that vibrational signals are often part of multimodal displays, have high information potential, and are considered important information, for example, at night, in dark and noisy environments. Because vibration signals are inherently associated with body movements that are visually perceptible in diurnal species, and often simultaneously generate acoustic signals in the air, examples among insects that rely solely on vibrations for communication are not necessarily common. Here we will present some examples of integration of vibration signals with signals from other modalities in insects, and discuss the benefits of such complex signalling in various social behaviours (e.g., courtship, rivalry) and predator-prey interactions.

A multicomponent acousto-vibratory courtship described for the first time in a model cricket species

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Crickets (Orthoptera, Grylloidea) are one of the main invertebrate models for the study of mating systems and communication. Their acoustic communication in sexual interaction has been intensively studied both behaviorally and neurophysiologically. Males produce sound by stridulation during the long-distance calling, territoriality, and the short-distance courtship and aggression. Research of the vibrational channel mainly concerned the substrate-borne components of their songs that were shown to improve communication. However, crickets exhibit additional types of vibrational behaviors during short-range interactions, which have received scarce attention in experimental research.

I recorded substrate vibration during courtship of the house cricket (Acheta domesticus) to investigate the function of body tremulation, known to be part of cricket courtship. Unexpectedly, I revealed a multicomponent male courtship display including stridulation, body tremulation, and leg drumming, the latter also clearly audible when emitted on a loudspeaker membrane. These components occur as spectrally diverse, temporally correlated signals, but with drumming varying greatly in persistence thorough the repetitive elements of the song. This persistence is inversely correlated with stridulation rate, reflecting physical demands of the display that likely represents a reliable substrate for female choice. I examined the relative importance of different components in copulation, by eliminating either male stridulation, substrate vibration transfer, or female hearing, and found a low impact of these treatments on female behavior. The results of this study put current understanding of field crickets' courtship behavior into a new perspective, suggesting it should be reinvestigated with the focus on vibrational signals. This shall improve our understanding not only of the function, but also of the evolution, of cricket signaling systems.

The subgenual organ complex in stick insects: Functional morphology and its implications for vibration detection

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In insects, a notable diversity of sensory structures is involved in detecting substrate vibrations. The subgenual organ or a subgenual organ complex is present in most insect lineages. The subgenual organ and associated organs consist of scolopidial sensilla, and the subgenual organ is a highly sensitive receptor organ for substrate vibrations. While in Orthoptera, the subgenual organ complex in the legs has been investigated in locusts, bushcrickets, and crickets, less information is available for several related taxa. Such information can also support the analysis of evolutionary diversification and adaptation of mechanoreceptors. In stick insects, the subgenual organ complex consists of the subgenual organ, spanning the proximal tibia, and the distal organ, extending distally in a linear set of sensilla. The two organs are located almost in perpendicular orientation to each other. The distal organ shows an elaborate neuroanatomy with the set of ~20 sensilla, but is not investigated physiologically in detail. The functional morphology of the subgenual organ complex is documented for possible coupling to different sensory input pathways from the cuticle, hemolymph channel, and tibial trachea. Especially structural coupling to the cuticle or tracheae could indicate possible inputs of vibration energy or airborne sound. The sensilla of the distal organ are located in the hemolymph channel, and are oriented in distal direction of the leg. There are different types of tissue strands connecting the organ to the inner cuticle. The position of the organ in the hemolymph channel and the direction of dendrites indicate an activation by forces acting in longitudinal direction of the tibia, which are likely vibrational stimuli transmitted in the leg's hemolymph. Further, there is a structural connection between the subgenual organ and the proximal part of the distal organ by a septum, which could indicate a functional coupling between the two organs.

