The hosts want to thank the Cocroft, Schul, and Gerhardt lab for help and support. Special thanks to Jennifer Hartwick, for her organizational skills, efforts and patience.
Location

The meeting takes place in the Christopher S. Bond Life Sciences Center on the University of Missouri campus. All talks (invited and contributed talks) are in the Monsanto Auditorium. Posters are displayed in the lobby before the auditorium and in the Research Display Area, above the lobby.

Meals

Box-lunches are served Sat.-Tue in the Monsanto Lobby (before the auditorium) in the Life Sciences Center. You can find quiet places to eat, rest, talk, argue, or frolic throughout the Life Sciences Center. The balconies (2.-5th floor) around the McQuinn Atrium have sofas and tables available.

Dinner Sat and Sun is in the Plaza 900 dining hall across Rollins Rd. (see map). You will need your swipe card; guests can also pay with cash ($8.50).

Breakfast is available in the Plaza 900 dining hall ($6.50).

Banquet

The Banquet takes place after the field trips on Monday evening in the McQuinn Atrium in the Life Sciences Center. A cash bar will be available.
Main talks

Saturday, 6/04, 10:30am  Public 'Saturday Morning Science' Lecture
David C. Marshall, University of Connecticut
Decoding the Din--Songs, Sex, and Speciation in Periodical Cicadas
(in cooperation with the Christopher S. Bond Life Sciences Center)

Sunday, 6/05, 8:30am
Peggy S.M. Hill, University of Tulsa
Sound or Vibration, or Does it Matter?

Dagmar and Otto von Helversen Lecture
Sunday, 6/05, 7:00 pm
Bernd Ronacher, Humboldt University Berlin
Processing of temporal patterns in a small brain: how much information can grasshoppers extract from song signals?

Monday, 6/06, 1:30 pm
Daniel F. Eberl, University of Iowa
Molecular Functions in Ciliated Auditory Mechanoreceptors in the Drosophila Antenna
(in cooperation with the Interdisciplinary Neuroscience Program)

Tuesday, 6/07, 1:30 pm
William E. Conner, Wake Forest University
Sound Strategies: Acoustic Aposematism, Mimicry, and Sonar Jamming in the Bat-Moth Arms Race
(in cooperation with the Division of Biological Sciences)
# Complete Schedule of Talks

## Saturday, June 4

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<td>David C. Marshall</td>
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- Opponent Asymmetries and the Role of Vibratory Signaling in Male-male and Female-female Jumping Spider Contests
- Males Increase the Efficacy of Courtship Signaling in Response to Female Receptivity Cues: A Test with Puppet Females
- Sources of Selection on Experience-mediated Plasticity in Female Preference Functions
- When Love Comes Calling: Measuring Sexual Selection on Sagebrush Crickets
- Temporal Pattern Preferences in Response to Dynamically Changing Temporal Features in Cricket Song Recognition and Localization in the Parasitoid Fly, Ormia ochracea
- Listening in Noise: Selective Filters and Spatial Release From Masking in Tropical Crickets
- Temporal Processing of Vibrational Communication Signals
- No Evidence for DPOAEs in the Mechanical Motion of the Locust Tympanum
- Selective Attention by Noise Avoidance in the Acoustic Parasitoid Fly Ormia ochracea
- Sound-induced motion of the Bushcricket Hearing Organs
- Cellular Mechanisms Underlying Stimulus-specific Adaptation in the Tettigoniid TN-1 Neuron
### Sunday, June 5

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<td>Peggy S.M. Hill</td>
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<td><em>Sound or Vibration, or Does it Matter?</em></td>
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9:30-10:00 **COFFEE BREAK (Monsanto Lobby)**

*Chair: D. Howard*

10:00   | 49   | **R.E. Hunt**    |
|        |      | *Reproductive Interference in Erythroneura Leafhoppers* |

10:20   | 95   | **S.M. Villarreal** and C. Gilbert |
|        |      | *1 Pulse, 2 Pulse, 3 Pulse, 4: Acoustic Communication in a Dueting Katydid, Scudderia pistillata* |

10:40   | 25   | **M.J.B. Eberhard** and S.H. Eberhard |
|        |      | *1 Pulse, 2 Pulse, 3 Pulse, 4: Acoustic Communication in a Dueting Katydid, Scudderia pistillata* |

11:00   | 36   | **S.D. Gordon** and G.W. Uetz |
|        |      | *Male Courtship and the Effects of Seismic Signals from Multiple Courting Males in the Wolf Spider Schizocosa ocreata* |

11:20   | 33   | **J. Gibson**    |
|        |      | *Vibrational communication: mate searching and directional accuracy in treehoppers* |

11:40   | 60   | **P. Marting**   |
|        |      | *Competitive signal masking during mate localization in a treehopper* |

12:00-1:00 **LUNCH (Monsanto Lobby)**

*Chair: M. Zorovic*

1:00    | 97   | **J.E. Yack** and C. Taylor |
|        |      | *Near-field Hearing in Monarch Butterfly Caterpillars (Nymphalidae: Danaus plexippus)* |

1:20    | 88   | **T. Takanashi**, N. Skals, A. Surlykke, H. Tatsuta, Y. Ishikawa, and R. Nakano |
|        |      | *Variation in Courtship Ultrasounds of Moths with Reference to Sex Pheromones* |

1:40    | 20   | **V.L. Bura**, D.H. Janzen, and J.E. Yack |
|        |      | *Sound Production in Silk and Hawk-moth Caterpillars (Bombycoidea): Taxonomic Diversity and Function* |

2:00    | 78   | **J.L. Scott** and J.E. Yack |
|        |      | *Evolutionary Origins of Vibration Signals in Caterpillars (Drepanidae: Drepanoidea)* |

2:20    | 31   | **K.H. Frederick-Hudson** and J. Schul |
|        |      | *Signal diversification and rapid speciation in temperate Neoconocephalus katydids* |

2:40    | 73   | **R.L. Rodriguez** and G. Höbel |
|        |      | *The Allometry of Advertisement Signals in Insects and Frogs* |

3:00-3:30 **COFFEE BREAK (Monsanto Lobby)**

*Chair: Z. Tang Martinez*

3:30    | 75   | **D. Rothenberg** |
<p>|        |      | <em>Insect Sound and Human Music: Convergent Evolution?</em> |</p>
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<td><strong>M. Greenfield</strong></td>
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<td>Temporal Resolution for Song Signals and Consequences for Pattern Discrimination by Crickets</td>
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<td>Are leader preferences in katydids the outcome of a sensory bias?</td>
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| 8:30   | 34   | **J.M. Gleason**, Y. Zhou, J.L. Hackett, and M.D. Greenfield<br>
|        |      | *Quantitative Trait Loci for an Acoustic Signal in the Lesser Waxmoth, Achroia grisella* |
| 8:50   | 56   | **N. Lee**, **D. R. Howard**, C. L. Hall, and A. C. Mason<br>
|        |      | *Female Choice in the Prairie Mole Cricket Gryllotalpa major*                      |
| 9:10   | 46   | **G. Höbel** and R. C. Kolodziej<br>
|        |      | *Individual Preference Functions and Sexual Selection in Gray Treefrogs*           |
| 9:30   | 69   | **R. Nakano**, F. Ihara, Y. Ishikawa, and T. Takanashi<br>
|        |      | *Dual Roles of Male Courtship Ultrasound in the Yellow Peach Moth*                 |
| 9:50   | 62   | **J.R. Marquess**, J.A. Anderson, and J.P. Chambers<br>
|        |      | *Implications of Stridulation Behavior in the Red and Black Imported Fire Ants, Solenopsis invicta buren and Solenopsis richteri forel, and Their Hybrid* |
| 10:10  |      | COFFEE BREAK (Monsanto Lobby)<br>
|        |      | Chair: P. DeLuca                                                                  |
| 10:40  | 23   | **J. R. Cooley** and P. Fonseca<br>
|        |      | *Song Pitch Displacement in 13-year Periodical Cicadas*                           |
| 11:00  | 29   | **P.J. Fonseca**, J. Cooley, and D.R. Hughes<br>
|        |      | *Sound Production in Three Closely Related Cicadas, Okanagana canadensis, O. rimoso and O. bella* |
| 11:20  | 98   | **V. Zgonik** and A. Cokl<br>
|        |      | *Triggers of the Male and Female Calling and Courtship Song in Southern Green Stink Bug (Nezara viridula)* |
| 11:40  | 35   | **K.R. Goodman** and D.O. Elias<br>
|        |      | *Rapid Diversification of Sexual Signals in Hawaiian Nesosydne Planthoppers (Hemiptera: Delphacidae)* |
| 12:00  | 22   | **J.A. Cole**<br>
|        |      | *Reproductive Character Displacement and a Song Cline after Secondary Contact in California Shield-back Katydids (genus Aglaothorax)* |
| 12:30  |      | LUNCH (Monsanto Lobby)                                                            |
| 1:30   | 9    | **Daniel F. Eberl**<br>
|        |      | *Molecular Functions in Ciliated Auditory Mechanoreceptors in the Drosophila Antenna* |
| 2:30   |      | FIELD TRIPS                                                                      |
| 6:30   |      | BANQUET (McQuinn Atrium)                                                         |
Tuesday, June 7

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| 8:30   | 84   | **J. Stout**, L. Samuel, and G. Atkins  
*Selective Processing of Calling Songs by AN2 Interneurons of Female Gryllus bimaculatus: Roles in a Temporally Selective Neuronal Network* |
| 8:50   | 90   | **T. Trilar** and M. Gogala  
*Present Status of Mountain Cicadas (Cicadetta montana s. lato) in Europe* |
*Delineation of Species Boundaries Between Field Cricket Species of the Genus Itaropsis (Orthoptera, Gryllidae, Gryllinae): A Test of Concordance Between Morphological, Molecular and Acoustic Datasets* |
| 9:30   | 64   | **G. Miller**  
*Male Song and Female Preference in Two Hybridizing Meadow Katydids (Orthoptera: Tettigoniidae)* |
| 9:50   | 68   | **G.K. Morris** and S.J. Gutierrez  
*Cuticular Acoustic Forms: Generator Structure for Ensiferan Signals* |
| 10:10-10:40 |  | **COFFEE BREAK** (Monsanto Lobby)  
*Chair: J. Windmill* |
| 10:40  | 15   | S. Alem, K. Koselj, B. M. Siemers, and **M.D. Greenfield**  
*Bat Predation and the Evolution of Leks in the Acoustic Lepidoptera* |
*Buzz-pollination by Bumblebees and its Influence on Pollen Ejection in Solanum rostratum Flowers.* |
| 11:20  | 17   | **N.W. Bailey**, E. Glidewell, and M. Zuk  
*Incommunicado Crickets: Different Mutant Wing Morphologies in Two Populations of Field Crickets Each Cause the Loss of Singing Ability* |
| 11:40  | 18   | **O. M. Beckers** and W. E. Wagner Jr.  
*Effects of Parasitism on the Host: Evidence for Host Manipulation?* |
| 12:00  | 52   | **A.L. Joyce**  
*The Impact of Host Plants on Courtship Vibration Transmission and Mating Success of Parasitoid Wasps (Hymenoptera: Braconidae)* |
| 12:30-1:30 |  | **LUNCH** (Monsanto Lobby) |
| 1:30-2:30 | 11  | **William E. Conner**  
*Sound Strategies: Acoustic Aposematism, Mimicry, and Sonar Jamming in the Bat-Moth Arms Race* |
| 2:30-3:00 |  | **COFFEE BREAK** (Monsanto Lobby) |
Tuesday, June 7 continued

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| 3:00 | 81   | **S. Sivalinghem** and J.E. Yack  
*Acoustic Communication in the Pine Engraver Bark Beetle, Ips pini (Coleoptera: Scolytinae)* |
| 3:20 | 61   | **S.M. Matheson** and J.E. Yack  
*Multi-component Vibration Signals of Group-living Caterpillars: Characteristics and Function* |
| 3:40 | 39   | **C. L. Hall**, A. C. Mason, D. R. Howard, and R. J. Smith  
*Description of Acoustic Characters and Stridulatory Structure of Nicrophorus Burying Beetles: A Comparison of Eight Species* |
| 4:00 | 40   | **J. Hamel**  
*Communication Between Treehopper Parents and Offspring About Changes in Predation Risk* |
| 4:20 |      | **Business Meeting** - Student Competition - Future of ISV |
| 5:00 |      | End of Meeting |

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*Motor Basis for Vibrational Communication in the Treehopper, Umbonia crassicornis*  
K. Christie, W.C. Smith, E. Sivan-Loukianova, M. Roy and D.F. Eberl |
| 2        | 21   | Eberl  
*Physiological and Anatomical Changes after Acoustic Trauma in the Fruit Fly Drosophila melanogaster* |
| 3        | 26   | M. J. B. Eberhard, F. A. Roemschied, B. Ronacher and S. Schreiber  
*Some Like it Hot - Effect of Temperature on Auditory Neurons in the Locust* |
| 4        | 28   | L.E. Fletcher  
*Potential Molting Signal in a Gregarious Sawfly Larva, Perga affinis (Hymenoptera: Pergidae)* |
| 5        | 32   | K. H. Frederick-Hudson, J. Schul  
*Comparing Phenotypic and Genetic Diversity in Three Sympatric Species with Acoustic Communication* |
| 6        | 37   | S. D. Gordon and J.F.C. Windmill  
*Morphological Plasticity Based on Environmental Conditions: Hearing in Gregarious vs Solitary Locusts (Schistocerca gregaria)* |
| 7        | 38   | R.N.C Guedes, S.M. Bond, B. Frei, M.L. Smith and J.E. Yack  
*Vibration Detection and Discrimination in the Masked Birch Caterpillar (Drepana arcuata)* |
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25  83  N. Stange and B. Ronacher  
  Which Information is Contained in the Songs of Chorthippus biguttulus?
26  86  C.A. Swatek, J.S. Gibson and R.B. Cocroft  
  Use of Amplitude Cues During Vibration Localization by a Small Plant-dwelling Insect
27  87  A. L. Sweger and G. W. Uetz  
  The Role of Acoustic and Seismic Communication in Gladicosa gulosa: Complex Vibration Signals in a Wolf Spider.
28  91  M. Tucker  
  Parallel changes in mate-attracting calls and female preferences due to auto-polyploidy
29  92  G.W. Uetz, J. S. Gibson, S. D. Gordon, J. A. Roberts and D.L. Clark  
  Active Space of Multimodal Signaling by Wolf Spiders in a Complex Environment.
30  94  V. Yu. Vedenina and G. Pollack  
  Courtship Behavior and Recognition of Courtship Song in the Field Cricket Gryllus assimilis
31  96  J.F.C. Windmill, D. Mackie and J. Sueur  
  Extremely High Sound Pressure Level from a Pygmy Aquatic Insect
32  53  B.J. Kensinger, B. Luttbeg, S. Heads, and J. Schul  
  A revision of the distributions, calling behavior, and taxonomy of two North American shieldbacks (Orthoptera: Tettigoniidae): Atlanticus testaceus and Atlanticus monticola
33  66  A. Mohsin and J. Schul  
  Sexual Dimorphism of Directional Hearing in a Katydid with Duetting Communication System
Musical Performance during the Banquet:

**David Rothenberg: a concert of original music made out of, and in collaboration with, the sounds of insects**

Musician and philosopher David Rothenberg is the author of *Why Birds Sing* (Basic Books and Penguin UK), also published in Italy, Spain, Taiwan, China, Korea, and Germany. In 2006 it was turned into a feature-length TV documentary by the BBC. Rothenberg has also written *Sudden Music, Blue Cliff Record, Hand’s End, and Always the Mountains*. His articles have appeared in *Parabola, Orion, The Nation, Wired, Dwell, Kyoto Journal, The Guardian, The Globe and Mail* and *Sierra*, and his writings have appeared in at least eleven languages. His latest book is *Thousand Mile Song* (Basic Books), about making music with whales, currently being developed into a feature documentary for Canal+ in France.

He is currently collaborating with researchers from CUNY, NYU, and the Netherlands Institute of Ecology on the quantification of the musicality of nightingale songs, a project that stems from his earlier book on bird song and music. His latest major label music CD, *One Dark Night I Left My Silent House*, a duet with pianist Marilyn Crispell, came out on ECM in May 2010.

Rothenberg is professor of philosophy and music at the New Jersey Institute of Technology. His next book *Survival of the Beautiful: Art, Science, and Evolution* will be published by Bloomsbury in 2011.

As a musician David Rothenberg has performed and recorded with Laurie Anderson, Scanner, Glen Velez, Karl Berger, Peter Gabriel, Ray Phiri, and the Karnataka College of Percussion., to name a few. Most of his performances and compositions involve many sounds and musical ideas from the natural world, most famously birds and whales, but for his next project he has chosen to tackle sounds of the insect world, a project he began at the First International Arts Festival in London in 2006, a tri-annual festival devoted to the “art of being an insect.” It’s coming to New York in 2012. Rothenberg’s future book on insects and music is scheduled to be published by St Martins in 2013, when the seventeen year cicadas next return to New York.

Birds and whales are known for their exuberant melodies, while insects are known for their rhythms and textures. In what sense are such sounds musical? Tonight’s performance, with Rothenberg playing clarinet and electronic sound transformations, will attempt to answer that question, by example.
Abstracts

Invited Talks
Decoding the Din – Songs, Sex, and Speciation in Periodical Cicadas

David C. Marshall
University of Connecticut, Dept. of Ecology and Evolutionary Biology, Storrs, CT, USA
Email: david.marshall@uconn.edu

The periodical cicadas, genus Magicicada, are one of the natural wonders of the world. Noisy, synchronous emergences of millions of insects per acre, after 13 or 17 years spent underground as nymphs, with as many as four distinct species appearing together in mixed choruses, provide an unmatched spectacle to residents of the eastern United States. The patchwork of geographically distinct broods (of which this year’s Brood XIX is the largest) provides opportunities for springtime study in most years, and almost every brood contains cicadas of three species groups, known as the -decim, -cassini and -decula groups, each with 13- and 17-year species. During the past sixteen years – not quite one generation for the 17-year forms! – substantial advances have been made in our understanding of the biology of the periodical cicadas. These discoveries range from acoustic biology and mating behavior to host-parasite interactions and life-cycle shifts. A new species has been discovered here in the Midwest – one that demonstrates a rarely observed stage in the speciation process. These discoveries are showing that the extraordinary periodical cicadas are more like other cicadas (and other insects) than had been thought, and knowledge of their biology can help to refine general theories.