Morphological coupling of mechanosensory organs in stick insects

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Insects can detect substrate vibrations by different types of sensilla. Chordotonal organs are particularly sensitive to vibrations, and the main vibration receptor for many insects, the subgenual organ, is a chordotonal organ located in all legs. In orthopteroid insects like locusts, crickets, mantids or cockroaches, the subgenual organ is present in the leg's tibia with additional chordotonal organs, termed together the subgenual organ complex. For the different organs, the stimulation by substrate vibrations or airborne sound is specified by the type of attachment structures to surrounding elements. In stick insects (Phasmatodea), the subgenual organ complex in the tibia shows a unique organisation with the subgenual organ and the distal organ. The distal organ consists of a linear set of sensilla, which are so far physiologically not well characterised, but likely also responds to substrate vibrations. The two organs are anatomically linked by a tissue strand, the septum, located between the distal end of the subgenual organ and the proximal end of the distal organ. It runs between the organs from the anterior to the posterior side of the tibia. This tissue strand does not contain neuronal elements like sensilla or their dendrites, as shown by axonal tracing. This connection was not described for related insect taxa. The septum appears to be tensed, and this apparently affects the morphology of the subgenual organ by stretching the distal end. Therefore, it may be relevant for the mechanosensory activity of the subgenual organ. By coupling the two chordotonal organs, it may cause similar mechanical responses between the subgenual organ and parts of the distal organ. The anatomical findings underline the complex sensory organisation in stick insects.

Exploring the role of plant heterogeneity on the transmission of insect vibrational signals

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For communication to be successful, signals need to travel from a signaller to a receiver through the environment. Thus, the environment in which an animals signals affects signal transmission and serves as a powerful source of selection on those signals. For the many insects that use substrate-borne vibrations to communicate, plants serve as primary channels for vibrational communication. We are interested in how plant architecture—which is often heterogenous and complex—might explain the diversity of vibrational signals observed in nature. Starting with simple structures, we are investigating whether there are general rules that can predict the properties of signals used on more complex structures. We use a scanning laser vibrometer to measure and model vibration transmission through simple structures to explore a range of questions. For example, are certain frequencies better for signal transmission towards or away from the extremities of a plant and how might such relationships change if a signaller moves elsewhere on a plant? Results thus far indicate that the transmission of substrate-borne vibrations through plants is far more complex than assumed.

Characterization of substrate-borne vibrational communication of *Bagrada hilaris*

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Bagrada hilaris (Hemiptera: Pentatomidae) is a main pest of Brassica crops. It is native of the temperate regions of Africa, India, and the Middle East. The mating of adults of B. hilaris was already described in literature as it is characterized by a particular behavioural sequence: male antennation of the female, mounting, and copulation. In other pentatomids, mating involves vibrational signals along with chemical compounds, but there is no mention of the vibrational communication of B. hilaris. The aim of this study was to characterize the substrate-borne vibrational signals involved in the *B. hilaris* mating behavior. Adult males and females (3-7 days old) of B. hilaris were recorded separately or in pairs (male-female) using two laser doppler vibrometers. For each condition, insects were recorded on two different substrates: a potted bean plant (Phaseolus vulgaris L.) and a loudspeaker membrane. The recordings lasted 15 minutes per replica. We identified three types of vibrational signals with a modulated harmonic frequency structure. Males emitted two signal types, MS1 and MS2 whose dominant frequency (mean ± SD) on plant were respectively 130±18.46 and 142.32±37.32 Hz and on membrane 210.67±278.93 Hz and 159.22±28.47 Hz. Females emitted only one signal type (FS, mean ± SD dominant frequency: on plant: 129.94±35.27 Hz; on membrane: 130±9.95 Hz). Males and females produce calling signals when alone or before contact with the mating partner. After touching the female and during mating, the male emits a series of repeated MS2 (i.e., a train). Thus, it appears that vibrations play a role before and after copula. Additional studies are needed to further understand how vibrations and pheromones interact with each other. As already seen in other stinkbugs, a clear understanding of the intraspecific communication might enable the development of an eco-friendly pest management strategy.

Unpredictable vibratory environments affect prey capture and web structure of the funnel-weaving spider *Agelenopsis pennsylvanica*