Until recently, no one knew precisely how males and females of each Magicicada species find the right partner in their dense, mixed-species aggregations. Female signals were unknown, and the conspicuous, risky male behaviors were compared to those observed on vertebrate leks, where males perform in groups and females choose mates of exceptional quality from the pool of suitors. We now know that female periodical cicadas are not silent players in the mating game, and that they communicate with their desired mates with acoustic and visual “wing-flick” signals that are precisely timed to the male’s song phrase. (These signals can be easily mimicked, and males consequently attracted, with simple finger snaps!) Instead of a lek system, mate choice appears to involve a “scramble competition” for mates. Paradoxically for an insect that invests 13 or 17 years in development, the adult life of a periodical cicada is a mad rush to find mates and lay eggs during a brief window of time lasting but a few weeks to a month. Female periodical cicadas select the first male to pass a set of “minimal criteria”, based in large part on song characters, and then begin the time-consuming business of egg-laying.
New discoveries suggest what females may be selecting against as they choose their mates. One possibility is a fungal parasite (genus *Massospora*) that waits in the soil for 13 or 17 years in order to infect emerging cicadas. Stage I of the life-cycle of the parasite keeps the adult cicada alive while converting parts of the cicada’s abdomen into infective spores that are spread to other adult periodical cicadas of the same emergence. These unfortunate individuals develop a similar-looking “Stage II” abdominal infection that produces spores that drop to the ground to wait for the next generation. Remarkably, the Stage I fungus manipulates the natural behavior of cicadas in ways that improve its chances of spreading by contact. Infected female cicadas allow males to attempt to mate repeatedly. Infected males, even more strangely, act like females by responding to the songs of other males with the same precisely timed wing-flick signals that females use. Similar alterations of behavior by *Massospora* in other cicada species have been observed. These findings undermine the most widely held adaptive hypothesis for the evolution of *Magicicada* life-cycles— that the long, prime-numbered periods spent underground allowed the cicadas to escape synchronized parasites and predators.

*Massospora* is not the only specialized parasite or predator known to have evolved to exploit this sort of male-female signaling system. In Australia, distantly related cicadas with similar pair-forming systems suffer acoustic “aggressive mimicry” by a predatory katydid (*Chlorobalius leucoviridis*) that can attract males of a wide range of cicada species. Predators and parasites like *Chlorobalius* and *Massospora* may create evolutionary pressures on insect songs and thereby drive isolated populations toward speciation more rapidly.

Decoding the pair-forming signals of periodical cicadas has helped to explain previously mysterious male acoustic behaviors. Courting males, for example, use specialized “interference” signals that obscure the part of a competitor male’s song that triggers the female reply— the oblivious competitor soon leaves to search elsewhere. Similar signals have been observed in other cicadas and unrelated insect groups such as katydids that also employ male-female signal duets. New hypotheses are now possible for the unique complex courtship signals of *Magicicada*. Again, these findings bring periodical cicadas more into line with general patterns of insect behavioral ecology.
Behavioral and genetic approaches have together unmasked the most surprising discovery of this past cicada-generation, a seventh *Magicicada* species (*M. neotredecim*) that is literally in the process of evolving its distinctive calling song. This new 13-year species, with a distribution centered on southern Missouri and Illinois, appears to have evolved recently from populations of 17-year *M. septendecim*, and, where it geographically overlaps its closest 13-year relative (*M. tredecim*), females of the two species distinguish their mates based on finely tuned preferences for song frequency. Away from the zone of overlap, males of *M. neotredecim* have the song frequency of the parent species, and playback experiments show that females prefer this pitch at those sites. This geographic pattern, called reproductive character displacement, is predicted to occur when songs evolve as a result of natural selection to avoid costly interspecific mating, yet it has only rarely been observed.

The most intriguing questions about periodical cicadas involve the evolutionary reasons for their long, prime-numbered life cycles. Although these questions are by no means solved, new observations of life-cycle variations in both 13- and 17-year species suggest that environmentally triggered shifts in life-cycle are a major factor in creating both new broods and new species of periodical cicada. (Yes – in a key sense, periodical cicadas are not really periodical.) Developmental flexibility allows large numbers of cicadas to change life-cycle together, maintaining the high population densities on which they have evolved to depend. If true, this connects *Magicicada* to a growing body of evidence for phenotypic plasticity, together with genetic change, as a key factor in the evolution of new species. The seemingly unique periodical cicadas have an important role to play in the development of biological theory.

Dr. John R. Cooley (University of Connecticut) is a key collaborator and co-discoverer of many of the findings presented here. Other collaborators include Dr. Richard D. Alexander (University of Michigan), Dr. Chris Simon (University of Connecticut), and Kathy Hill, M.Sc. (University of Connecticut). Research funding from the following sources has been important for this research: Frank W. Ammermann Endowment, Univ. of Michigan Museum of Zoology; National Science Foundation grants to Dr. Chris Simon (Univ. of Connecticut); National Geographic Grant to Dr. John Cooley (Univ. of Connecticut); Royal Society of New Zealand ISAT grant to Kathy Hill.
Sound or Vibration, or Does it Matter?

P. S. M. Hill*
University of Tulsa, Department of Biological Sciences, Tulsa, OK, USA
*correspondence with: peggy-hill@utulsa.edu

In his 1949 leafhopper monograph, *Insect Drummers*, Frej Ossiannilsson commented on making a distinction between sound and vibration:

This discussion has been made more complicated by many workers having felt obliged to separate a perception of air-born vibrations by a specific auditory sense from a perception of the vibrations by the tactile sense. This presentation of the problem will, in my opinion, very easily turn into a battle of words. Even in insects with a well developed tympanal organ apparently specially constructed for the interception of vibrations of the air, we shall of course never be able to gain a real conception of how the animal subjectively apprehends these...I believe that the vibrations produced by the tymbal organ of one specimen are conducted to other individuals mainly by the solid substratum--as a rule some part of a plant--and only in a less degree by air. If it could be established that the animals do in this way apprehend calls of each other as such--is this to be termed hearing or not? A matter of taste! (1949, 136).

This concern of Ossiannilsson has been noted by others since then, but never fully reconciled in the literature of our discipline.

My own interest in the distinction between sound and vibration emerged and was refined by my work with the prairie molecricket, *Gryllotalpa major* Saussure. Males signal through stridulation with their forewings from a burrow chamber with a surface opening, producing an airborne component (sound) of a song that will carry for up to 400 meters. Flying females receive this airborne component as a sexual advertisement signal, but the same...
stridulation event excites the soil (vibration) and is detected by neighboring males at a distance of 3-4 meters from the focal male. Thus, one behavioral event produces both sound and vibration in the popular connotation of the two terms. We now recognize that both stridulation and drumming on the substrate typically produce both airborne and substrate-borne waveforms. However, which of these is the necessary and essential stimulus in a communication system, or are both required for signal transfer and processing? Or, do the two signals encode information for different targets? It is difficult to discuss these concepts across taxa without a common language!

We distinguish between sound and vibration based on sensory perception, which is probably the most commonly used method for separation of the two. It is common knowledge that sound is what we hear with our ears, while vibration is felt with the body. However, in the strictest use of the term, vibration refers to particle motion in a fluid medium, or in an elastic body, whether it is airborne, waterborne or substrate-borne. *Sound* is used typically to refer to airborne or waterborne compressional acoustic waves, which are detected by an animal with pressure receivers, or pressure difference receivers, but it is rarely used to describe a subset of a larger category of vibration. *Vibration* in the sense most commonly used actually refers to substrate-borne vibration, which is detected from particle displacement of the substrate. Thus, substrate-borne vibration is only one subset of all physical vibrations, which includes sound. To further complicate, signals carried via airborne, waterborne or substrate-borne vibrations all could be considered acoustic.

We can distinguish between sound and vibration based on the reception of the event with some sort of auditory organ (sound) or via a tactile sense (vibration). Sound in vertebrate animals would be projected from the cochlea of the ear to the auditory cortex of the cerebrum for decoding, and vibration would be projected via the spinal cord to the primary somatosensory cortex, or its equivalent. However, what if substrate-borne vibrations are conducted through the skeleton of an animal to the middle ear, avoiding the eardrum in an extratympanic pathway? The information is detected in the cochlea and transmitted through the vestibulocochlear nerve, or its analog, to the brain. Is this sound or vibration?

Further, we know that invertebrate animals are capable of detecting substrate-borne vibrations with a wide array of receivers, but whether or not these receivers are used in communication or simply serve as part of a mechanism to alert the individual of a vibrational event is not yet known in most cases. What we do know is that in almost every documented case of animal communication via the substrate-borne vibration channel the waveform is a boundary wave: a Rayleigh wave or a bending wave. At the boundary between a fluid and a solid, energy is transferred from one to the other. An event that excites the substrate is transferred to the air, and vice versa. A loud noise can be both felt and heard.

The issue is further complicated when we examine the evolution of hearing in invertebrates. There is ongoing discussion of whether the auditory organ in insects, for example, is derived from the subgenual organ, which is a vibration receiver, or whether there have been multiple incidences of
convergent evolution of invertebrate hearing organs and multiple incidences of loss of anatomical elements.

Until we know more about the functional role of substrate-borne vibration receivers and the central processing of any signals they detect, we will continue to be confronted with this gray area. Is this a sound or a vibration, or does it even matter?

I wish to thank the organizers of the 2011 Invertebrate Sound and Vibration meeting for their kind invitation to participate and their hosting of this talk. I also thank those friends who share my fascination with sound and vibration who have helped me learn and grow as they provided insightful comments and excellent conversation over the years, especially Dr. John Shadley, my mechanical engineering colleague, without whom none of my ideas would have come to fruition.
Dagmar and Otto von Helversen Lecture

Processing of temporal patterns in a small brain: how much information can grasshoppers extract from song signals?

Bernd Ronacher, Institut für Biologie der Humboldt Universität zu Berlin, 10099 Berlin, Germany

*correspondence with: bernhard.ronacher@rz.hu-berlin.de

Many grasshopper species use acoustic signals to attract and to identify potential mates. The correct interpretation of these signals is under strong selective pressure, since it directly influences the mating success and the production of offspring. In pioneering studies, Dagmar and Otto von Helversen have shown that the temporal pattern of amplitude modulations provides the crucial cues for signal recognition. We investigate the processing of sound patterns in the auditory pathway of grasshoppers in a combination of behavioural tests, neurophysiological recordings and theoretical approaches.

In my talk I will try to draw a line between two – at first glance rather disparate – topics: (i) sexual selection exerted by choosy females on grasshopper males, and (ii) the variability of neuronal

![Fig. 1: Correlation between hind femur length of Chorthippus biguttulus males and the onset accentuation at the begin of song syllables. (terminology after von Helversen and von Helversen 1997; J Comp Physiol A 180: 373-386). P = 0.0239, r = 0.307; Pearson, two-tailed; Nicole Stange, unpublished data.](image-url)
signals. Taking the viewpoint of a grasshopper's central nervous system, we asked how much information can be extracted from the spike trains of auditory neurons, and how noise will influence the discrimination of communication signals. All information about the external world must be conveyed to the brain via trains of action potentials. At different stages of the auditory pathway we observe a considerable amount of "intrinsic noise" that leads to a trial-to-trial variability of spike trains.

However, an important question is whether the observed variability of spike trains is of any relevance for the animals. Conceivably, external noise sources that degrade acoustic signals on their way from sender to receiver may be completely dominant, thus reducing intrinsic noise to a minor problem. In a quantitative approach, using a spike train metric (after van Rossum 2001), we show that intrinsic noise can not be neglected and constitutes an important limit for signal recognition and discrimination between similar signals – which is important in the context of sexual selection. These considerations will lead to the final question: how much information about a sender's condition and health may a female grasshopper extract from a song signal. Nicole Stange in my lab found a series of interesting correlations between specific features of individual grasshopper songs and morphometric parameters of the sound producing males (see also Poster by Nicole Stange), correlations that a female could, in principle, use to evaluate the quality of potential mates by means of acoustic cues.
Molecular Functions in Ciliated Auditory Mechanoreceptors in the Drosophila Antenna

Daniel F. Eberl*
1The University of Iowa, Department of Biology, Iowa City, USA
*correspondence with: daniel-eberl@uiowa.edu

Sensory cilia are as diverse as the sensory signals they transduce. They are involved in transducing mechanical signals such as touch and hearing, as well as many kinds of chemical and visual signals. In insects, the stretch receptive chordotonal sensory organs, which innervate both tympanal hearing organs as well as flagellar or antennal hearing organs, exhibit specialized ciliary features in the dendrites of sensory neurons. In particular, the ciliated segments are relative long, and display a ciliary dilation that subdivides the cilium into morphologically and functionally distinct segments. The distal segment is the sensory compartment, lacks dynein arms in the axoneme, and is the localization site of the TRPN mechanosensory ion channel encoded by nompC. The proximal segment is the localization site of the TRPV channels encoded by inactive (iav) and nanchung (nan), important for propagation of the sensory signals, and the axoneme in this segment also exhibits dynein arms, suggesting that this segment could be motile.

Among the genes we have studied that are important for the development or function of the Drosophila auditory sense organ, the Johnston's organ (JO) in the antenna, I will present three vignettes that illustrate different dimensions of ciliary biology. First, these sensory cilia are constructed by intraflagellar transport (IFT). Second, these sensory cilia require a specialized ionic milieu provided by the scolopale cell. Third, the functionally distinct proximal ciliary segment may provide the putative active motility that underlies amplification, non-linear mechanics and tuning.

Ciliary assembly in Johnston's organ requires the machinery of IFT. The first genetic clue was the identification of the beethoven (btv) mutation, which strongly reduced hearing, as the IFT retrograde motor protein, the cytoplasmic dynein DHC1b. These mutants show defective cilia and delocalized ciliary proteins. Furthermore, mutations in subunits of the anterograde motor, kinesin II, completely failed to assemble cilia,
and showed truncation at the basal bodies. A number of IFT particle proteins play key roles in JO ciliary assembly and ciliary compartment establishment and specialization. Finally, assembly of dynein arms in the proximal ciliary compartment requires the action of two leucine-rich repeat proteins encoded by the \textit{touch-insensitive larva B (tilB)} gene and the \textit{smeana (smet)} gene.

To transduce mechanical signals, the mechanoreceptive ion channels must allow ion flow across the ciliary membrane, driven by a transmembrane potential. The endolymph-like compartment enclosed by the scolopale cell, the scolopale space, provides a critical functional milieu for effective transduction. The scolopale cell enwraps the sensory dendrites of each scolopidium, forming the sizable extracellular scolopale space sealed with septate junctions, and fills it with specialized extracellular matrix proteins such as that encoded by the \textit{eyes shut (Eys)} gene, also known as \textit{Spacemaker (Spam)}. The space is also thought to contain a receptor lymph that is likely to be K$^+$-rich. Our studies show that expression of the Na$^+$/K$^+$ ATPase is highly enriched in the scolopale cell, and that it is required specifically in the scolopale cell for the morphological integrity of the scolopale space, and the functional integrity of the sensory cilium.

The recent progress in understanding the auditory mechanics of the \textit{Drosophila} antenna have revealed an exquisitely sensitive and intricate organ. Energy-dependent antennal motion is derived from the scolopidia of JO, and most likely from the sensory cilia in the JO neurons. A likely source of this movement is active motility of the cilium itself, probably the proximal ciliary compartment, which we have shown contains axonemal dynein arms. One model is that these active movements generate spontaneous oscillations of the antenna in the absence of sound, dynamic range compression, and sound-level dependent tuning of the antennal mechanics. If these functions require active axonemal motility, then the dynein arms are likely candidates as the motors. This is consistent with loss of these activities in several mutants that disrupt axonemal integrity including dynein arm loss. We propose that this can be directly tested by introducing specific mutations into axonemal dynein heavy chains that, instead of disrupting function, alter their functional properties. We have experiments in progress to introduce temperature-sensitive mutations into these motors, and are testing whether the antennal mechanics are altered in the predicted ways.

In summary, genetic studies of the \textit{Drosophila} auditory system are contributing important insight into the development and function of this sense organ, and are revealing a mechanical and biological beauty in this exquisitely sensitive organ that previously could not have been fathomed.

I am pleased to acknowledge support by NIH grant DC004848, the hard work of many lab members, and productive collaborations with several colleagues.
The interactions of insectivorous bats and their prey can be thought of as an evolutionary arms race. Bats began the race with the evolution of sophisticated, high frequency sonar with which they echolocate flying insects and track them through space. Many nocturnal insects including moths countered with the evolution of sonar-detecting devices – ears – that alert insects to the echolocation cries of approaching bats. Moths take evasive action in the form of loops, spirals, and power dives and impressive aerobatic “dog fights” ensue. Tiger moths (Lepidoptera: Arctiidae) have added a new twist to the fray. Tiger moths answer bats with a series of intense ultrasonic clicks produced by paired thoracic structures called tymbals.

I have been lucky enough to have three fantastic graduate students study bat/moth interactions at Wake Forest. They are Nickolay Hristov, Jesse Barber, and Aaron Corcoran. Our laboratory research using big brown bats, *Eptesicus fuscus* (Figure 1), and tethered tiger moths has supported three functions for the moth clicks: acoustic warning, acoustic mimicry, and sonar jamming (Figure 2).

Principal component analyses of species with anti-bat moth sounds find that species cluster into two groups: one group with species using sounds of simple structure and low duty cycles indicative of moths that warn and mimic and a second group of species using sounds with more complex sound
structures and high duty cycles indicative of the sonar jamming function (Figure 3).

Figure 2. Tiger moth acoustic defense strategies. Column 1: Species name and defensive strategy; Column 2: Image of moth species; Column 3: Scanning electron micrographs of the tymbal organs of each species; Column 4: Spectrogram of tymbal sounds; Column 5: Palatability of species compared to noctuid controls.

We continue to study the bat-moth arms race, but now, in the field at the Southwestern Research Station near Portal, Arizona where 18 species of bats battle with over 30 species of tiger moths. Each night reveals new and exciting strategies on the part of both predator and prey.
Figure 3. Classification of anti-bat moth sounds plotted in acoustic space along maximum duty cycle (% of time occupied by sound) and modulation cycle complexity (# of clicks per modulation cycle) axes. Each number represents a species. The sonar-jammers cluster contains *Bertholdia trigona* (B) and the aposematic/mimetic cluster contains *Cynia tenera* (C) and *Euchaetes egle* (E). Colored areas show proposed acoustic strategies on a multi-species level.

References


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Contributed Talks and Posters
Bat predation and the evolution of leks in the acoustic Lepidoptera
Sylvain Alem¹, Klemen Koselj², Björn M. Siemens² & Michael D. Greenfield¹

¹ Institut de recherche sur la biologie de l’insecte, CNRS UMR 6035, Université François Rabelais de Tours, 37200 Tours, France
² Max-Planck Institute for Ornithology, Sensory Ecology Group, Eberhard-Gwinner-Straße, D-82319 Seewiesen, Germany

*correspondence with: michael.greenfield@univ-tours.fr

Theories of lek evolution generally invoke enhanced mating success experienced by males signalling in aggregations. Reduced predation has also been acknowledged as a potential factor driving lek formation but its role is more ambiguous. Although lekking is a complex behaviour, few empirical studies have investigated the role of both claims. We studied the potential pressures imposed by mating success and predation in an acoustic pyralid moth, Achroia grisella, in which males gather in leks and broadcast a calling song attractive to females. We exploited the ability to manipulate the distribution of singing males in laboratory arenas to create different sized leks and tested female preferences for these aggregations. Because A. grisella are vulnerable to predation by bats while in flight and on the substrate, we also tested the responses of a potential predator, Rhinolophus ferrumequinum, a bat species that feeds on moths and will glean them from the substrate, to the experimental leks. We found that the per capita attractiveness of A. grisella males to females rose with increasing lek size. R. ferrumequinum also oriented toward experimental A. grisella leks, but this attraction did not increase at larger leks. Thus, a male’s per capita exposure to predation risk declined as more moths joined the lek. A. grisella males appear to benefit from advertising in larger leks in terms of both increased mate attraction and reduced predation risk. Our results support the idea that multiple factors operating simultaneously may maintain lekking behaviour.

Achroia grisella;
Lepidoptera : Pyralidae

Rhinolophus ferrumequinum

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Motor basis for vibrational communication in the
treehopper, *Umbonia crassicornis*

B. Allison¹, Q. Su², C. Cribbs¹ and C. I. Miles¹

¹Binghamton University, Dept of Biological Sciences, Binghamton, NY USA,
²Binghamton University, Dept of Mechanical Engineering, Binghamton, NY

*Correspondence with: cmiles@binghamton.edu*

Male and female treehoppers *Umbonia crassicornis* (Hemiptera: Membracidae) communicate by vibrational signals they send through branches of the trees on which they live. The calls consist of a frequency and amplitude modulated tonal component in the 100-200Hz range as well as broadband high frequency clicks in the 400-1000Hz range (1). We investigated the methods by which *U. crassicornis* generate their signals, using video recordings, as well as anatomical and electrophysiological methods. Video recordings from calling males showed that signals are produced as the insect vibrates its abdomen in the dorso-ventral plane. Anatomical studies revealed two pairs of muscles that cross the thoraco-abdominal border. Their contractions would move the abdomen ventrally as it pivots about a pair of lateral hinges. Electrophysiological recordings from these muscles reveal activity that correlates with the vibrational signal recorded on the substrate where the insect sits (Fig. 1).

**Fig. 1.** Abdominal muscles produce communication signals. Top trace is accelerometer recording of the signal produced on the substrate, bottom trace is the activity of abdominal muscles.

In contrast, the click signals do not correlate with activity of the abdominal muscles. Instead, these are produced by the large metathoracic leg muscles. This conclusion is based on electrophysiological recordings from the muscles while clicks are recorded in the substrate. If the legs are then held away from the substrate, the click on the substrate disappears, despite continuing activity from the muscle (Fig. 2).

**Fig. 2.** Metathoracic legs produce clicks. Top trace in each pair is activity of the metathoracic leg muscle; bottom is substrate movement. All recordings are from the same individual. A. all legs in contact with substrate. B. metathoracic legs not in contact with substrate. C. metathoracic legs returned to contact substrate.

(1) Cocroft & McNett (2006) Vibratory communication in treehoppers (Hemiptera: Membracidae)


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Incommunicado crickets: Different mutant wing morphologies in two populations of field crickets each cause the loss of singing ability

N.W. Bailey¹*, E. Glidewell², M. Zuk²

¹University of St Andrews, School of Biology, St Andrews, Scotland
²University of California, Riverside, Department of Biology, California, USA
*correspondence: nwb3@st-andrews.ac.uk

Homoplasy, or morphological similarity, is a common evolutionary phenomenon, but determining its evolutionary causes presents challenges. It requires knowledge—or an educated guess—of the ancestral states of different populations or taxa, sources of selection on the traits of interest, and knowledge of phylogenetic relationships.

I will present data on the rapid evolution of male elytral structures in the field cricket *Teleogryllus oceanicus* to examine evidence for parallel evolution in acoustic communication in this species. Within the short span of about 20 generations, a novel mutation arose and spread in a wild population *T. oceanicus* on the island of Kauai, in Hawaii. The mutation eliminates the harp, mirror, scraper and most of the file on male elytra (see figure). Although males still stridulate, the lack of sound-producing structures means that they cannot produce sound. The mutation rapidly spread from an initial frequency of 0% to over 95% of males, apparently due to selection imposed by a co-occurring, deadly, acoustically orienting parasitoid tachinid fly.

The mutation, *flatwing*, appeared on the neighboring Hawaiian island of Oahu soon after its initial emergence on Kauai. A seemingly logical explanation is that *flatwing* mutants migrated between the islands, but we investigated this scenario more carefully using a morphometric analysis of males from both islands reared in a common lab environment. The results were surprising. Males from Kauai and Oahu were morphologically different. Kauai males’ wings lack a mirror and the harp is almost completely eliminated, whereas the reduction in the harp of Oahu males’ wings is significantly less extreme (see figure). Why? I will discuss several mechanisms and evolutionary scenarios that might explain this morphological (but not functional) difference, including variation in genetic control of the mutant phenotypes, rapid evolution of regulatory genes, and possible environmental influences, and assess where the weight of evidence currently lies.

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Effects of parasitism on the host: evidence for host manipulation?

O. M. Beckers\textsuperscript{1}, W. E. Wagner Jr.\textsuperscript{1}

\textsuperscript{1}University of Nebraska. School of Biological Sciences, Lincoln, USA

*correspondence with: beckersom@unlserve.unl.edu

Parasites can influence host traits in various ways. In some cases, parasites appear to cause their hosts to express phenotypes that are beneficial for the parasite. By manipulating host traits, parasites may increase their fitness within the host, increase their probability of transmission to the next host, or, in the case of parasitoids, increase adult fitness.

In California, the parasitoid fly Ormia ochracea uses the mating calls of the field cricket Gryllus lineaticeps to locate hosts for its lethal larvae. Adult flies preferentially orient to higher chirp rates and longer chirp durations, and other studies have shown that they benefit from avoiding superparasitism and benefit from placing their larvae on larger hosts. We tested whether larval infestation influences the host’s phenotype. First, we tested if parasitoid infestation affects male singing activity and/or song characters (1, 3, and 5 days following infestation). Second, we tested whether the parasitoids benefit from infesting larger hosts, and whether infestation affects host weight in a manner that would benefit the parasitoids.

Infested male crickets were significantly less likely to produce song on any of the recording days compared to non-infested crickets. Additionally, infested crickets that did sing, sang less frequently. These effects occurred the day following infestation and persisted in the subsequent time periods. Song characters, however, did not differ between infested and control crickets. Reduced singing by the host following infestation may reduce the risk of costly superparasitism for \textit{O. ochracea} larvae. We also found that the weight of \textit{O. ochracea} pupae was significantly and positively related to the host’s weight on the day of infestation. Importantly, infested crickets gained weight after infestation, whereas control crickets did not. Furthermore, larvae in crickets that gained more weight had greater pupal weights.

In conclusion, larval infestation resulted in behavioral castration of the host and in an increase in host weight. Both of these changes benefit larval development and may even increase the reproductive success of adult \textit{O. ochracea}, supporting the host manipulation hypothesis.

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Are leader preferences in katydids the outcome of a sensory bias?
S.L. Bush, K. Frederick-Hudson, and J. Schul
University of Missouri, Division of Biological Sciences, Columbia, MO, USA
*correspondence with: BushSL@missouri.edu

Males of several Neoconocephalus species produce discontinuous calls with regularly repeated verses. Durations of verses range from a few tens of ms (e.g. N. spiza) to longer than 1 s (N. nebrascensis) and verse repetition rates from 0.3 Hz to 5 Hz. Discontinuous calls are limited to one monophyletic clade of the Neoconocephalus phylogeny ('discontinuous clade'), which also includes several species with continuous calls.

Males of these species synchronize their verses with those of neighboring males. In one species (N. spiza), such call synchrony is the consequence of female preference for leading calls. Here we test the previously proposed hypothesis that this leader preference arises from a sensory bias of the katydid hearing system. This hypothesis predicts that species with continuous calls (the ancestral state in Neoconocephalus) should exhibit a preference for leading calls when responding to synchronized discontinuous calls, i.e. that species with continuous calls possess a hidden leader preference.

We tested female preferences during phonotaxis on a walking compensator in N. nebrascensis, a species with discontinuous calls, and in four species with continuous calls: N. bivocatus (which is sibling species to N. nebrascensis), N. retusus, N. triops, and N. ensiger. Of these five species, N. ensiger is the only one with a biologically significant leader preference; all others tracked the midline of the two loudspeakers for any delay tested.

These results indicate that the female preference for leading calls is most likely not a preexisting sensory bias in N. spiza and N. ensiger, but evolved following the evolution of discontinuous calls. Because some species with discontinuous calls have a leader preference while others do not, there are most likely two evolutionary trajectories leading to call synchrony in this group.

Orientation of Neoconocephalus females in the presence of two male calls spatially separated by 105º. The call at loudspeaker (LS) 2 was delayed relative to LS1. Only N. ensiger (filled triangles) exhibited a leader preference.

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Sound Production in Silk and Hawk-moth Caterpillars (Bombycoidea): Taxonomic diversity and function

V.L. Bura¹, D.H. Janzen² and J.E. Yack¹*  
¹Carleton University, Department of Biology, Ottawa, Canada. ²University of Pennsylvania, Department of Biology, Philadelphia USA.  
*correspondence with: jyack@connect.carleton.ca

Anti-predator strategies have been widely studied in caterpillars. Most studies focus on visually communicated defenses (e.g. visual crypsis, mimicry, warning colours) and little has been reported on the role of acoustic signals in caterpillar defense. In this study we report on the taxonomic diversity of defensive airborne sounds in the large silk- and hawk-moth caterpillars (Bombycoidea) and test hypotheses on the mechanisms associated with sound production, and the function of these sounds.

We conducted a survey of late instar caterpillars from North America, Europe and Costa Rica. In total, 43 species were tested and we found that 16 (37 %) produced sounds upon disturbance. Sound production was identified in two families (Saturniidae and Sphingidae) and five subfamilies, and our preliminary mapping studies provide preliminary evidence that sound production has arisen multiple times. Four different sound producing mechanisms are reported; mandible clicking, mandible stridulation, whistling through spiracles, and air expulsion through the buccal cavity. Larval signals shared characteristics with those of other defensive sounds; they are clearly audible at close range (10cm), individual units (chirps or clicks) typically lasted less than 100 ms and they are broadband, with dominant frequencies ranging from 10 to 40 kHz depending on the species.

Experimental trials with simulated and live avian predator attacks support the hypothesis that sounds are defensive. More specifically, some species (e.g. *Amorpha juglandis*) appear to use sounds as deimatic displays, to startle predators, while in other species (e.g. *Saturnia pyri*) sounds are accompanied or followed by a chemical defense and are believed to function in acoustic aposematism. Sound characteristics and trials with live predators suggest these defensive sounds are directed at birds and possibly bats and rodents.

We conclude that sound production in Bombycoidea caterpillars is probably a widespread, but until now, poorly understood component of their defensive repertoire. Factors leading to the origins and diversity of these interesting sounds will be discussed.

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Physiological and Anatomical Changes after Acoustic Trauma in the Fruit Fly *Drosophila melanogaster*

K. Christie, W.C. Smith, E. Sivan-Loukianova, M. Roy and D.F. Eberl

Department of Biology, University of Iowa, Iowa City IA USA 52242
correspondence with: mailto:daniel-eberl@uiowa.edu

Hearing loss due to traumatic exposure to noise is a growing and pervasive health issue, and its physiological mechanisms are not fully understood. Most studies to date have used various mammalian model organisms (mouse, rat, chinchilla). These animals have high maintenance costs, coupled with (relatively) long generation times. Our study develops the fruit fly *Drosophila melanogaster* as an inexpensive and powerful model system for studying the physiological and genetic effects of noise-induced hearing loss (NIHL). During courtship, *Drosophila* males produce acoustic tones and pulses to excite females and elicit copulation. These vibrations are detected via an array of antennal chordotonal mechanoreceptors called the Johnston’s organ (JO). Like vertebrate hair cells, JO neurons are ciliated and respond to mechanical stimulation with subsequent receptor potentials.

We exposed two wild-type laboratory fly strains (Canton-S, 40AG13), and flies heterozygous for a known auditory mutant (*nrv3*) to acute acoustic trauma consisting of 24-hr exposure to computer-generated continuous pulse song played at > 105 dB SPL. We measured the physiological and anatomical changes associated with acoustic trauma both immediately subsequent to and 7 days after exposure. JO ultrastructure was examined using EM and immunohistochemistry, while sound-evoked electrophysiological responses were measured from the auditory nerve.

Immediately after the 24-hour exposure, we consistently found a significant decrease, on the order of 30% reduction, in the amplitudes of sound-evoked potentials. Preliminary EM analysis showed no obvious morphological changes at this timepoint.

After 7 days, the reductions in sound-evoked potentials persisted in traumatized flies. At this timepoint, JO neurons from control animals exposed to trauma exhibited a significant decrease in mitochondrial size, and an increase in mitochondrial number. These changes suggest the possibility of mitochondrial fission ahead of apoptosis. The effects on mutant animals, which demonstrate altered mitochondrial morphology without noise exposure, was even more pronounced.

Future studies include analysis of JO cell morphological changes with longer times post-trauma, mutants in pathways likely to suppress or enhance susceptibility to trauma, such as oxidative and metabolic cellular stress pathways. We also plan to use genome-wide gene expression approaches to characterize the genomic response to acoustic trauma in JO.

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Reproductive character displacement and a song cline after secondary contact in California shield-back katydids (genus *Aglaothorax*)

J.A. Cole
Science Division, Johnson County Community College
*correspondence with: jcole32@jccc.edu

Upon secondary contact, lineages are expected to fuse unless barriers evolve that reduce gene flow. I studied three species of shield-back katydids that are sympatric in the Transverse Ranges that run west to east across Southern California. In the west, two syntopic species are divergent in calling song pulse rates: *A. diminutiva* with 5 pulses/s and *A. morsei* with 15 pulses/s. Across the range of *A. morsei* from west to east, pulse rates decrease clinally from 15 pulses/s to 5 pulses/s along an 80 km transect. The third species *A. longipennis* with a 12 pulse/s intermediate rate is found within the range of *A. morsei* within the song cline.

I asked first whether pulse rates displaced as a consequence of secondary contact. Molecular phylogenetic analysis of nuclear DNA sequences resolved two clades: *A. diminutiva* and *A. morsei-longipennis*. In the *A. morsei-longipennis* clade, Eastern *A. morsei* with slow pulse rates (5 pulses/s) are basal, while western *A. morsei* with fast pulse rates (15 pulses/s) are derived. Parsimony and likelihood reconstructions of ancestral ranges show the *A. diminutiva* and *A. morsei-longipennis* clades entered into secondary contact in the western Transverse Ranges. Independent contrasts indicate rapid song evolution occurred in western *A. morsei* populations at nodes where secondary contact was reconstructed. These results strongly supports song evolved in *A. morsei* in response to secondary contact with *A. diminutiva*, and suggests that song may be involved in species recognition at the contact zone.

The *A. morsei-longipennis* song cline may be the result of gene flow of high pulse rate alleles out of the contact zone, where they are selectively advantageous for species recognition, east across *A. morsei* and *A. longipennis* populations, where they are selectively neutral. Mating of western high pulse rate individuals with eastern low pulse rate individuals will ‘diffuse’ pulse rate over distance. To investigate hypotheses explaining cline formation, a preliminary population genetic data set was generated for *A. morsei* and *A. longipennis* that consists of genotypes for more than 500 AFLP loci. Spatial autocorrelation and population structure analyses show introgression of western contact zone *A. morsei* alleles penetrating east into the cline. Genotypes of *A. longipennis* are scattered among genotypes of *A. morsei* throughout the cline center with no distinct population structure. Gene flow out of the contact zone is therefore evident, and furthermore, this gene flow may be causing the fusion of two incipient species.

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Song pitch displacement in 13-year periodical cicadas

J. R. Cooley, and P. Fonseca

1The University of Connecticut, Storrs, CT, USA, 2The University of Lisbon, Lisbon, Portugal
*correspondence: cicada@magicicada.org

In 1998, while studying Brood XIX in northern Arkansas, periodical cicada choruses with two peak acoustical frequencies (≈1.1 and ≈1.7 kHz;) were found within the “anomalous zone” reported by Martin and Simon, in which two mtDNA haplotypes of 13-year M. –decim could be found. The high-pitched cicadas that we found corresponded to the northern haplotype (A) and the low-pitched cicadas corresponded to the southern haplotype (B). A series of playback experiments demonstrated that the two types of 13-year M. –decim were reproductively isolated, so the northern type (mtDNA lineage A) was named M. neotredecim while the southern type retained the name M. tredecim.

Where M. neotredecim and M. tredecim overlap, they exhibit a pattern of reproductive character displacement in calling song pitch and female pitch preferences. Within the zone of displacement, the dominant male call pitch of M. neotredecim is 1.7 kHz, while outside the contact zone, its call pitch is 1.4 kHz, identical to that of its putative ancestor, M. septendecim.

We report our latest findings from a detailed acoustical and neurophysiological study of Magicicada calling songs in and outside the Midwestern zone of reproductive character displacement. This project makes use of peripheral and central nervous system monitoring and stimulation, high quality acoustical recording, and laser vibrometric measurements of timbal and eardrum activity.
Buzz-pollination by bumblebees and its influence on pollen ejection in *Solanum rostratum* flowers

P.A. De Luca¹, L.F. Bussière², D. Souto-Villaros², D. Goulson², A.C. Mason¹ & M. Vallejo-Marín²

¹Biological Sciences, University of Toronto Scarborough, Toronto, ON, Canada
²Biological and Environmental Sciences, University of Stirling, Stirling, UK

*correspondence with: paul.deluca@utoronto.ca

Buzz-pollination is a plant strategy that promotes gamete transfer by requiring a pollinator, typically bees (Apoidea), to vibrate a flower’s anthers in order to extract pollen. Pollen collected by the bee is brought back to the nest where it is used as larval food, but uncollected pollen adhering to the bee’s body is available for transfer to the stigma of another flower as the bee continues foraging, thus promoting fertilization for the plant. Although buzz-pollination is widespread in angiosperms with over 30,000 species using it, little is known about the functional connection between natural variation in buzzing vibrations and pollen ejection. We characterized variation in buzz features (Fig. 1) within a colony of *Bombus terrestris* bumblebees, and then used these data to evaluate their effects on pollen ejection in the flowers of *Solanum rostratum*. We found substantial variation in three properties (duration, peak frequency, and peak amplitude), both within and among workers from a single colony. Of these, only peak amplitude was significantly correlated with body mass. We then constructed 294 artificial buzz stimuli that independently varied within three standard deviations of the mean for all three parameters for use in a playback experiment. Each stimulus was broadcast to a separate *S. rostratum* flower, and the pollen grains that were ejected were collected and counted. Peak amplitude, and to a lesser extent duration, exerted strong effects, with larger amplitude and longer buzzes ejecting more pollen. There was no effect of frequency on the amount of pollen ejected. Given that higher amplitude buzzes remove more pollen, our findings suggest that foraging by heavier individuals may result in the highest amount of pollen removed per bee, and this could have significant consequences for the success of a colony. Future research will examine the effect of buzzing features on plant species with different floral morphologies, and will also evaluate whether the observed effects of buzzing translate into selection on bees to maximize pollen collection, and on plants to minimize pollen lost to pollinators while maximizing pollen export to other flowers.