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Mounting evidence suggests that air- and water-borne noise are pervasive and emergent threats to animal fitness. Yet we know little about the extent and consequences of substrate-borne noise, despite the ancient and ubiquitous use of substrate-borne vibrations as animal signals and cues. The funnel-weaving spider Agelenopsis pennsylvanica is prevalent across urban and rural habitats in North America, and these spiders rely on web vibrations to detect prey. To determine if and how experience with different vibratory environments affects prey capture and (presumably) associated web building behavior, we collected penultimate female A. pennsylvanica from urban and rural habitats demonstrated to differ in natural noise levels. Upon maturation, we exposed adult females to two 3-week periods of substrate-borne vibration playbacks (6 weeks total) using a fully crossed 2 x 2 design of 'quiet' (Q) and 'loud' (L) treatments. In addition to our four treatment groups (QQ, QL, LQ, LL), we had a 'silent' control group that did not receive any playbacks (SS). The treatments differed by 13 dB to match naturally recorded amplitude differences between our focal urban and rural sites. Twice a week across the 6 weeks, we measured the latency to attack (i) a live cricket and (ii) an artificial 'prey' stimulus. We also assessed web structure at the end of each three-week period by estimating (a) web denseness, (b) variability of denseness, and (c) dry mass. To see if our treatments influenced foraging and web building behavior, we compared time to attack live and artificial prey and our quantified web characteristics across our time periods. We found differences in attack latency between treatment groups and interactions between treatment groups and origin on web characteristics. Our results suggest that increased amplitudes of noise negatively impact prey capture and that A. pennsylvanica may adjust their web structure to changing vibratory conditions based on prior habitat experience.

Does male vibratory courtship influence female predatory behaviour in the cursorial spider, *Pisaura mirabilis*?

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Male courtship can serve various purposes such as species recognition, indication of quality or mating status. Spiders are known for sexual cannibalism; therefore, we can expect that male traits evolved to reduce the risk of being cannibalized. Spiders are also known for using substrate-borne vibrations to sense their environment. In orb-web spiders, male vibratory courtship can delay female predatory behaviour, presumably to protect males from female attack as they traverse the web. *Pisaura mirabilis* is a cursorial spider that does not make a web, but males produce substrate borne vibratory courtship when they encounter female dragline silk. This raises the question of whether male vibratory courtship similarly delays female predation in P. mirabilis as was shown for an orb-web spider. We investigated whether male vibratory courtship signals delay female predatory response. We tested this hypothesis by playing back male vibratory courtship, white noise or a silent control while simultaneously exposing females to prey (N=52). We found no delay of female predatory response to prey, nor other differences in female predatory behaviour between treatments. Our results suggest that male vibratory courtship does not serve to reduce female aggression towards courting males in *P. mirabilis*.

Rethinking communication and sexual selection in spiders

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The last few decades have seen a dramatic increase in research investigating the field of biotremology. Vibratory communication has been used to ask and answer questions about wide-ranging topics from biophysics to evolution and test broad principles in behavioral and evolutionary ecology. This talk will review some of the progress that has been made on spider vibratory communication over the last two decades, particularly research on the Paradise Jumping Spiders from the North American genus *Habronattus*. Finally, the talk will discuss more recent work that has suggested that rethinking complex signal function and evolution may be needed.

Applied biotremology towards the future

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In 2022, the first ever vibrational device for insect pest management, a bimodal (i.e., pheromones + vibrations) trap to capture the Brown Marmorated Stinkbug, Halyomorpha halys, entered the market and within a few weeks was sold out to farmer organizations. This is the completion of a long path that started in the early 80s, when disruptive signals were for the first time transmitted to plants by loudspeakers as airborne sounds to interfere with a leafhopper behavior. Since then, the potential of vibrations to be instruments of crop protection has been tested in numerous experiments. In fact, biotremology can be seen as a vivid demonstration of the feasibility of bridging between basic and applied research. From basic research, involving for example studies of animal behavior, neurophysiology and morphology, it is possible to attempt a technology transfer by means of lab, semi-field and field tests that finally allows the production of crop protection devices. Thanks also to recent technology advancements and international policies towards smart agriculture, applied biotremology is spreading worldwide while the word "semiophysicals" finally begins to be recognized as an official term that designates the use of vibrations to interfere with animal behavior. Indeed, vibrations embody at the same time, the concepts of sustainability, by not producing undesired residuals (unlike most chemicals) and that of smart technology by introducing high-tech devices in orchards and greenhouses. In this review, I will present the story of applied biotremology, by reporting the range of insect and plant species object of investigation and commenting on the outcomes. A surprisingly high number of insect pests have been the object of experiments of applied biotremology, from different parts of the world, with original and often creative approaches. The collection of all available information in this field, will serve to create a database useful for future investigations.