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Vibrational Communication in Mantophasmatodea

M. J. B. Eberhard\(^1\), and S. H. Eberhard

\(^1\)Humboldt-Universität zu Berlin, Department of Biology, Berlin, Germany

\*correspondence with: Monika.Eberhard@biologie.hu-berlin.de

The insect order Mantophasmatodea (heelwalkers) was newly described in 2002, nearly a century after the last insect orders had been established. Extant members of this order are only known from semi-arid and arid regions of Namibia and south-western South Africa. Most species are strictly allo- or parapatric, with the majority of them having a limited distribution range. So far, 17 extant species have been described. Male and female Mantophasmatodea communicate via percussive signals transmitted through the branches of the bushes in which they reside. Vibrational signals are produced by tapping the abdomen on the surface; males have a pronounced drumming organ on the subgenital plate, females tap in the absence of any specialized organ.

Vibrational signals were recorded and analyzed from males and females of 13 species from 15 localities in the Western Cape Region (South Africa) and 2 localities in Namibia. Several call parameters were measured and used in a principal component analysis (PCA). Male calls were mapped onto an existing molecular phylogenetic tree to track evolution of the communication signals. Behavioral playback experiments were performed to investigate the responses of males and females to various calls.

Female calls consist of single pulses whereas male calls comprise repeated pulse trains (groups of pulses). Calls of different species are of similar general structure but differ in temporal characteristics. PCA of male call parameters resulted in three principal components (PCs) explaining 99.4% of total variance. The three PCs separate most of the 13 species very well from each other. Mapping male calls onto the phylogenetic tree indicates a slowly diverging drift in call pattern in the allopatric species, as can be similarly found in the structure of male and female genitalia. *Karoophasma biedouwense* Klass et al., 2003 and *Viridiphasma clanwilliamense* Eberhard et al., 2011, which occur syntopically at Clanwilliam Dam, Western Cape Region - the only well supported case of sympatry so far - exhibit great differences regarding their calls, indicating reproductive character displacement. Behavioral playback experiments revealed that males and females of *K. biedouwense* reacted positively to the call of their conspecific mates but reaction was depressed when they received the playback calls of the heterospecific, sympatric species (*V. clanwilliamense*).

Vibrational signals of Mantophasmatodea are species- and gender-specific. They are of great importance for species recognition and mate location for these fascinating wingless insects.
Some like it hot - Effect of temperature on auditory neurons in the locust

M. J. B. Eberhard¹, F. A. Roemschied²,³, B. Ronacher¹,³, and S. Schreiber²,³

¹Humboldt-Universität zu Berlin, Department of Biology, Berlin, Germany
²Humboldt-Universität zu Berlin, Institute for Theoretical Biology
³Humboldt-Universität zu Berlin, Bernstein Center for Computational Neuroscience Berlin

*correspondence with: Monika.Eberhard@biologie.hu-berlin.de

Temperature influences basic properties of nerve cells such as spike rate, conduction velocity, and spike amplitude. This is relevant for ectothermic animals whose body temperature changes with ambient temperature. Here, we investigate the effect of temperature on signal processing in the grasshopper acoustic communication system. For these insects, the decoding of temporal characteristics of conspecific calls is crucial for mate recognition and may be impaired by temperature differences between sender and receiver.

The processing of auditory input starts within the metathoracic ganglion, where the first steps of song pattern recognition and analysis of sound direction are accomplished. Receptor neurons, local interneurons, and ascending interneurons constitute the first three processing stages, forming a hierarchically organized feed-forward network. Previous studies revealed an improvement of temporal resolution at higher temperatures due to a higher precision of spike timing. However, neurons of the three processing stages were not equally affected by variation in temperature.

In the present study, we analyzed responses of locusts’ auditory receptors, local, and ascending interneurons at two different temperatures (30°C and 20°C). Intracellular recordings were conducted to obtain spike rate vs. intensity curves, using short acoustic broad-band stimuli (100 ms; 1 – 40 kHz) delivered at intensities rising from 32 to 88 dB. Based on these data, temperature coefficients ($Q_{10}$) were determined.

Our results confirm an increase of spike count with higher temperature. The shape and duration of action potentials, as well as first spike latencies were also affected. However, the overall response pattern and the shape of the intensity-response curve did not change considerably. Remarkably, ascending interneurons and receptors exhibited lower $Q_{10}$ values than local interneurons. This might be caused by different temperature compensation at different processing stages.

To understand these phenomena, Hodgkin-Huxley-type neuronal models were used to reproduce the observed electrophysiological responses at each processing stage. We investigated how the observed temperature compensation can arise from specific cell-intrinsic mechanisms or, alternatively, from the network structure of the metathoracic auditory pathway.

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Opponent asymmetries and the role of vibratory signaling in male-male and female-female jumping spider contests

Damian O. Elias*1, Carlos A. Botero3, Maydianne C. B. Andrade2, Andrew C. Mason2, and Michael M. Kasumovic4

1Department of Environmental Science, Policy and Management, University of California, Berkeley, Berkeley, CA, USA, 2Integrative Behaviour and Neuroscience Group, University of Toronto Scarborough, Toronto, Canada, 3National Evolutionary Synthesis Center (NESCent) Durham, NC, USA, 4Evolution & Ecology Research Centre, The University of New South Wales, Sydney, Australia

*correspondence with: doelias@berkeley.edu

Opponent asymmetries often determine the probability of winning a fight in agonistic situations. In many animal systems, the asymmetries that drive the dynamics and outcome of contests are related to resource holding potential (RHP) or territory ownership. Ritualized signaling is predicted to evolve when the costs of fighting outweigh the benefits of winning a single contest. We examined these predictions in two contexts, male competition for mates and female competition for nest sites in the jumping spider *Phidippus clarus*. We document several key differences between the sexes in the role of RHP and territory ownership in determining contest outcome. We also document several differences in the role and reliability of vibratory signaling in contests. We interpret these differences in light of the different natural history and the economics of fighting between the sexes.

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For any arthropod, molting is a risky endeavor. Growth within an exoskeleton requires periodic shedding of the cuticle, leaving an organism vulnerable until the new cuticle hardens. Most solitary organisms look for a safe place to molt and this is no different for group-living insects, such as pergid sawflies. However, while solitary individuals often find places that are hidden or elevated off the ground, the safest place for social individuals may be within their group. Here I present preliminary observations of a molting signal used by gregarious larvae of the Australian sawfly, *Perga affinis*. *P. affinis* larvae live in colonies for their entire larval stage. During the day they reside in tight clusters and at night they process to a foraging area where they disperse for feeding. The larvae use vibrational signals to coordinate their activities and to re-aggregate after separation. Observations of molting activity revealed that larvae were significantly more likely to molt during the day, while residing in tight clusters, than at night when they were dispersed. Additionally, on at least two occasions I witnessed a potential molting signal given by a larva about 30 minutes prior to ecdysis. In both cases, the molting signal affected the behavior of the other group members, suggesting that it is a form of communication. During normal conditions, tight clusters undergo a series of synchronous group contractions that increase in frequency prior to departure for feeding. The two witnessed molting signals occurred as the tight clusters were preparing for departure to feed and in both instances, the molting signals caused all of the group contractions to stop. They did not resume until the individual had completed its molt. Potential benefits for a molting signal will be discussed on the poster. Additionally, a video of the behavior will be presented.

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Sound production in three closely related cicadas, *Okanagana canadensis*, *O. rimosa* and *O. bella*

P.J. Fonseca (1), J. Cooley (2) and D.R. Hughes (3)

(1) Departamento de Biologia Animal and Centro de Biologia Ambiental, Faculdade de Ciências da Universidade de Lisboa, Bloco C2, Campo Grande, Lisboa, Portugal.

(2) The University of Connecticut, Storrs, CT, USA.

(3) Naval Undersea Warfare Center Division, Newport, 1176 Howell Street, Newport, Rhode Island, USA.

correspondence: pjfonseca@fc.ul.pt

Mate attraction in singing cicadas is usually mediated by a stereotyped male calling song. The basic song pattern is produced with powerful timbal muscle contractions that apply the force to the timbal plate through an elastic ligament, the timbal apodeme. The convex ribbed timbal buckles inward producing sound. The elasticity of the timbal, at least in part due to the presence of resilin, is responsible for the return of the system to its equilibrium upon muscle relaxation, which may also be accompanied by sound. The *Okanagana* species in this study produce a series of sound pulses, one per rib buckled, during timbal muscle contraction, while the outward timbal recovering is essentially silent. Tensor muscle contraction, responsible for strong song amplitude modulations in other species, appears to have a minor effect in these species, while the extension and vertical abdominal movements have a marked effect on sound output.

Simultaneous monitoring of both timbal motoneurons activities during singing, elicited as after effect of brain electrical stimulation, revealed a common bilateral alternating stable pattern in *O. rimosa* and *O. bella*, but a surprising variability in *O. canadensis*, where single or doublet motoneuron action potentials to each timbal muscle may present modifications in their bilateral time pattern suggesting a certain degree of bilateral independence of the central pattern generation (CPG) network. Moreover, and as a response to self produced sound, we not only observed a very early activity in the auditory nerve that could not be attributed to sound, as reported years ago by Franz Huber and collaborators, but also recorded a strong response to the almost silent sound generated during the outward timbal release. This sensory feedback may play a role in CPG functioning.
An individual’s prior experience of sexual signals can result in variation in mate preferences, with important consequences for the predicted form of selection on sexual displays. We test four hypotheses about potential sources of selection shaping experience-mediated plasticity in mate preferences: mate availability assessment, mating assurance, mismating avoidance and acquired preference. We exposed females of two members of the *Enchenopa binotata* species complex of treehoppers (Hemiptera: Membracidae) to 4 treatments that varied their experience with signal frequency, the male sexual signal trait varying most among species and showing the strongest female preference (as a closed function). The treatments consisted of experience with: low frequency non-preferred signals; mean frequency preferred signals; high frequency non-preferred signals; silence; or a mixture of low, mean and high frequency signals.

Females experiencing preferred signals (mixed and mean frequency treatments) showed greater mate preference selectivity than females in the other treatments. Females in the mixed treatment showed the highest selectivity. Females did not vary in their peak preference across treatments. These patterns of plasticity support the mate availability assessment hypothesis and the mating assurance hypothesis. These patterns of plasticity predict the strongest selection on sexual displays when there are a variety of mates in the social environment. By influencing the expression of mate preferences, experience-mediated plasticity may influence the course of sexual selection.
Signal diversification and rapid speciation in temperate *Neoconocephalus* katydids

K. H. Frederick-Hudson, J. Schul

Missouri University, Department of Biology, Columbia MO, USA,

*correspondence with: khfrederick@gmail.com

Evolution of communication systems is inherently complex, requiring coevolution between sender and receiver mechanisms. **Here we use phylogenetic methods to study the relationship of signal diversity and biogeography in *Neoconocephalus* katydids.**

Ancestral state reconstruction indicated that among the calls of *Neoconocephalus* species three derived temporal patterns occur: (1) a double-pulses pattern with alternating pulse periods evolved 5 times independently; (2) discontinuous calls with pulses grouped into chirps/verses evolved in two clades convergently, and (3) slow pulse rates (less that 70 pps) had at least three independent origins.

*Neoconocephalus* is ancestrally a tropical genus. Most temperate species form one monophyletic clade. Call diversity in this temperate clade represents the total call diversity of the genus, with all derived patterns present. In contrast, genetic diversity within the 7 species of the temperate clade was less than found in a single species (*N. triops*) over a comparably large geographic range.

An ultrametric (time) tree approach indicates that tropical clades are older and genetically more diverse than their sister temperate clades. Together with the high signal diversity of the temperate clade suggest radiation during post-glacial expansions. Thus, the diversity of the temperate clade likely evolved during inter-glacial periods, potentially within the last 10-20,000 years.

![Figure 1: *Neoconocephalus* mitochondrial tree (COI), each branch represents a single species, except *N. triops* (shaded). Shapes indicate call phenotypes; X is ancestral call type. Specious temperate clade also contains all call diversity in the genus.](image-url)

Thank you to NSF and Orthoptera society for providing funding as well as the Schul lab and R. Snyder for aiding in data collection and analysis.
Comparing phenotypic and genetic diversity in three sympatric species with acoustic communication

K. H. Frederick-Hudson1*, J. Schul1

University of Missouri, Division of Biological Sciences, Columbia MO, USA,
*correspondence with: khfrederick@gmail.com

In insects with acoustic communication, male calls are among the most diverse traits. Typically, species-specific call traits have little variation within each species and serve as a pre-zygotic barrier among species. We studied the population genetics and call diversity among three closely related Neoconocephalus species with sympatric ranges to determine if genetic diversity can predict call diversity. Each species in this study has one unique call trait. N. robustus calls have the ancestral temporal pattern of this genus but a derived spectrum. N. nebrascensis and N. bivocatus each have one derived temporal call trait with the ancestral spectrum. We recorded calls of each male and compared the phylogenetic relationship among the individuals using mitochondrial (COI) and random genomic (AFLP) markers.

The mitochondrial haplotype of N. nebrascensis differed significantly from the other two species; there was no significant difference between N. bivocatus and N. robustus haplotypes, however most N. bivocatus formed a distinct cluster within this haplotype (Figure 1). AFLP data had a similar pattern to mtDNA data, indicating incomplete lineage sorting between N. bivocatus and N. robustus.

True hybrids were found using both genetic and call analyses. Most hybrids have intermediate call types, a pattern typical for Orthopteran hybrids. While there was little genetic diversity among the three species and in particular between N. robustus and N. bivocatus call phenotypes were distinctly different between the three species and did not strictly follow population structure.

![Figure 1: Mitochondrial haplotype map built from COI data. Each oval represents an individual, coded by call trait. Each branch and/or node represents one base pair change. N. nebrascensis has its own unique haplotype, however, N. robustus and N. bivocatus share a haplotype due to incomplete lineage sorting.](image)

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Vibrational communication: mate searching and directional accuracy in treehoppers
Jeremy S. Gibson*, Reginald B. Cocroft
Univ. of Missouri
*correspondence with: jsgth5@mail.missouri.edu

The strategies used by animals to search for food, mates and habitat will be influenced by the reliability of the sensory information that guides directional decisions. For actively searching animals, however, it is challenging to determine when decisions are made or what sensory input guides those decisions. We investigated the relationship between information quality, directional accuracy, and search behavior in a small plant dwelling insect. In thornbug treehoppers (Hemiptera: Membracidae: Umbonia crassicornis), males search for stationary females by homing in on the female’s plant-borne vibrational signals. Searching is punctuated by decision points during which the male stops to produce vibrational advertisement signals that elicit a female’s response, the male either continues in the same direction or turns around. We recorded the vibrational information available at each point for 17 males individually on a host plant with a receptive female. Males made more accurate decisions when signal amplitude was high; when the propagation velocity of the vibrational waves was low; and when the vibratory motion of the stem was aligned with the male’s dorsoventral axis. Males changed their searching behavior along the search path: at greater distances from the female, where signal quality was lower, accuracy was low and males moved farther between samples. This research provides insights into mechanisms of vibrational localization, the evolution of signal traits, and decision-making in the face of uncertain information.
Quantitative trait loci for an acoustic signal in the lesser waxmoth, *Achroia grisella*

J.M. Gleason¹, Y. Zhou¹,², J.L. Hackett¹, and M.D. Greenfield³

¹University of Kansas, Department of Ecology and Evolutionary Biology, Lawrence, KS, USA,
²Present address: University of Vermont, Department of Biology, Burlington, VT, USA
³IRBI, CNRS, Université Rabelais de Tours, Tours, France

*correspondence with: jgleason@ku.edu*

Male lesser waxmoths, *Achroia grisella*, broadcast an ultrasonic calling song by buckling their tymbals with downward pressure of the wings. Traits important to female response include pulse rate (PR), pulse amplitude (PA) and the asynchrony interval (AI) caused by differences in striking by each wing. We examined the genetics of these traits, as well as development time (DT) and adult weight (W) through quantitative trait loci (QTL) mapping of a backcross between two inbred lines from Kansas and Florida. From a new EST library we derived 85 informative single nucleotide polymorphism (SNP) markers. The markers segregated into 29 linkage groups. Significant QTL were found for all traits except AI. Weight was significantly correlated with all other traits, but the QTL for this trait was different from those of the other traits. DT was significantly correlated with PA and shared a QTL. DT and PR were not significantly correlated and had linked QTL. The limitations and implications of these results will be discussed.

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Rapid diversification of sexual signals in Hawaiian *Nesosydné* planthoppers (Hemiptera: Delphacidae)

Kari Roesch Goodman*1,2* and Damian O. Elias1
1 U.C. Berkeley, Dept. of Env. Science, Policy & Management, Berkeley, CA
2 Bishop Museum, Honolulu, HI
*correspondence with: krgoodman@berkeley.edu

Despite repeated observations of diversification in sexual signals, it is difficult to pinpoint the initial causes of divergence. Detailed population genetic and phylogeographical analyses coupled with fine-scale study of sexual signal diversification can lead to significant insights into the timing of factors associated with the speciation process. In this study, we assess signal diversification in *Nesosydné chambersi* (Hemiptera: Delphacidae), an insect from the island of Hawaii, testing whether: a) ecological specialization precedes divergence in sexual behavior, b) divergence in sexual behavior is associated with the maintenance of reproductive isolation, and c) trait displacement is greater between populations in sympatry than in allopatry. Our data show that signal traits diverge quickly both in the absence and presence of ecological shifts and that they are associated with reproductive isolation among ecologically similar populations in secondary contact. *N. chambersi* offers a rare window into the early stages of signal evolution and speciation from a natural system.

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Male courtship and the effects of seismic signals from multiple courting males in the wolf spider *Schizocosa ocreata*

S. D. Gordon$^{1,2,*}$ and G. W. Uetz$^2$

$^1$University of Cincinnati, Cincinnati Ohio, USA,
$^2$University of Strathclyde, Glasgow, UK

*correspondence with: shira.gordon@eee.strath.ac.uk

Signaling between two individuals is rarely isolated and signals may be received by both intended and unintended receivers within a communication network. As a consequence, the signaler may be forced to contend with signals from other animals and need to adjust behavior to best transmit its signal. However, information obtained from other signaling animals (eavesdropping) also may benefit the signaler.

We tested the effects of seismic signaling cues from other males on behavior of the wolf spider, *Schizocosa ocreata*, by measuring focal male behavior when courting (in the presence of chemical cues from female silk) or not courting (no silk) with and without seismic cues from other courting males. We found that when courting in the presence of female silk and seismic signals from multiple stimulus males, focal males reduced the vigor of their courtship (rate of percussive signals). The opposite was true for the focal males that were not courting (i.e. without female silk cues present); seismic signals from other courting males induced courtship of a focal male where the female silk cue was lacking.

A courting male may reduce vigor in an attempt to reduce interfering or jamming signals. Alternatively, as vigor can be a condition-dependent trait, reduction of vigor may be a means to evaluate condition relative to the other males, thereby saving energy. The initiation of courtship by the non-courting focal male (without female cues) is an example of eavesdropping on cues not intended for the receiver. Using such cues may be advantageous to males, as they may encounter or attract a potentially cannibalistic female nearby before her silk triggers a courtship response. These data highlight the importance of considering the communication network of animals when trying to understand their communication behaviors.

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Morphological plasticity based on environmental conditions: hearing in gregarious vs solitary locusts (*Schistocerca gregaria*)

S. D. Gordon$^1$* and J. F. C. Windmill$^1$

$^1$University of Strathclyde, Glasgow, Scotland UK

*correspondence with: shira.gordon@eee.strath.ac.uk

Animals, based on differing capabilities to receive signals from the environment, are sometimes best suited to their habitat. For example animals that see in dark conditions often have larger eyes or eyes with tapetum to reflect light. Animal ears too may be adapted to most efficiently receive predator or courtship signals. Often such morphological traits are under constant evolution, driving the physical feature in one direction. However, some animals show different phenotypes based on environmental conditions. For instance, genetically identical locusts exhibit two behavioral and morphological phases (solitary and gregarious) determined by their environment. This form of epigenetic change is triggered within the locust’s life cycle by several features of the animal’s environment, centering primarily on social crowding conditions. The locusts in these phases have different colors, sizes, and behaviors. Recent studies demonstrate differences in visual abilities and corresponding brain size between the phases suggesting the insect’s capabilities match the needs of each phase.

While much research focuses on hearing in locusts aimed at understanding basic tympanal ear principles; phase has never been taken into consideration as an element that may differentiate hearing abilities. This study focuses on the hearing of locusts in the different phases. Specifically, we measure frequency and amplitude sensitivity of the tympana as well as determine general morphology of the tympana of the solitary and gregarious locusts (*Schistocerca gregaria*).

Understanding phase morphological and behavioral changes provides insight not only into how the environment can change the animal, but also to the evolution of which traits are better adapted to different environmental situations.

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Photo: *Schistocerca gregaria*, taken by S. D. Gordon
Vibration Detection and Discrimination in the Masked Birch Caterpillar (*Drepana arcuata*)

R.N.C Guedes*1,2, S.M. Bond*1, B. Frei*1, M.L. Smith*1 and J.E. Yack*1

1Department of Biology, Carleton University, 1125 Colonel By Drive, Ottawa, Canada K1S 5B6
2Departamento de Biologia Animal, Universidade Federal de Viçosa, Viçosa, MG 36571-000, Brazil
*correspondence with: jyack@connect.carleton.ca

Vibrational signals are believed to be important to larval insects for purposes of conspecific communication and predator detection. However, little is known about how larvae detect, and discriminate between relevant and non-relevant signals in a complex vibratory landscape. We measured vibrations in the environment of the territorial masked birch caterpillar *Drepana arcuata* (Drepanidae), and assessed its ability to detect and respond to different vibratory cues, including conspecific and predatory intruders, as well as wind and rain. Resident caterpillars were shown to rely on low amplitude vibrations generated by crawling movements of an approaching conspecific, since removal of the vibratory cues through leaf incision prevented the resident from responding. Residents did not signal in response to vibration disturbances caused by wind and rain, but did respond to approaching conspecifics under windy conditions, indicating that they can filter out non-relevant large amplitude vibrations caused by wind. When exposed to the vibrations of an approaching predator (*Podisus maculiventris* (Heteroptera: Pentatomidae)), resident caterpillars signaled at significantly shorter distances from the intruder, and at higher rates than when approached by a conspecific. Our results demonstrate that *D. arcuata* is capable of detecting and discriminating between relevant signals in a ‘vibrationally noisy’ environment.
Description of Acoustic Characters and Stridulatory Structure of *Nicrophorus* Burying Beetles: A Comparison of Eight Species

C. L. Hall¹,², A. C. Mason³, D. R. Howard¹, and R. J. Smith²

¹Augustana College, Dept. of Biology, Sioux Falls, SD, USA,
²Idaho State University, Dept. of Biological Sciences, Pocatello, ID, USA
³University of Toronto Scarborough, Dept. of Biological Sciences, Scarborough, ON, Canada

*correspondence with: carrie.hall@augie.edu

The burying beetles of the *Nicrophorus* genus are well known for their reproductive behaviors in which they sequester dead vertebrate carcasses beneath the soil to use as a food source for their developing offspring. Interspecific and intrasexual competition for the ephemeral carrion resources can be physically intense and cooperative burial and brood care between the male and female that win the carcass increases reproductive success. During all stages of carcass preparation and reproduction, *Nicrophorus* beetles stridulate by rubbing *plectra* located on the underside of the elytra across the *pars stridens* located on the dorsal surface of the fourth (females) or fifth (males) abdominal segment. To date, no study has characterized the stridulatory sounds produced by North American species of the *Nicrophorus* genus. This study asked, 1) what are the spectral and temporal characteristics of the stridulations of eight *Nicrophorus* species of interest, and are there species-specific differences in the sounds of these niche-partitioned conspecifics? In addition to the characterization of sound, we asked, 2) are there differences in stridulatory structure and body size measurements that differ by species or by sex, and if so, is there an inverse relationship between body size and dominant frequency as in other insects? We found that sound does differ by species and by sex, but the biphasic structure of the sound is broadband with weak spectral characterization. Stridulatory structure also differs by species, but not by sex, and does not relate to sound character differences or body size. It is likely that sounds produced by *Nicrophorus* beetles are not under selection as a species isolating mechanism, and may serve a more generalized function, such as alarm signal or aggregation signal, where the identity of the sender is either unimportant or unambiguous, respectively, as is the case in many Coleopterans.

The figure shows an Artist’s rendition of the species-specific differences in stridulatory structure. The beetle shown is *Nicrophorus marginatus* with the *pars stridens* located under the elytra of the fifth abdominal segment of this male. The inset drawings are of the *pars stridens* of each species: a) *Nicrophorus americanus*, b) *Nicrophorus defodiens*, c) *Nicrophorus guttula*, d) *Nicrophorus investigator*, e) *Nicrophorus marginatus*, f) *Nicrophorus orbicollis*, g) *Nicrophorus pustulatus*, and h) *Nicrophorus tomentosus*. (Original artwork by Nicole Lindsey.)
Communication between treehopper parents and offspring about changes in predation risk

J. A. Hamel\textsuperscript{1} and R. B. Cocroft\textsuperscript{1}

\textsuperscript{1}University of Missouri, Division of Biological Sciences, Columbia, USA, *correspondence with: jahtf7@mail.missouri.edu

In group-living species, individuals may estimate predation risk from the behavioral cues or signals of other group members. If there is a cost to prolonged vigilance for group members, then we expect to see communication about risk reduction when a predator is no longer present. However, communicating about a decrease in risk poses two challenges: individuals must decide when a predator has left, and receivers must discriminate between signals about risk increase and risk reduction. We present results of a laboratory playback experiment with a treehopper species in which mothers defend offspring groups from predators. Offspring elicit maternal defense by repeatedly producing repetitive, synchronized vibrational signals. Mothers produce vibrational signals after predator encounters have ended. We hypothesized that maternal signaling after predator eviction communicates reduced risk to offspring. We simulated predation and compared post-predation offspring signaling rates during playback of maternal signals, wind (which inhibits vibrational signaling in treehoppers), and silence. As predicted, offspring signaled less when maternal signals or wind were played than when no signal was played. We propose that maternal signals communicate decreased risk to the offspring group and elevate offspring signaling thresholds. In these parent-offspring groups, the mother and offspring solve detection and signal discrimination challenges by partitioning communicative roles. The offspring detect the predator and signal increased risk to their mother, the mother evicts the predator and then communicates decreased risk to her offspring, and maternal and offspring signals differ greatly in spectral and temporal features.

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The role of wing pigmentation and abdominal vibrations for species recognition in scorpionflies

M. Hartbauer*, J. Gepp*, K. Hinteregger and S. Koblmüller
Department of Zoology, Karl-Franzens University Graz, Austria
*Institut für Naturschutz und Landschaftsökologie Steiermark, Austria
*correspondence with: manfred.hartbauer@uni-graz.at

Premating behaviour in the genus Panorpa (Insecta, Mecoptera), also known as scorpionflies, includes repeated sequences of wing flagging and abdominal vibrations executed by both sexes. These behaviours may be species-specific and important for the maintenance of reproductive isolation of scorpionfly species living in sympatry. In this study substrate vibrations spontaneously generated by isolated individuals was well as wing morphometry was studied in the Central-European scorpionfly species *P. communis*, *P. germanica* and *P. alpina* by means of laservibrometry and image analysis.

The length of right forewings showed only little intraspecific variation (coefficient of variation = 3 - 6%). Wing length and associated body size increased in the following order: *P. alpina* < *P. germanica* < *P. communis*. By means of the number of dark spots found on forewings and the percentage of pigmented wing area individuals can be assigned to the correct species with high accuracy (ignoring sex-specific differences).

Sequences of abdominal vibrations are only of short duration (mean = 0.85 s) and induce substrate vibrations consisting of individual pulses of variable amplitude. Individual variability of inter-pulse period is about as high as intraspecific variability of this signal parameter. Nevertheless, inter-pulse periods of males and females of *P. alpina* were significantly shorter compared to *P. communis* females. Mean inter-pulse period of substrate vibrations generated by males and females of *P. germanica* was not different from all other species. Interestingly, across species evaluation showed that the average individual inter-pulse period significantly increased with wing length.

Phylogenetic inference based on partial COI sequences of 35 individuals showed that all tested individuals belong to either *P. communis*, *P. germanica* or *P. alpina*. This result argues against the existence of interspecific maternal geneflow between sympatrically occurring scorpionfly species. Results of wing morphometry suggest that in addition to pheromones, produced by *P. alpina* and *P. germanica* males, wing patterns carry species-specific information as well. In contrast, a high individual variability of inter-pulse period and pulse amplitude questions the role of vibratory signals for species recognition. However, scorpionflies may be able to estimate the size of other individuals solely on the basis of substrate vibrations.
Encoding of leading and following calls in the ascending auditory pathway of *Neoconocephalus*

G. A. Hartman*, K. H. Frederick-Hudson, and J. Schul
University of Missouri, Biological Sciences, Columbia, MO, USA
*correspondence with: rh844@mail.mizzou.edu

In many insects and frogs with discontinuous calls, males synchronize their chirps with those of neighboring males. Females commonly prefer leading calls and males compete for the leading position. One evolutionary explanation for the female leader preference is that it is the outcome of a sensory bias. Römer et al. (2003; Eur J Neurosci 15: 1655-1662) presented an elegant model, how directional processing in katydids might result in a leader preference: the lateral inhibition mediated by the omega neuron might suppress the responses to the following call.

In *Neoconocephalus*, females of at least one species (*N. spiza*) have a significant leader preference (Greenfield and Roizen 1993, Nature 364: 618-620). However, several other species do not have preferences for leading calls: females orient along the midline between leading and following calls (Bush et al. this volume). Here we tested how the leading and following calls were represented in the auditory pathway ascending to the brain. We used *N. triops*, a species without leader preference in this study.

Call models were presented from one loudspeaker on each side of the insect, either alone or simultaneously with varying delays between them. We recorded the summed ascending activity of the cervical connectives using hook electrodes. The spikes of a large auditory neuron (TN1), which does not contribute to call processing, were removed by subtracting its average spike waveform. The remaining signal showed tonic spiking activity in response to the calls, likely representing the activity of AN1 and AN2. We rectified the recordings and averaged them over 25 stimulus repeats and measured the area under the averaged recording exceeding the background level.

When stimulated with one call model, the activity of the ascending pathway had a significant directionality. When two call models were presented simultaneously (0 ms delay), activity was similar to that during ipsilateral stimulation with one model. For delays between 9 and 81 ms, responses did not differ significantly between leading and following side; if anything, responses on the following side were stronger.

Future experiments will show whether the representation of leading and following calls differs among species with and without leader preference. This will inform the question whether the leader preference in *Neoconocephalus* is the outcome of a sensory bias and generated during directional processing in the ascending auditory pathway.
When to give up bi-directional communication: Effect of female response song and of female phonotaxis on mating frequency in a bush-cricket (Orthoptera: Phaneropteridae: Poecilimon affinis)

Dagmar von Helversen φ¹, Otto von Helversen φ¹ and K.-G. Heller¹,²*
¹Dep. Zoology II, Friedrich-Alexander-University Erlangen-Nürnberg, Germany
²Grillenstieg 18, 39120 Magdeburg, Germany
*correspondence with: heller.volleth@t-online.de

Acoustical communication systems with the purpose to find a mate are in the simplest case formed by one partner (usually the male) singing and one partner (usually the female) recognizing the signal and approaching the sender phonotactically. Such systems are typical for crickets (Grylloidea) and most bush-crickets (Tettigonioidae). In some tettigonioid families, however, more complex acoustical communication systems evolved with the females producing response songs. In such a system the phonotactic approach has not to be done alone by the female. Both sexes may move towards each other or the male has to take the risky approach alone in addition to his calling costs. Yet surprisingly this flexible system was given up several times independently, and the species returned to the unidirectional system with singing males and moving females.

We wanted to get a clue to the reasons of this reduction and studied the mating behaviour of a species with bi-directional system, Poecilimon affinis, in the field. Within this genus, the acoustical female response behaviour has been lost at least three times independently. To imitate the effect of a reduction, we produced mute females (by cutting off one tegmen). In a comparison of the female mating frequency, there was no difference in a population at high density - ca. 40% of both types of females mated per night, but a highly significant difference at low density (37% intact to 5% mute).

These results indicate that in species evolving at high densities the costs of responding may be not balanced by advantages, at least if these are measured in the number of matings (and obtained spermatophores).
Female crickets rely almost exclusively on the analysis of the pattern envelope in order to discriminate conspecific from heterospecific songs. Here, the temporal resolution for details of the song pattern was examined for female crickets, *Gryllus bimaculatus*, by using a behavioural gap detection paradigm at different modulation depths. The limit for gap detection was determined at 6 - 8 ms. An extensive analysis of songs of males revealed gaps within pulses and intermittent sounds during the usually silent opening phase of the wings for numerous individuals. However, the magnitude of these variations in the song pattern was below the gap detection threshold of females. Variability in the temporal detail of the song pattern is therefore unlikely to provide a basis for discrimination of individual males and for sexual selection. Evidence from further behavioural and electrophysiological measurements suggested that the observed limits for pattern discrimination are at least in part due to central mechanisms of auditory pattern processing.
Neuroethology of an auditory illusion: no evidence for perceptual restoration in field crickets
S. Hirtenlehner and H. Römer*
Karl-Franzens-University, Zoology, Graz, Austria
*correspondence with: heinrich.roemer@uni-graz.at

The ability in humans to restore missing speech sounds is well known: when listening to a sentence interrupted by silent gaps we perceive a continuous stream of speech if noise pulses fill in those gaps. Since this continuity illusion facilitates communication in noisy environments it is not surprising that it has been found in other taxonomic groups (nonhuman primates, birds) as well. A recent study on frogs, however (Seeba et al. 2010) suggested that the increased attractiveness of added noise is a result of a sensory bias, rather than indication of an illusion of perceiving missing pulses. Here we tested perceptual restoration in field crickets, and in a combination of behavioural and neurophysiological experiments provide data in support for the sensory bias hypothesis.

We analyzed the preferences of female *Gryllus bimaculatus* for synthetic male calling songs in behavioural experiments on a trackball system. In no-choice and two-choice tests we measured the lateral deviation during phonotaxis when presenting (i) a standard calling song (complete song: 150 chirps/min); (ii) a calling song where every second chirp was deleted (incomplete song; 75 chirps/min) and (iii) a calling song with bandpass-noise filled in these silent gaps (noise-filled song; see figure, upper trace). In addition, we analyzed the responses of a pair of auditory interneurons (AN1) under the same stimulus conditions.

As expected, the complete song caused the strongest lateral deviation in the no-choice paradigm, and was preferred by females compared with the incomplete song in the two-choice test. But there was no preference when compared with the noise-filled song.

Although female crickets prefer the noise-filled song to the incomplete song there is no evidence for perceptual restoration. Neurophysiological analysis of responses to the noise filled song indicate that noise pulses simply increase the total amount of excitation in response to this signal (figure, lower trace), and the amount of excitation correlates well with the lateral deviation measured in behavioural experiments. These results are consistent with the sensory bias hypothesis, rather than illusory perception as in humans or other taxa.

Female mate preferences are an important component of sexual selection. Preferences can be described by preference functions, which plot female responses across a range of display values. The shape of preference functions (i.e., open or closed) interacts with the distribution of display values to determine the form of selection on displays. Preferences can be further broken down into separate components, like peak preference, selectivity, and responsiveness. Exploring variation in preference shape, and in the components of preference is important, because this variation can influence the strength and direction of sexual selection. In Gray Treefrogs (*Hyla versicolor*), the population-level preference function for call duration is open, and that for pulse rate is closed. We show that there is substantial among-female variation in preference shape, with open and closed functions possible for both call duration and pulse rate preferences. There is also substantial variation in the components of preference. We explore potential trade-offs between preference shape and preference components, as well as between preference components, and discuss their implications for sexual selection.

We thank Diana Kim, Patrick Walsh, and Jessica Prepodnik for help with collecting and testing frogs.
Great strides have been made in explaining the function and evolution of male sexual traits in a wide variety of animal taxa. However, variation in female mate-choice behaviours has not been studied as extensively. Like male sexual traits, female mate-choice behaviours are predicted to be condition dependent. Although previous research details acoustic preferences exhibited by populations of female gray treefrogs (*Hyla versicolor*), variation among females in mate choice is largely unexplained. In this study, we examined how total reproductive effort is allocated to egg production to determine whether condition contributes to variation among females in the form or strength of mating preferences. Our study addressed whether mate choice is related to female 1) size; 2) condition; or 3) investment in eggs. Phonotactic preferences for longer call durations were tested using two experimental paradigms: in two-speaker playback tests, we recorded movement toward stimuli of differing amplitude to measure preference strength; in single-speaker playback tests, we recorded latency to move to the stimulus to describe individual preference functions. After collecting behavioural data, we measured body size (TFL), mass before and after egg deposition, number of eggs deposited and egg diameter. We found that size, but not condition, significantly affected preference strength. Energetic reserves not dedicated to egg-laying (residual condition) impacted response times to moderately loud (75 dB SPL) advertisement calls of various durations. This condition-dependent variation in female mate choice likely contributes to the continuing variation in male advertisement calls over evolutionary time.