Five years of vibrational mating disruption in the vineyard

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The use of vibrations as a tool in integrated pest management is a novel solution that has been proposed in the recent years to control insects communicating by vibrational signals. Vibrational mating disruption was developed and used against two major grapevine pests: *Scaphoideus titanus* (vector of Flavescence dorée) and *Empoasca vitis*. A specific signal was designed and tested to interfere with their sexual vibrational communication and has been proven effective to reduce the number of mating in laboratory and in semi-field conditions. This innovative technique has contributed to the set-up of the first vibrational vineyard in 2017 in Trentino, Italy. Since then, the system has been implemented and is being evaluated in commercial vineyards in northern Italy.

Here, we present how technical and biological monitoring has been carried out to evaluate the efficiency of the system after five years of field testing. The method efficacy was evaluated in two ways: (i) monitoring the mini-shakers efficiency by assessing the transmission of vibrations trough the trellis system using a numerical model of the vineyard and (ii) monitoring the population density of the two target leafhoppers and non-target organisms by visual inspection of the leaves for immature stages and adult leafhoppers and yellow sticky traps for adults.

The first applied vibrational mating disruption technique was proven to be effective to reduce population density of the two key pests of grapevine: *S. titanus* and *E. vitis*, as long as the safety threshold of vibrations is maintained. Non-target organisms are not affected by the species-specific vibrations transmitted along the trellis of the vineyard. Vibrational mating disruption is therefore a promising tool for the control of insects using vibrational signals, the environmentally friendly technique relying on the use of mini-shakers autonomously operating on solar energy is a further step to integrate smart technology into agricultural practices.

Substrate-borne vibrations reduced the infestation of the tobacco whitefly *Bemisia tabaci* (Hemiptera, Aleyrodidae): an experimental assessment in tomatoes, *Solanum lycopersicum*

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While pest management using insecticides is probably the most conventional option among various control methods, the overuse of insecticides often causes the resurgence of pests due to the acquisition of resistance, and also often negatively impacts the ecosystem. As an alternative, increasing attention has been paid to the physical management of insect pests utilizing substrate-borne vibrations and/or sounds, as this pest management tool has modest ecosystem impacts. This method exploits acoustic communications used by insects for mating and the perception of enemy attacks, provoking behavioral responses in an ingenious manner. We aimed to examine whether substrate-borne vibrations effectively drive away tobacco whiteflies, Bemisia tabaci (Hemiptera: Aleyrodidae), which are serious agricultural pests. To do so, B. tabaci were artificially introduced in greenhouses where tomato (Solanum lycopersicum) plants were reared. A substantial averaged reduction in the average density of B. tabaci nymphs and adults was achieved by transmitting vibration stimuli on the plants. No obvious reduction was found in the number of tomato plant flowers. Although the performance of the vibration device and transmission procedures require further improvement, the present results shed light on the potential of substate-borne vibrations as a promising alternatives for pest management. This study was partly supported by the Research Program on Development of Innovative Technology Grants (JPJ007097).

Substrate-borne vibrational signals and stridulatory organs for sexual communication in leafminer, *Liriomyza sativae* (Diptera: Agromyzidae)

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The vegetable leafminer (*Liriomyza sativae* (Burgess)) is a highly polyphagous pest that threatens vegetables and horticultural plants. Although sexual communication is a key component of the animal behavioral repertoire, the mechanism underlying sexual communication in *L. sativae* remains to be elucidated. Here, we used laser vibrometry to characterize the vibrational signals emitted by *L. sativae* during pair formation. By emitting trains of vibrational pulses (male calling) the male initiated communication on the host plant. The female then became immobile and responded to the male calling by emitting replies (female replies), which in turn triggered male replies consisting of a rapid series of chirps and trills. If the female replies, a continuous exchange of male and female replies ensued, representing a duet. In playback trials, a playback signal caused responses from the opposite sex. Moreover, scanning electron microscopy revealed vibration-producing stridulatory organs in both male and female individuals. The files in males were more developed than those in females, and older male specimens had more signs of abrasion. The results provide new insight into the mating biology of *L. sativae*.