![Graph showing relationship between average response time to standard call and proportion of body mass invested in eggs.](image)
Functional coupling of tympanal membrane motion and tympanal nerve response

J. Hummel\textsuperscript{1*}, M. Kössl\textsuperscript{1}, and M. Nowotny\textsuperscript{1}

\textsuperscript{1}Goethe University, Department of Cell Biology and Neuroscience, Frankfurt am Main, Germany

*Correspondence with: jhummel@stud.uni-frankfurt.de

In bushcrickets, two tympanal membranes are located on both sides of the foreleg tibiae, with the hearing organ complex between them. In contrast to mammals, the tympana are not the main sound input above a certain cut-off frequency (e.g. Lewis, 1974\textsuperscript{b}, J. Exp. Biol. 60, 839-851). Here, the sound enters the body via a spiracle opening on the lateral side of the thorax and travels through the auditory trachea towards the actual site of its perception. Therefore, the function of the tympana in sound transmission is still not resolved. Separated by the dorsal wall, their inner surface is divided into a dorsal part that borders on a hemolymph channel and a ventral part that contacts the air filled trachea. It is assumed that sound induced outward movement of the tympana could have a stretch-and-pull-effect on the dorsal wall that holds the hearing organ complex on top of it. As a consequence, the tympanum vibration might be functionally coupled to sensory cell activity.

We combined electrophysiological recordings of tympanal nerve activity with Laser-Doppler-Vibrometer measurements of tympanal membrane motion. When using far-field stimulation (4-78 kHz), in nerve recordings the frequency of most sensitive hearing, which matches a resonance frequency of tympanal membrane vibration, was at \textasciitilde 16 kHz. If the tympanum is locally stimulated, despite of it not being the main site of sound input, receptor cells still do respond to lower stimulus frequencies at higher levels. These findings indicate a mechanical influence of the tympana in the sound transmission process, rather than a mere pressure release function. Hence, tympanum motion seems to be functionally coupled to sensory cell activity.

One could assume that larger tympanum displacement amplitudes would result in higher spike activity. During far-field stimulation, however, a second prominent displacement amplitude maximum of tympanum motion at \textasciitilde 7 kHz only correlated with increased nerve activity at higher stimulus intensities \textgtr\textasciitilde 70 dB SPL. Moreover, manipulations of the system, such as closing the spiracle or local stimulation of individual sites of sound entry, lead to considerable discrepancies between the responses of tympanum and nerve fibers. The functional coupling, therefore, appears to be indirect. Additionally, the tympana seem to act like pressure receivers that are dominated by an internal component (sound via the spiracle) and are influenced by a secondary external component (the sound-induced resonance of the tympana). Both components seem to be important for tympanal vibration pattern and thus the tuning properties of the sensory cells at the resonance frequency of the tympana.

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Reproductive interference between species occurs in many animals, especially those that share similar communication channels and signals. However, few studies have considered the implications of reproductive interference in an ecological context. That is, how reproductive interference might influence the population dynamics of interacting species and ultimately the structure and composition of animal communities (see Gröning and Hochkirch 2008). The leafhoppers *Erythroneura aclys* and *E. bistrata* are specialists on redbud trees. They are found frequently in large numbers on the same trees, although *E. aclys* is often numerically dominant. The objectives of my study were to determine the role of vibrational signals in mate recognition and courtship in each species and whether vibrational signals are involved in intra- and interspecific reproductive interference.

The overall sequence of behaviors that lead to copulation is similar for both species, although the structure of calls is species-specific. In single male and female trials, males of both species emit simple pulses; females respond to these pulses forming a duet. Males then search and after locating the female they emit a very complex courtship signal prior to mating. Reproductive interference occurred in both species when two males were paired with a single female. In *E. aclys*, males emitted simple pulses when the other male was duetting or courting a female. These pulses differed in structure and frequency from those observed in single male trials. In *E. bistrata*, males also disrupted courtship by emitted relatively high amplitude, broad-band jamming signals. In addition to vibrational interference, misdirected courtship (males courting males) was observed in both species. Studies of how signals used in intraspecific interactions might be co-opted during interspecific interactions and how such interactions influence reproductive success are underway.

The vast majority of research on the role of intra- and interspecific competition in structuring animal communities focuses on competition for food and space; much less is known about how reproductive interference may contribute to community organization. The *Erythroneura* leafhopper system has the potential to serve as an important model system for understanding the role of reproductive interference in structuring communities and potentially in driving signal divergence and speciation.

Literature Cited

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Auditory neuron arrays in a 2:1 resonance for sound amplification

J. C. Jackson\textsuperscript{1,2*}, J. F. C. Windmill\textsuperscript{1}, and D. Robert\textsuperscript{2}

\textsuperscript{1}Department of Electronic and Electrical Engineering, University of Strathclyde, 204 George St, Glasgow G1 1XW, UK,
\textsuperscript{2}School of Biological Sciences, University of Bristol, Woodland Rd, Bristol BS8 1UG, UK

*correspondence with: joseph.jackson@eee.strath.ac.uk

Arrays of sensor/actuator units, such as force-generating neurons, can theoretically be used to provide nonlinear signal processing useful for hearing. We describe a generic model for an ensemble of active sensors coupled to an external passive sensor, and show how a specific mathematical relationship, namely a 2:1 resonance, between the stimulus frequency and the neuronal refractory period can yield marked nonlinear features such as amplitude-dependent gain and hysteretic amplification.

A typical model neuron can be described as having three distinct phases – quiescent, active, and refractory. An auditory neuron responding cycle-by-cycle to a sound stimulus has an upper frequency limit due to the refractory period limiting the rate at which the neuron can fire. Should the sound stimulus be of a frequency slightly greater than this limit, then the neuron can only fire once every two cycles. For two neurons, however, firing can occur every sound cycle if they fire in antiphase, such that, every cycle, one or the other is able to fire. This idea can be extended to work in an ensemble of many thousands neurons, such as that found in the mosquito ear.

This hypothesis can be used to model the nonlinear antennal dynamics of the mosquito ear. The emergence of neuron pairs generating force in antiphase with each other acts as a switch to generate amplification and hysteresis of the antennal motion. Simulations of this phenomenon replicate the experimental behavior of the mosquito ear as a function of the sound intensity.

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Delineation of species boundaries between field cricket species of the genus *Itaropsis* (Orthoptera, Gryllidae, Gryllinae): A test of concordance between morphological, molecular and acoustic datasets

Jaiswara. R.¹, Robillard. T.², Rao. K.¹,³, Cruaud. C.⁴, Desutter-Grandcolas, L.² and Balakrishnan, R.¹*

¹Centre for Ecological Sciences, Indian Institute of Science, Bangalore 560012, India
²Museum National d'Histoire naturelle, Rue Buffon, Paris, France
³Current affiliation: Department of Biochemistry, Indian Institute of Science, Bangalore 560012, India
⁴Genoscope. Centre National de Séquençage. 2, rue Gaston Crémieux, CP5706, 91057 Evry Cedex, France.

Delimitation of species boundaries in most taxa is achieved based on differences in morphology or DNA sequences obtained from phenetic or phylogenetic analyses. In the case of crickets, acoustic mating signals or calling songs are known to be species specific and this serves as an additional tool to infer species boundaries. In this study, we used acoustic, morphological and molecular datasets to test the concordance in species boundaries in the field cricket genus *Itaropsis*. This genus is known by only one species, *Itaropsis tenella* with a very broad distribution ranging from peninsular India to Sri Lanka. We sampled specimens from four sites spread across peninsular India. Two kinds of acoustic analyses were performed. Firstly, using each call feature, a comparison was made between samples from different sites. There were significant differences between most call features between sites, suggesting the existence of multiple species. Secondly, a cluster analysis combining information from four call features resulted in three groups, implying the presence of three putative species. Phylogenetic analysis based on molecular datasets and a combination of all datasets resulted in three clades, which were broadly concordant with the acoustic clusters. Therefore, we propose that the genus *Itaropsis* may be represented by three species in peninsular India. The broad concordance in implied species boundaries resulting from phylogenetic analysis of DNA sequences and cluster analysis of acoustic features of calling songs suggests that the latter could provide an important and powerful tool to infer species boundaries and identify cryptic species of crickets.

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The impact of host plants on courtship vibration transmission and mating success of parasitoid wasps (Hymenoptera: Braconidae)

A.L. Joyce

1University of California Merced, Sierra Nevada Research Institute, Merced, California, USA,
*correspondence with: ajoyce2@ucmerced.edu

Male parasitoid wasps of a number of species in the family Braconidae fan their wings during courtship, producing substrate vibrations that females must detect prior to mating. These parasitoid wasps develop on herbivorous Lepidoptera larvae. Our prior work demonstrated that natural and artificial rearing substrates impact transmission of male courtship vibrations, which in turn related to mating success. Physical differences among leaves from distinct host plant species may similarly impact transmission of courtship vibrations and reproductive success of these wasps. In managed agricultural systems, parasitoid wasps are often moved from one host plant to another for biological control. Host plant physical characteristics could positively or negatively impact mating success and establishment. We investigated the mating success and courtship vibration transmission of the parasitoid Cotesia flavipes on three host plants. Cotesia flavipes is a gregarious parasitoid with 40-50 offspring developing from each host larva. Courtship vibrations were recorded from courting male-female pairs on rice, corn and sugarcane plants. Each leaf used for a recording was marked in 2 cm increments using liquid paper white out so the distance from the recording device to the courting pair was known. All courtship vibrations used for comparisons were 0-6 cm from the recording source, a phonograph cartridge. Each plant leaf and each insect pair were used for one recording.

After each recording, the leaf was removed from the plant to determine leaf density. In separate trials, the mating frequency of pairs was observed on each host plant species. We found that both courtship vibration duration and amplitude, along with mating success, varied with leaf density. Host plants in natural systems may be a selective force on the courtship vibration signals of parasitoid wasps.

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A revision of the distributions, calling behavior, and taxonomy of two North American shieldbacks (Orthoptera: Tettigoniidae): *Atlanticus testaceous* and *Atlanticus monticola*

B.J. Kensinger*, B. Luttbeg¹, S. Heads², and J. Schul³

¹Oklahoma State University, Department of Zoology, Stillwater, OK, USA, ²University of Illinois, Illinois Natural History Survey, Champaign, IL, USA, ³University of Missouri, Department of Biology, Columbia, MO, USA, ⁴*correspondence with: bart.kensinger@okstate.edu

The genus *Atlanticus* Scudder as currently defined comprises 24 species of flightless shield-backed katydids (Tettigoniidae: Tettigoniinae) distributed over eastern North America and northeastern Asia. Of the nine species found in North America (Rehn and Hebard 1916), all are early emerging generalist feeders (Caudell 1967). This genus is in great need of taxonomic revision in order to determine how many true species exist within the clade (Capinera et al. 2004). The purpose of this study is to: 1) describe a distinct and previously unrecognized species found west of the Mississippi River and hitherto clustered with the eastern species *Atlanticus monticola*; 2) revise and redescribe the current distribution and calling behavior of *Atlanticus testaceous* and this new species.
Vibratory communication in the soil: pupal signals deter larval intrusion in a group-living beetle *Trypoxylus dichotoma*

W. Kojima¹, Y. Ishikawa¹, and T. Takanashi²

¹ Graduate School of Agricultural and Life Sciences, The University of Tokyo, Japan
² Forestry and Forest Products Research Institute, Ibaraki, Japan,

*correspondence with: aa107001@mail.ecc.u-tokyo.ac.jp

Pupae of several insect species are known to generate air-borne sounds and/or substrate-borne vibrations, the functions of which are not well understood. Here we revealed a new class of vibratory communication between pupae and larvae of a group-living Japanese rhinoceros beetle, *Trypoxylus dichotoma*, which inhabits humus soil. The last-instar larvae of this beetle construct their own pupal cells to ensure normal pupation and eclosion. However, since these cells are fragile, and pupae and larvae co-inhabit the same patches of humus, the pupal cells are subject to damage from burrowing larvae. In laboratory experiments, we found that pupal cells harbouring live pupae were less likely to be broken by larvae than were those harbouring dead pupae. Based on our preliminary observation that pupae produced vibrations in response to larvae approaching the pupal cells, we hypothesized that the vibrations act as defensive signals. High-speed video and vibration analyses showed that pupae regularly emitted 3–7 pulses at 1.3-sec intervals by beating their pronotum against the inner wall of pupal cells. The pupal vibration was of low frequency with a maximum energy at ≈100 Hz. The drumming behaviour was more frequently observed in the presence of an approaching larva than in its absence. When we played back recordings of the pupal vibrations, the cells were rarely disturbed by the larvae. These results suggest that pupae generate vibrations to deter conspecific larvae, thereby preventing damage to the cells. This larval response to pupal vibrations may have evolved through preexisting anti-predator and/or sib-killing-avoidance behaviour.

We thank R. Nakano for preliminary vibration recordings. This work was supported by Grants-in-Aid from the Ministry of Education, Culture, Sports, Science, and Technology of Japan.
Temporal pattern preferences in response to dynamically changing temporal features in cricket song recognition and localization in the parasitoid fly, *Ormia ochracea*

D. Koucoulas*, N. Lee, and A.C. Mason

Biological Sciences, University of Toronto Scarborough, Toronto, ON, Canada

*correspondence with: dean.koucoulas@utoronto.ca

Reproductive success in the acoustic parasitoid fly *Ormia ochracea* depends on their ability to recognize and localize the calling song of individual singing field crickets, often in the presence of multiple sound sources. The dominant frequency of the sound pulses within the call song of field crickets are generally at 5 kHz, while species-specific song differences occur in the temporal organization of these sound pulses. Successful host localization requires the auditory system to correctly segregate the timing of sound pulses that correspond to a single source and ignore irrelevant sources. Our previous work in *O. ochracea* walking phonotaxis has described temporal features in the call song important to song recognition such that walking responses occur to pulse durations and interpulse interval combinations that make up a range of acceptable pulse rates. To examine song recognition in regulating directional responses, *O. ochracea* tethered on a spherical treadmill were subjected to the simultaneous broadcast of 1) two control songs with a static pulse rate typical of their natural host, or 2) a control song versus an alternative song with dynamically varying temporal parameters from speakers situated ± 180 degrees relative to the midline axis. Total distance walked was measured from phonotactic responses as an indicator of song recognition while both steering velocity and angular heading (instantaneous direction of approach) were analyzed over the course of a response to determine the effects of song recognition in modulating localization behaviour. Results demonstrated that flies respond to changes in call temporal properties that occur during an ongoing bout of phonotaxis. These findings indicate that *O. ochracea* exhibit selective filtering that is updated during the course of stimulus presentation, and suggest future directions for elucidating the role of temporal cues in host song recognition and localization.

We thank P.A. De Luca and M.E. Jackson for helpful discussion and members of the Integrative Behavior and Neuroscience Group for animal care. Sources of funding were NSERC PGSD3 to NL and NSERC to ACM
How does signal perturbation affect song recognition in grasshoppers?

Stefanie Krämer*, Bernhard Ronacher
Humboldt-Universität zu Berlin, Germany
*correspondence with: stefanie.kraemer@hu-berlin.de

The acridid Grasshopper *Chorthippus biguttulus* employs acoustic communication as a central mechanism for mate recognition, localization and species isolation. Decisive for song recognition is the characteristic temporal pattern of the signal’s envelope, i.e. a sequence of syllables and intermittent pauses (e.g. v.Helversen et al. 1997). However sender and receiver face constraints given in the biotope. The signals are exposed to distortion and masking, factors that may notably impair song recognition. Our aim was to investigate at which temporal position in the signal’s envelope distortions would be most detrimental to recognition. We therefore systematically degraded a male model song by imposing perturbations to its envelope. Perturbations consisted of a combination of accentuations and gaps, or gaps only. These envelope distortions were placed at the onset, the middle or ending part of the syllables. In behavioral tests we found that females tolerated perturbations in the song envelope. Remarkably, songs containing perturbations at the syllable onset turned out to be very attractive. Female reaction decreased to songs with distortions at middle and ending positions. When the syllables contained gaps only, perturbations in the onset and middle part were more detrimental to song attractiveness than at the syllable’s ending (see also v. Helversen et al. 1998). We employed the same stimuli in intracellular recordings on auditory interneurons, to better understand the behavioral data. Receptors and 2nd order interneurons increased firing rates across envelope accentuations and showed a decrease of spikes during gaps (see figure). On the other hand some of recorded third order neurons showed inhibitions during the mentioned perturbations (AN3, AN4). It seems likely that spike trains elicited for envelope distortions at the syllable onset nevertheless provide information about the species specific syllable pause ratio (fig. A). In contrast, accentuations in the middle and ending parts (fig. B, C) may cause misleading period information about the signal. A spike train metric combined with a cluster algorithm was applied to assess whether spike patterns may correlate with the behavioral findings.

A) Perturbation at the onset  B) ...the middle       C) ...the ending of syllables.

Raster plots of 2 neurons shown across an examplary time window.
**Female Choice in the Prairie Mole Cricket**

*Gryllotalpa major*

N. Lee¹, D. R. Howard¹,²*, C. L. Hall³ and A. C. Mason¹

¹University of Toronto Scarborough, Department of Biological Sciences, Scarborough ON, Canada

²Augustana College, Department of Biology, Sioux Falls, SD, USA

³Idaho State University, Department of Biological Sciences, Pocatello, ID, USA

*presenting author and correspondence with: daniel.howard@augie.edu

The prairie mole cricket *Gryllotalpa major* is a rare subterranean insect endemic to relict fragments of the tallgrass prairie ecosystem. In mating season males construct spatially aggregated acoustic burrows from which they project their call song to entice flying females that visit for the sole purpose of mating. Previous work has described aspects of male spacing in mating aggregations, song correlates of male body size, and female attraction success as a function of location in an aggregation, but none have looked at female preference for call song features – a male trait likely under strong sexual selection. We conducted a field study to measure the relationship between call song parameters and female attraction and discovered that the most attractive males produced songs with a higher dominant frequency. In two-choice phonotaxis experiments, captured females were subjected to the broadcast of song models that varied in the extreme values for each temporal and spectral parameter of the call song. In subsequent tests, females were also presented with a choice between a conspecific or heterospecific song. Walking responses were initiated with small head turns and leg raises in the direction of both alternative sources and continued with walking bouts interrupted by brief pauses. Analyses reveal no differences in measures of meander (directedness in localizing a single song model), walking durations, and the number of pauses in response to different song models. Females displayed strong preference for louder conspecific songs at higher chirp rates and dominant frequency. Preference for higher dominant frequency songs is consistent with field measures of mate attraction but such song corresponds to smaller males. This mis-match in preference may be driven by species recognition mechanisms as the closely related sympatric mole cricket *Neocurtilla hexadactyla* advertise with similar calling songs at a slightly lower dominant frequency. Our results support the view that females may simply be localizing the most detectable conspecific song.