Exploitation of vibration sensing for pest management in whiteflies

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Many insects have sensitivities to substrate-borne vibrations that carry information on approaching individuals, including predators. Because vibrations induce various behaviors of insects, e.g., predator avoidance, vibration sensing can be used for physical pest management to disrupt the behaviors of insects that are harmful to agricultural crops. Here we investigated vibration sense and its application to pest management in two whitefly pests, namely, Trialeurodes vaporariorum and Bemisia tabaci (Hemiptera: Aleyrodidae), which cause severe damage to tomato Solanum lycopersicum and other crops worldwide. Adults of T. vaporariorum displayed startle and flight behavior in response to vibrations with 50–600Hz. Moreover, microscopic observation indicated that they have putative vibrational receptors in their leg chordotonal organs. Subsequently, we conducted field experiments in several tomato greenhouses installed with vibrational exciters made by magnetostrictive materials. Vibrations transmitted to tomato plants by the exciters reduced infestations and population densities of adult and larval whiteflies in comparison to the plants without transmitted vibrations. Furthermore, vibrations positively affected fruit set of tomato due to vibrational pollination. Further studies will lead to the development of vibrational technologies for pest management as alternatives to chemical pesticides. We discuss the mechanism of behavioral disruption and pollination by vibrations and their potential of vibrational technologies for pest management and crop cultivation in agriculture.

This study was partly supported by the Research Program on Development of Innovative Technology Grants (JPJ007097).

Not just mating: The unexpected side-effects of the disturbance noise on the flight activity and oviposition behavior of leafhoppers

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Vibrational Mating Disruption (VMD) is a novel pest management strategy that exploits species-specific vibrational signals to interfere with the mating communication of the target pest species and thus reduces the population density. VMD has been applied in a commercial vineyard against two leafhoppers, Scaphoideus titanus and Empoasca vitis. However, only the direct effect of the "disturbance noise" (DN) playback on the mating duet has been evaluated. Since, in many animals, substrate-borne vibrations are known to affect several physiological aspects and behaviors, we tested the effect of the DN used for VMD on two crucial behaviors of S. titanus: flight and oviposition. Flight was tested in laboratory conditions, individuals were released in a plexiglass cage on grapevine potted plants. Trials included two treatments with DN, (1) only males and (2) pairs (males and females), and (3) a silent control with pairs. We measured the flight activity in terms of number of jump/flight episodes in a given time. As expected, we found that when exposed to the DN, both males and females flew more than in the silent conditions. In particular, the flight activity of males exposed to vibrations was not different from single males that in absence of females displayed the typical call-and-fly behavior. In a second experiment, we subjected mated females to DN and counted the number of eggs laid in one week in comparison with females left in a silent condition as a control. Interestingly, females exposed to the DN laid significantly fewer eggs than females in silence. In conclusion, the DN used for VMD affects also behaviors other than mating. Even though these side-effects were unsolicited in the first development of the pest control strategy, they uncover new information on the mechanism of action of VMD. Additionally, by interfering with multiple crucial behaviors of the target species, the DN might be a more resilient solution to control the population density.

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Vibrational monitoring of invasive hoppers in the apple agroecosystem

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Field monitoring of insect pests is often difficult or inaccurate. In the case of Auchenorrhyncha (leafhoppers and planthoppers), the most common systems to date are the use of colored sticky traps or direct collection (by frappage, sweep net, aspirator). These methods are time-consuming and lack accuracy. In addition, the information may be significantly delayed from the actual first pest colonization due to the necessity of human operators to make the survey.

Recent advances in biotremology have the potential to provide a more reliable monitoring method. For example, by means of insect vibration detectors applied to plants (e.g., with accelerometers), it would be possible to recognise the intraspecific vibrational signals associated with target species and define the presence or absence of these insects in a given area. The first objective of this study was to create a vibrational library of the signals emitted by four Auchenorrhyncha species, potentially harmful to apple orchards in Trentino (Italy): *Orientus ishidae, Metcalfa pruinosa, Agalmatium flavescens, Acanalonia conica*. To identify the vibrational signals and the period of the day in which they are emitted, insects were set in cages containing a potted apple plant with attached accelerometers that recorded the signals of single males and couples for 24 hours.

To test the detection efficiency of this technique, we identified an apple orchard infested by the target species and applied the accelerometers to the apple branches for 24 hours. The results confirm the possibility of using biotremology methods as a tool for the real time monitoring of insect pests presence.