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Selective Attention by Noise Avoidance in the Acoustic Parasitoid Fly *Ormia ochracea*

N. Lee* and A. C. Mason

1University of Toronto Scarborough, Department of Biological Sciences, Scarborough Ontario, Canada

*correspondence with: norman.lee@utoronto.ca

Localizing sound sources of interest in noisy environments is a sensory challenge encountered by all organisms that depend on hearing for behavioural decisions. Reproduction in the acoustic parasitoid fly *Ormia ochracea* (Diptera: Tachinidae) requires successful localization of species-specific calling songs from singing field crickets that serve as hosts for the flies’ developing larvae. Both song recognition and sound localization require that the auditory system precisely measure, and segregate temporal information that corresponds to individual sources and these tasks may be compromised by masking noise. In walking phonotaxis experiments with tethered females, we examined the ability of *O. ochracea* to detect and localize song in the presence of random noise at different signal-to-noise ratios (SNR) and when song and noise were spatially grouped or separated. Our results indicate no support for spatially-mediated release from masking in *O. ochracea*. Flies walked significantly less in the presence of noise. Greater SNR resulted in improved signal detection that modulated walking velocity to the cricket song and resulted in greater walking distances. Noise caused flies to divert walking responses away from noise source locations and thereby biased orientation to song sources. Responses were diverted even further with greater song and noise separation. Diverted walking responses were mainly attributed to changes in steering velocity that depended on the location of the noise source. Our results show a form of selective attention expressed as directional noise avoidance behaviour that may be a feature of hyperacute directional hearing in *Ormia ochracea*.

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Sound and Vibration Signals in the Mountain Pine Beetle, *Dendroctonus ponderosae* (Coleoptera: Curculionidae, Scolytinae)

A. A. Lindeman\(^1\)*, A. J. Fleming\(^1\), and J. E. Yack\(^1\)

\(^1\)Carleton University, Department of Biology, Ottawa, ON, Canada,
*correspondence with: amanda.lindeman@gmail.com

The Mountain Pine Beetle (*D. ponderosae*) poses a major threat to North American forests. Through stridulation of a file and scraper mechanism on the elytra and abdominal tergites, these insects produce signals which are suggested to play a role in a variety of antipredator and social interactions. Experimental evidence is lacking regarding most aspects of acoustic communication in bark beetles, including the characteristics and function of signals, and even how they detect signals. Here we characterize and compare sounds produced by males in three different behavioral contexts: distress, male-female interactions and male-male aggressive interactions.

Acoustic signals varied in their temporal and spectral properties depending on the behavioral context. For example, male distress signals were ‘simple’ chirps, characterized as a series of uninterrupted toothstrikes (mean: 28), and an average duration of 43ms. These chirps were broadband (13 to 27 kHz at -10 dB) with distinct peaks at around 9, 28, 56 and 75 kHz and an average dominant frequency at 8.91 kHz. Conversely, male chirps during male-female interactions were complex, with 3 to 5 distinct components (see image). These chirps were twice as long as distress chirps, and had most dominant energy below 5 kHz. Other recorded signals were simple and complex male-male aggressive chirps, simple female chirps, and clicks during male-female encounters. Solid-borne vibrations were also recorded on the phloem layer during natural interactions, and signals were detected at up to 3cm.

Our results demonstrate that these bark beetles produce an elaborate repertoire of signals that vary between different social and antipredator contexts. These results provide insight into the structure and function of acoustic signals in bark beetles, and provide a necessary step towards new research on the sensory ecology and neuroethology of acoustic communication in this interesting and economically important group of insects.

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Ultrasonic Receivers: from insect ear to next-generation ultrasound sensor

D. Mackie1* and J. F. C. Windmill1

1Centre for Ultrasonic Engineering, Department of Electronic and Electrical Engineering, University of Strathclyde, Glasgow, UK,
*correspondence with: david.mackie@eee.strath.ac.uk

For over 50 years the auditory systems of insects have been of great interest to researchers in the field of acoustic systems. Recent advances in technology have allowed a far more detailed approach to the study of the mechanics of insect ears.

The physiology of insect ears is of interest to engineers primarily because the structures appear much simpler than those of the mammalian auditory system. However, they possess some remarkable characteristics, having the capability to process sound in unexpected ways. Also, many insects can hear and process ultrasound frequencies. A variety of morphologies have been observed in different species, each displaying unique ways of ‘capturing’ and processing sound.

This research aims to investigate the interesting and potentially valuable characteristics of insect ears. The properties and geometry which define the system are studied using a combination of Scanning Laser Vibrometry and Scanning Electron Microscopy. Thereafter a three-dimensional computer model (see figure below), representing the auditory system, is built and finite element analysis applied. For a wide range of stimuli, the model can be used to predict the unique membrane behaviour.

This allows us to understand the mechanical processes undergone by the ear structures, with a view to eventually translating this new knowledge into the development of novel ultrasonic sensor systems.

Figure - 3D Model of Schistocerca gregaria tympanal membrane – inset shows membrane with surrounding shell. Scale bar is 0.5mm.

I would like to thank both Dr Joseph Jackson and Dr Shira Gordon for their invaluable input. This work was financially supported by funding from the BBSRC, EPSRC and the Royal Society.
Competitive signal masking during mate localization in a treehopper

Peter R. Marting* and Reginald B. Cocroft
University of Missouri, Division of Biological Sciences, Columbia, USA,
*correspondence with: martingp@missouri.edu

Many plant-dwelling insects use vibrational signals in their duetting communication system. Mate-searching males produce vibrational advertisement signals, and the vibrational responses of receptive females provide localization cues. A competing male can disrupt this exchange with masking signals that overlap the advertisement signal of other male. Signal masking is a ubiquitous problem in animal communication, because individuals must often communicate in the presence of noise. However, the problems faced by duetting animals subject to competitive signal masking may be especially severe. In contrast to incidental masking sources such as wind or signaling by other nearby species, or even the competitive signal timing interactions of chorusing species in which multiple individuals are producing advertisement signals, masking signals are presumably under selection to maximize the disruption of communication. We studied competitive signal masking in a treehopper (Hemiptera: Membracidae: Tylopelta gibbera), focusing on how variation in masking signals influences their effectiveness at disrupting male-female duets. In T. gibbera, receptive females (which mate only once) will reply to more than one searching male, and mate with the first to arrive. Males frequently produce a distinct, tonal signal during the advertisement signal of competing males, and vibrational playbacks show that this behavior reduces the female’s probability of replying. We will present work in progress on the importance of masking signal features (e.g., timing relative to the advertisement signal, frequency, duration) in preventing female replies, and compare the properties of optimal masking signals with those of the masking signals used by competing males.
**Multi-component Vibration Signals of Group-living Caterpillars: Characteristics and Function**

S.M. Matheson and J.E. Yack

1Carleton University, Department of Biology, Ottawa, Canada,

*correspondence with: jyack@connect.carleton.ca

Early instar caterpillars often live in groups, but the mechanisms used for communication are poorly understood. We introduce and characterize multi-component vibratory signals in gregarious Lepidoptera larvae (*Drepana arcuata*, Drepanidae), and test hypotheses on their function.

First and second instar larvae live in small groups of 2-7 individuals in leaf shelters, and produce four unique vibratory signals: buzz scraping, mandible scraping, anal scraping and mandible drumming (see image). The functions of these signals are not known. We tested the hypothesis that signals are used for vibratory-mediated spacing by analyzing over 40 hours of video footage and laser vibrometer recordings of undisturbed groups, and by staging encounters between groups and a conspecific ‘intruder’.

Several lines of evidence support the spacing hypothesis. First, caterpillars have a regular preferred inter-individual distance which is maintained through escalation of signaling rate as a conspecific caterpillar approaches their ‘personal space’. Second, certain signals (e.g. buzz scrape and mandible scrapes) are positively correlated with movement, suggesting that these signals advertise the location of a moving individual within a group. Third, while feeding, early instars regularly produce anal scraping signals, suggesting that these signals are used to indicate their position at ‘the table’. Alternative hypotheses, such as recruitment, defense, auto-echolocation, and vibrotomy have not yet been supported by our studies, but will be discussed.

Our results to date support the hypothesis that early instar *D. arcuata* caterpillars are constructing ‘vibratory fences’ to maintain personal space in a number of different contexts within a group.

Thanks to Tiffany Timbers, Becky Lynes and many other helpful contributors. Funding provided by NSERC, CFI and ERA to JEY.
Stridulation elicits a variety of behavioral responses in the Formicidae: distress, alarm and recruitment of nestmates. The intent of my research is to broaden the understanding of stridulation by investigating the morphology, and the multiple behaviors in which stridulation has been observed in two closely related species, *Solenopsis invicta*, *S. richteri*, and their hybrid.

A SEM examination of head width and the stridulatory organs of imported fire ant workers found the number of ridges on the “file” (*pars striden*) to be positively correlated with body size. The increase in ridge number in relation to body size suggests that the number of pulses in each pulse train of the stridulation signal should increase as body size increases.

Absence of stridulation upon initial discovery of the food source and low amount of stridulation observed with ten or less ants present at the food source indicates that stridulation does not serve as an initial short range recruitment signal to nearby nestmates. Furthermore, over 90% of the total stridulation observed was recorded with 30 or more ants present at the food source. Finally, the time between calls decreased and the number of stridulations increased as more ants arrived at the food source.

Stridulation in dyadic encounters between ants occurs almost exclusively during non-nestmate conspecific interactions. Restrained ants or “defenders” accounted for 92.9% of the total stridulation observed compared to just 3.4% for “attackers.” Restrainment between the head and thorax or “neck” evoked the highest level of stridulation in majors. Stridulation during non-nestmate interactions is size specific, as trials involving majors had nearly twice as much stridulation (88.3%), than trials with mediums (48.3%) and minors (41.7%). IFA workers used two different types of calls during food source and nestmate/non-nestmate trials: single stroke (SS) and full stroke (FS) stridulations. Due to the rapid attenuation of the signal, full stroke stridulations are more valuable to communicating acoustically, compared to single stroke stridulations. The use of FS stridulations when trying to attract nestmates farther than 1 cm away would be of greater benefit to the restrained ant over a mixture of SS and FS. However, SS stridulations may be more efficient (and FS unnecessary) when nestmates are within 1 cm or in contact with the stridulating ant (as was seen in the foraging trials).

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If a bird flies in the forest, does a butterfly (or any other insect) hear it?
L. E. McMillan¹, J-P. G. Fournier¹, and J. E. Yack*¹
¹Carleton University, Department of Biology, Ottawa, ON, Canada
*correspondence with: jyack@connect.carleton.ca

Hearing organs are widespread in insects and mediate diverse dedicated behaviors in various social and anti-predator contexts. However, there remain certain cases where the function of hearing is unknown. For example, some butterflies possess tympanal hearing organs (see image) which have been shown to be sensitive to sounds, but at present, little is known about their function. In the present study, we hypothesize that butterflies (and other insects) use ears to detect the flight sounds of predatory birds.

Insectivorous birds are known to pose a strong predation pressure on many types of insects. We predict that approaching avian predators produce sounds that are available to an insect. By attracting birds in the wild to tethered insects, we show that birds produce flight sounds that are pulsed, broadband, and overlap with the hearing range of many insects. For example, eastern phoebe flight sounds were found to be broadband (>50 kHz at -20 dB) repetitive, with a peak frequency in the lower sonic range (>1 kHz). We then conducted playbacks of bird flight sounds to butterfly and moth extracellular neural preparations in the lab. Both moth and butterfly auditory recordings (respectively sensitive to 20-40 kHz, and 1-6 kHz) showed neural responses to bird flight sounds played at sound levels that represent a bird approaching from over 2.5 meters away. In response to increasing playback sound levels that simulate an approaching bird, the number of action potentials increased, while the latency and inter-spike interval decreased in the auditory nerve, suggesting that insects may have the ability to discriminate the proximity of an avian predator. Bird flight sounds also elicited motor responses in model insects (moths, butterflies) in both lab and natural settings.

The results of our study show that birds produce sounds while attacking insects, and that insects are capable of detecting and producing motor responses to these sounds in the lab and in the field. Our study provides evidence for a novel function for invertebrate hearing; specifically, to the sounds produced by an approaching avian predator.

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Male song and female preference in two hybridizing meadow katydids (Orthoptera: Tettigoniidae)

G. Miller
Longview Community College, Natural Sciences Division, Lee’s Summit, MO, USA
*correspondence with: Ginger.Miller@mcckc.edu

Understanding how reproductive isolation evolves is difficult as we can not observe speciation directly. As an alternative to studying full species in which trait differences may have resulted from divergence following isolation, we may study partially diverged taxa, in which limited gene exchange exists and reproductive isolation can be studied as it is occurring.

I examine species discrimination between two acoustic meadow katydids, *Orchelimum nigripes* and *O. pulchellum*, that are incompletely isolated (hybridizing) and for which no song differences have been previously documented. *Orchelimum nigripes* and *O. pulchellum* are allopatric throughout most of their native ranges. *Orchelimum nigripes* is found throughout most of the Central United States, extending east to the Appalachian Mountains. *Orchelimum pulchellum* is found east of the Appalachian Mountain Range, extending to the East Coast of the United States. *Orchelimum nigripes* and *O. pulchellum* have been described as different species based upon consistent morphological differences across their distributions.

There is evidence of gene flow between *O. nigripes* and *O. pulchellum*. My study focuses on a hybrid zone which extends across much of Louisiana, Mississippi, and Alabama south of the Appalachian Mountain Range. This older zone likely formed from secondary contact in the Pleistocene.

Males of *O. nigripes* and *O. pulchellum* both sing broadband songs that consist of two repeated song elements. Both species’ songs have a series of ticks followed by a brief silent interval, a buzz, then a longer silent interval. I show that the calls of *O. nigripes* and *O. pulchellum* differ significantly in multiple temporal characteristics. These differences in male signals may be used by females to correctly diagnose species of males.

To isolate the acoustic preference of females for male song from other signals and exchanges, I tested female song preference on a walking compensator (a “servosphere”) with playback of male song. I demonstrate that female preference in both species is more complex than a simple preference for increased call energy, and that females of both species will orient to male songs of either species.
Temperature-dependence and procaine-induced changes of DPOAEs in insect ears

D. Möckel¹, J. Lang¹, M. Nowotny¹, E.-A. Seyfarth¹, and M. Kössl¹

¹Institut für Zellbiologie und Neurowissenschaft, Goethe-Universität Frankfurt, Siesmayerstrasse 70, D-60323 Frankfurt am Main, Germany

*correspondence with: Moeckel@bio.uni-frankfurt.de

Tympanal organs of insects emit distortion-product otoacoustic emissions (DPOAEs) that are indicative of nonlinear ear mechanisms. They are evoked by simultaneously stimulating the ear with two pure tones (f1 < f2), and they appear as additional spectral peaks, with the 2f1-f2 emission being the most prominent. Insect DPOAEs are similar to those measured in vertebrate ears although insect tympanal organs possess very different auditory receptors, i.e., the characteristic scolopidia [Möckel et al. J Comp Physiol A 193, 2007; J Comp Physiol A 197, 2011]. We use locusts and bushcrickets to narrow down the origins of DPOAE generation in insect ears. Each of the two animal models has distinct technical advantages based on the anatomical properties of its tympanal organ.

(i) Locusts were used for our measurements of temperature effects. Their tympanal organs lie in the 1st abdominal segment. The devices for stimulation and recording of DPOAEs were placed close to the tympanal membrane, to which the scolopidia are directly attached. The body temperature of the animals was decreased by 10°C relative to room temperature, and then increased by 15°C. The amplitudes of the low-level component of the DPOAE growth functions decreased by 5 dB and increased by as much as 20 dB, respectively. Such level-dependent effects occurred only for stimulation frequencies below 12 kHz, and were reversible, if the body temperature was changed back to its initial value. The high-level component of the DPOAE growth functions, however, was not affected by a body temperature change.

(ii) In bushcrickets, the main site of sound input (spiracle) and the location of the tympanal receptor organ (in the foreleg tibiae) are anatomically separated. Hence the situation is suitable for applying pharmacological test substances without interfering with the acoustical measurements. We found that application of the local anaesthetic procaine (in concentrations of 740 to 74 mM) caused distinct level-dependent effects on the DPOAE-amplitudes: emission amplitudes evoked by low-level stimuli increased by 10 to 20 dB, while emissions evoked by high stimulus-levels remained unchanged or dropped by 3 to 5 dB. These effects recovered to normal ca. 40 to 60 min after application.

Both experimental treatments, i.e., changed body temperature and procaine-application, resulted in reversible, level-dependent effects on DPOAEs. The low-level component of the DPOAE growth function was physiologically much more vulnerable than the high-level component. Such separation of effects suggests that two level-dependent mechanisms are involved in the generation of DPOAEs and that these are active processes.

We thank Bernd Grünewald for his advice on the tests with procaine. Supported by a stipend from the Evangelisches Studienwerk to DM and by the DFG.
Sexual dimorphism of directional hearing in a katydid with duetting communication system
Arooj Mohsin and Johannes Schul*
Biological Sciences, University of Missouri, Columbia, MO, USA
*correspondence with: Schulj@missouri.edu

The Phaneropterinae katydid Scudderia texensis has a duetting communication system with females responding acoustically to male calls, and males approaching the response calls of females. This results in strong selective pressure on the males’ ability to detect and localize female response calls. Phaneropterines have sexually dimorphic ears. In females the acoustic tracheas are small and do not touch along the midline (figure, top right), while in males the acoustic tracheas are large and touch along the midline (top left).

Blocking the contralateral acoustic spiracle significantly decreased the directionality of hearing in males (bottom left, thick blue line: mean, thin lines: individual measurements), demonstrating that sound crosses from one acoustic trachea to the other. Thus, the male ear functions as a pressure gradient receiver with sound reaching the ear drum from directly from the outside, and through a second pathway from the inside. In females, blocking the contralateral acoustic spiracle had no effect on directional hearing (bottom right), indicating that female ear functions as pressure receiver with sound acting only on the outside of each eardrum. Thus, sexual selection has generated morphological and functional differences between male and female S. texensis that recapitulate the differences in hearing organs between different orders of Ensiferans. This highlights the significant phenotypic differences resulting from differential gene expression (due to sex determination).