By having larger and more updated libraries available, it would be possible to detect the presence of many species even at the earliest stages of a pest colonization and, in the case of alien species, their occurrence in environments potentially susceptible to invasion.

Vibrational disruption approaches for interfering with vectorborne plant pathogens transmission

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The increasing demand for safe and sustainably produced food is leading to the development of pest control tools and strategies alternative to pesticides, such as Vibrational Disruption (VD). VD has been mainly used to disrupt pest mating behavior and for mass trapping. However, recent studies suggest the playback of intra-specific vibrational signals on the host plant might have relevant impact on insect feeding, thus possibly also on the behaviors associated with pathogen transmission. The main goal of this project was to evaluate whether and how VD might interfere with transmission of the phytoplasma Chrysanthemum yellows (CY) by the leafhopper *Euscelidius variegatus*. Here we present our preliminary results regarding: i) the characterization of *E. variegatus* vibrational communication; ii) EPG-assisted observation of infective and non-infective individuals leafhoppers feeding on CY infected and healthy plants "treated" with vibrations. The results of this study could help validating VD as an environmentally-safe strategy for the containment of vector-borne plant pathogens.

Potential use of acoustic communication for pear psylla IPM

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Animals use many ways to communicate including acoustically. Insects are no exception. Acoustic communication encompasses both air-borne vibrations as well as the more innocuous substrate-borne vibrations. This talk will focus specifically on substrate-borne vibrations of a pear pest, the pear psylla (*Cacopsylla pyricola*). Pear psylla uses vibrational communication to search for and attract mates. Interestingly, there has not been any hard record of what these vibrational songs sound like until recently. These vibrational songs are dynamic and can be affected by some environmental factors. Recording pear psylla mating behavior and aspects of how they find mates show potential in using acoustics as a way to disrupt mating and reduce populations in pear orchards. Some potential evidence can be seen in a smaller-scale greenhouse experiment using potted pear plants and vibrational playback devices. There should be further exploration of this signal modality because it can have broader impacts on the way we develop integrated pest management strategies.

Potential of biotremology for monitoring and control of stink bugs: a Brazilian experience

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Because their general phytophagous habit and wide host plant spectrum many species of stink bugs are serious agricultural pests. In Brazil they are serious pests of different main cultures as soybean, maize, beans and others. The main method for control of stink bugs is the use of synthetic insecticides and because their negative effects on environment and human health alternative management methods are demanded by growers and society. Behavioural manipulation of stink bugs could offer a new strategy for stink bug management. Reproductive behaviour of stink bugs includes communication involving interchange of chemical, mechanical and visual signals. Knowledge of these signals and their interactions could help to identify opportunities to interfere in their communication systems and develop biorational tools for pest management. In this talk will be present recent advances of this approach showing results of experiments of communication interference using rivalry signals, interaction of chemical and vibratory signals and the efficiency of incorporating vibratory signals in traps for population monitoring.

How to teach biotremology in experimental home lab classes under Covid-19 lockdown conditions

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In the years 2020 and 2021 Covid-19 infection risk reduction required widespread adaptations all over the world. Universities had to restructure there teaching programs and to switch to digital distance learning. Lab courses which are regarded as crucial and essential in teaching natural science seemed to be impossible and were often cancelled or replaced by online demonstrations or computer simulations.

Starting in April 2020 I implemented experimental home lab classes, in which students were individually provided with experimental set-ups for doing experiments at home supervised through continuous video meetings. The concept turned out to be extremely successful in all our experimental classes including many aspects of entomology like dissection, study of microscopic slides, collection, identification and preservation of insect specimen, and projects on insect behaviour like insect orientation and communication.

For many years I had included in my animal behaviour classes experiments on perception of substrate vibrations using standard laboratory equipment (mini shakers, amplifiers and function generators for playback, accelerometers, amplifiers and oscilloscopes for signal calibration and control) – equipment that can be provided for a (small) number of student groups in laboratory classes, but cannot easily be included in a box with materials that students take home individually for longer periods of time.

Using extremely simplified but still well calibrated set-ups I was able to provide students with equipment for doing vibrational playback experiments and collecting data on behavioural thresholds of vibration perception in insects at home as accurately and efficiently as in lab courses.

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