Poster #33
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No evidence for DPOAEs in the mechanical motion of the locust tympanum

Hannah M Moir*, Joseph C Jackson, and James FC Windmill
Department of Electronic and Electrical Engineering, University of Strathclyde, Glasgow, UK
*correspondence with: hannah.moir@eee.strath.ac.uk

Distortion-product otoacoustic emissions (DPOAEs) are present in nonlinear hearing organs. For low-intensity sounds the DPOAEs are thought to be a by-product of active processes, and these emissions are produced when an ear is stimulated with two tones of different frequencies. Previous work acoustically recorded DPOAEs from the locust auditory organ. However, the location of the generation of these DPOAEs and the physiological mechanisms causing their emission from the locust ear has yet to be understood. The current study recorded locust tympanal membrane vibration using a laser Doppler vibrometer in order to identify a distinct place of DPOAE generation on the membrane. Two species of locust were investigated over a range of frequencies and sound levels of acoustic stimulus, mirroring earlier acoustic recording studies. The laser system allowed the membrane motion to be measured directly for the presence of distortion products, in particular at the neuron attachment sites that were previously suggested to be the most likely site of DPOAE generation.

The figure shows laser Doppler vibrometry scans the entire membrane of both species investigated. The scans indicate the velocity of the membrane at the largest expected DPOAE of 2f1-f2 = 12 kHz. The scale bar shows the outward (red) and inward (green) velocity over four phases of the oscillation cycle; the side view of the tympanum is also shown. The two tones applied were f1 = 12.25 kHz and f2 = 12.5 kHz at sound levels of 45/55 dB SPL for f2/f1 respectively. There are no coherent points of deflection on the membrane.

Vibrometry measurements failed to find evidence of mechanical motion on the tympanal membrane at expected DPOAE frequencies. The results of the current study therefore could not confirm the presence of DPOAEs in the locust ear through the mechanics of the tympanal membrane. The location of the mechanical generation of DPOAEs in the locust’s ear, and therefore the basis for the related physiological mechanisms, thus remain unknown.

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Cuticular Acoustic Forms: Generator Structure for Ensiferan Signals

G.K. Morris, S.J. Gutierrez
Department of Biology, University of Toronto Mississauga, ON, Canada
*correspondence with: glenn.morris@utoronto.ca

Cuticular exoskeleton of acoustic orthopteran insects is modified for transduction of airborne sound. Among crickets and katydids sound-adapted cuticle forms well-known stridulatory structures that are part of the tegmina: speculae, scrapers, file teeth etc. But adjacent body regions are also important, as for example the posteriorly projecting pronotum of Acanthacara, which forms a subnotal chamber about the insect’s reduced forewing (Figure). The loading of the tegminal radiators by the air of such spaces, both subnotal and subalar, greatly affects sound generation. Generator forms are adapted for radiation, damping, amplification, the shaping of broadcast fields and for phase-shifting. Size, shape, mass, flexibility, stiffness, surface area and elasticity are all important morphological features of cuticle-associated stridulatory structures.

Unstudied is the fibrous composite microstructure of the cuticle itself, and how this varies within generator structures and among generators of different species: for example between speculae as sound radiators and costal fields as damping barriers to short-circuiting. The elastic protein resilin is important in the biomechanics of insect flight, but its presence has not been investigated for any possible role in stridulation – nor of how it might have evolved for stridulation in relation to its ongoing role in ensiferan flight. Preliminary studies suggest a function for resilin in the production of ultrasonic sound pulses in Metrioptera sphagnorum through elastic regions deposited between veins near the forewing base. This paper attempts a brief overview of our present very incomplete knowledge of how ensiferan cuticular structure is adapted for sound generation.
Dual Roles of Male Courtship Ultrasound in the Yellow Peach Moth

R. Nakano¹,², F. Ihara¹, Y. Ishikawa³ and T. Takanashi²,⁴
¹National Institute of Fruit Tree Science, National Agriculture and Food Research Organization, Ibaraki, Japan,
²Neurosensing and Bionavigation Research Center, Doshisha University, Kyoto, Japan,
³Graduate School of Agricultural and Life Sciences, The University of Tokyo, Tokyo, Japan,
⁴Forestry and Forest Products Research Institute, Ibaraki, Japan
*correspondence with: rnakano@affrc.go.jp

Several groups of moths have developed intra-specific ultrasonic communication subsequent to the acquisition of tympanal organs for detection of predatory bats, which echolocate using ultrasonic pulses. Ultrasonic songs of moths are in general attractive to mating partners, and accordingly, contribute to the reproductive success of males. Recently, males of the Asian corn borer moth, Ostrinia furnacalis (Lepidoptera, Pyraloidea, Crambidae), are found to produce quiet courtship songs after they come into close proximity to a female, which increases copulation opportunity by making the female motionless. The female response is considered to be equal to the bat-avoiding ‘freeze response’ because females are unable to discriminate between male songs and bat calls. We predict that males of many more moth species exploit females’ ability to hear ultrasound in order to increase their mating success.

Here we examined the possibility of acoustic communication in the yellow peach moth, Conogethes punctiferalis (Lepidoptera, Pyraloidea, Crambidae), an important pest of peach and chestnut in Asia. Subsequent to the orientation flight toward a female releasing sex pheromone, the male emitted loud ultrasonic clicks while hovering around the female. Shortly after the male’s sound production, the female raised her wings, and then the male landed on her side in order to attempt copulation. Deafening of females or muting of males totally abolished the female behavioral response of ‘wing raising’. Playbacks of male songs were shown to evoke the same response from females. While resting males did not show any apparent response to the song, flying males ceased orientation flight toward calling females when a male song was played back. These findings indicate that the male song in this species play dual roles in mating. The male song elicits a specific response from females that is essential for inducing subsequent behavioral response from the male. In addition, the male song appears to suppress the orientation flight of rival males, thereby preventing possible disturbances from other males.

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**Sound-induced motion of the bushcricket hearing organs**

M. Nowotny1*, A. P. Udayashankar, J. Hummel, K. Wolf and M. Kössl

1Goethe University Frankfurt, Department of Cell Biology and Neuroscience, Frankfurt am Main, Germany,
*correspondence with: nowotny@bio.uni-frankfurt.de

Our *in-vivo* measurements focus on the auditory organs in bushcrickets which are located in their foreleg tibiae. Sound enters the body via the spiracle, an opening at the lateral side of the thorax and passes through a horn-shaped acoustic trachea before reaching the high frequency hearing organ called the *crista acustica* (CA). In addition to the spiracle and the trachea as structures that transmit incoming sound towards the hearing organ, bushcrickets also possess two tympana, specialized plate-like structures, on the anterior and posterior side of each tibia. They provide a secondary path of excitation at low frequencies for the sensory receptors.

We investigated the mechanics of the tympana and CA in the tropical bushcricket *Mecopoda elongata*. For CA preparation, the cuticle lying directly above the CA was carefully removed, and the surrounding hemolymph replaced with Fielden ringer solution. We captured the frequency-dependent motion response of the CA by recording the sound-induced vibration of the CA using a Laser-Doppler-Vibrometer (LDV) system. Pure tones and frequency modulated tones were used for sound stimulation.

The measurements of the tympanal membrane motion reveal the existence of two velocity-amplitude maxima at about 7 and 16 kHz and a complex motion pattern at higher frequencies (>30 kHz). During pure tone stimulation of the CA we could elicit travelling waves along the length of the hearing organ that move from the distal high frequency to the proximal low frequency region. The resulting distribution of the velocity response along the CA was exponential. In addition, distinct velocity maxima in the CA velocity response could be measured (~7, and ~17 kHz).

While the travelling-wave-induced tonotopy provide the basis for mechanical frequency discrimination through the CA, the additional resonances in the motion pattern of the tympanum and CA correlate well with the first two distinct peaks found at about 7 and 17 kHz in the song spectra of *Mecopoda elongata*. Thus, our results confirm that the mechanical response of the hearing organ in bushcrickets is tuned to behaviorally relevant frequencies.

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When Love Comes Calling: Measuring Sexual Selection on Sagebrush Crickets
G. D. Ower1*, and S. K. Sakaluk1
1Illinois State University, School of Biological Sciences, Normal, IL, USA
*correspondence with: geoff.ower@illinoisstate.edu

In crickets, acoustic signaling by males plays an important role in mate attraction and is thought to impose high energetic costs upon males, potentially making song an honest indicator of male quality. The objective of this study was to determine which acoustical features of male song in the sagebrush cricket, Cyphoderris streptans (Orthoptera: Haglidae), are attractive to females and to measure the strength and shape of sexual selection acting upon these characters. While mating, female sagebrush crickets feed on the hind wings of males, which allows the mating status of males to be ascertained by simply inspecting their hind wings for the wounds inflicted by females.

Populations in Grand Teton National Park were regularly censused throughout the breeding season and once they had reached a ratio of approximately 50:50 virgin to mated males, males were captured and their songs were recorded. Several acoustical characters were measured: pulse duration (a), interpulse duration (b), dominant frequency, train duration (c), and intertrain duration (d) and their selection surfaces analyzed using a dichotomous fitness measure (virgin = 0, non-virgin = 1). Multivariate selection analysis revealed significant linear and nonlinear selection on male song, with each of the five measured song characters contributing to male attractiveness.
Vibration detection in the treehopper, *Umbonia Crassicornis*

A. E. Payne\(^1\)\(^*\), Q. Su\(^2\), and C. I. Miles\(^1\)

\(^1\)Binghamton University, Department of Biological Sciences, Binghamton, USA,
\(^2\)Binghamton University, Department of Mechanical Engineering, Binghamton, USA

\(^*\)correspondence with: apayne2@binghamton.edu

For the treehopper *Umbonia crassicornis* (Homoptera, Membracidae) plant-borne vibrations play an important role in their mating behavior. Males and females engage in a vibrational duet, where roving males locate stationary females by following their vibrational calls. Directional cues can be encoded in vibratory signals as time delays and amplitude gradients. However, for small insects like *U. crassicornis*, such features are not easily detected. In a previous study, the mechanical movements of the bodies of female *U. crassicornis* were shown to differ depending on whether the vibration originated from in front or behind the insect (Cocroft *et al.* 2000). This directional response is also shown by the legs, where the vibration sensitive sensory neurons are located. The transfer of directional cues from the body motion to the leg sensory receptors could be the key to the insect’s ability to determine the direction of the vibration source.

While the previous work focused on females, we have extended this to include males, which we know actively seek the females based on their vibrational signals (Cocroft *et al.* 2000). In addition, we have recorded from sensory neurons in the male *U. crassicornis* leg as he is stimulated with directional vibrations, as a first step in examining how the nervous system may encode the direction of the signal. By using a custom built bending wave simulator, vibrations originating from in front or behind the insect were produced. The pronotal movement of male *U. crassicornis* was recorded using a laser vibrometer. It was found that males’ bodies exhibit a clear directionally oriented mechanical response to substrate vibrations, similar to that of females. Also similar to previous work on females, the greatest amount of mechanical response and therefore the greatest potential source of directional information occurred when the frequencies of the vibrations were within the range of *U. crassicornis* call frequencies (Cocroft *et al.* 2000).

Sensory responses to vibration stimuli were recorded in freely moving *U. crassicornis* males using fine wire electrodes. Individuals were presented with vibrational stimuli that covered a range of frequencies and amplitudes. The lowest intensity thresholds and greatest sensitivities occurred within the 100Hz to 1000Hz range, consistent with the range of frequencies for *U. crassicornis* calls. Thus, the sensory system appears to be tuned to detect vibrations over a behaviorally relevant range.

The allometry of advertisement signals in insects and frogs
R.L. Rodríguez and G. Höbel
Biological Sciences, University of Wisconsin-Milwaukee, USA
*correspondence with: rafa@uwm.edu

Sexual traits vary a great deal in how they scale relative to body size (i.e., in their static allometry). They often grow disproportionately large in large individuals. However, they also often vary in direct proportion with body size, and some types of sexual trait even grow disproportionately large in small individuals. A recent hypothesis seeks to explain this astonishing variability by positing a relationship with variation in the level of condition-dependence. Under this hypothesis, stronger condition-dependence leads to steeper allometric relationships.

We take a novel approach to test the condition-dependence hypothesis for variation in allometry by exploring the allometry of sexually-selected behavioral traits. We describe the allometry of signal traits for one species of plant-feeding insect that communicates with substrate-borne vibrational signals, and for three frog species that communicate with airborne acoustic signals. We find surprisingly variable scaling of signal traits on body size (see figure comparing allometric slopes for body and signal traits, where each symbol is a slope estimate for a trait in one of the four species). Our findings suggest that advertisement signals overall may be less reliably indicative of body size than usually anticipated, but that certain signal traits may be unusually reliable indicators.

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Listening in noise: selective filters and spatial release from masking in tropical crickets.

H. Römer* and A. K. D. Schmidt

1 Karl-Franzens-University, Zoology, Graz, Austria

*correspondence with: heinrich.roemer@uni-graz.at

Due to call frequency overlap and masking interference, the air-borne sound channel represents a limited resource for communication in species-rich habitats like the tropical rainforest. We studied the frequency tuning of an identified auditory neuron (AN1) mediating phonotaxis in the rainforest cricket Paroecanthus podagrosus suffering from strong competition, in comparison with the same, homologous neuron in European field crickets G. bimaculatus and G. campestris where such competition does not exist. As predicted, the rainforest species show a more selective frequency tuning compared to the European counterparts. The filter reduced background noise levels by 26 dB, compared to only 16 and 10 dB in the two European species. Furthermore, the filter of the rainforest cricket performed significantly better in representing the species-specific amplitude modulation of the male calling song, when embedded in background noise. The neuronal representation of the calling song pattern within receivers is maintained for signal-to-noise ratios of about -9 to -12 dB, due to the more sharply tuned sensory system and selective attention mechanisms (figure 1).

However, when the same preparations were placed in the nocturnal rainforest and tested for masked thresholds, the SN-ratios were strongly improved to values of up to -24 dB. Because noise spectra outdoors and those used for playbacks in the lab were quite similar we interpret our finding as resulting from the difference in the experimental approaches of common lab masking experiments (noise and stimulus are being presented from one side) compared to real world situations, where the various noise sources are separated in time and space.

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Insect Sound and Human Music: Convergent Evolution?
David Rothenberg
Professor of Philosophy and Music
New Jersey Institute of Technology, Dept. of Humanities, Newark, NJ, USA,
correspondence with: terranova@highlands.com

It is easy to see the influence of animal sounds in human music throughout history; particularly the songs of birds, and to a lesser extent, whales, are well-documented as influencing our music from ancient times to the present, from classical to popular forms. Insect sounds, though admired and enjoyed by people for thousands of years, have not always been considered musical in a way people can appreciate them. There are famous exceptions, of course, such as Josquin des Prez’s “El Grillo” from the fifteenth century, to Rimsky-Korsakov’s “Flight of the Bumblebee” in 1899, but by and large insect music as been heard as different enough from human music to not inspire direct imitation or adaptation.

However, in our present century attitudes on what constitutes music have evolved tremendously. With the rise of electronic sounds as musical tools and the definition of ambient forms of music that express the whole environment, either artificially reconstructed, or based on field recordings from the natural world, the whole realm of insect sounds becomes much more potentially musical. The more “noise-like” sounds we accept into our music, the more we may come to appreciate the beauty of what insects have been singing for millions of years.

Through audio and visual examples I will examine how careful listening to individual singing insects and group choruses offer profound ideas for coming to a greater understanding of how to make sense of nonlinear, textural music, and at the same time, a rhythmic analysis of the various songs of insects may help science understand the role of rhythm in insect communication, as musical approaches have helped in the study of whale song and bird song already.

Perhaps humans learned the value of complex timbres from tuning in to their swirling, complex tonalities. Maybe we learned the importance of rhythm in music from the repeating sounds of insects all around us as our cultures evolved. And think of the tremendous gestation cycles of periodic cicadas, the longest of such cycles in the animal world, one of the most reliable grand rhythms we know.

Neuronal basis of singing pattern generation in field crickets

Stefan Schöneich¹* and Berthold Hedwig¹

¹University of Cambridge, Department of Zoology, Downing Street, Cambridge CB2 3EJ, United Kingdom

*correspondence with: ss817@cam.ac.uk

Acoustic signalling in crickets is based on genetically determined motor rhythms that represent classical examples of fixed action patterns driven by a central pattern generator (CPG). For mate attraction male crickets generate stereotypic sound patterns by rhythmically opening and closing their forewings. A short sound pulse is produced during each closing movement and several pulses are sequentially grouped in the species-specific style to match the sharply tuned auditory recognition mechanism of the conspecific females. Although the neuronal mechanisms underlying cricket singing behaviour attracted much scientific interest over the last decades, it remained nevertheless a largely unsolved neuroethological question.

Currently we identify the neuronal components of the singing CPG in Gryllus bimaculatus by intracellular recording and staining of participating interneurons in the CNS of fictively singing males. Singing is elicited by microinjection of Eserine into the brain and extracellular motoneuron recording from a wing nerve monitors the fictive motor pattern. Although the singing motoneurons are housed in the mesothoracic ganglion, we identified local and descending interneurons in the metathoracic and ascending interneurons in the abdominal ganglia as elements of the singing CPG. These interneurons discharged in phase with the singing rhythm and perturbing their activity with intracellular current injection modified or reset the motor pattern.

Understanding the singing CPG at the level of identified neurons will not only provide insight into the control mechanisms of one of the most conspicuous insect behaviours. Linked with a genetic approach this will also provide the opportunity to reveal the neural modifications that caused song pattern modification during evolutionary segregation of cricket species.

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Response properties of auditory interneurons: species specific encoding or release of selection?

Johannes Schul*, Tim Ostrowski, & Katy H. Frederick Hudson
Biological Sciences, University of Missouri, Columbia, MO, USA
*correspondence with: Schulj@missouri.edu

As neurobiologists, we tend to interpret quantitative differences among species as being functional and related to species specific differences in neuronal processing. Considering an evolutionary context, however, may lead to very different conclusions.

The calls of Neoconocephalus species have ancestrally very fast pulse rates (200/s) with a single pulse pattern. Neoconocephalus bivocatus and N. triops both have a derived double pulse pattern. The derived call pattern evolved independently in the two species. Females of both species recognize the rate of the double pulses (ca. 100/s) and respond well to signals with long single pulses replacing the double pulses. We recently described qualitative differences of the response properties of the ascending interneuron AN1 between the two species: in N. bivocatus, AN1 responds with one AP per pulse (i.e. 2 AP per double pulse), while in N. triops AN1 generates only one AP per double pulse (Triblehorn & Schul 2009, J Neurophysiol 102:1348). We suggested that this represents differences in the processing underlying call recognition.

Subsequently, we quantified the encoding of the double pulse pattern in these two species. While the average responses confirmed our previous findings, we found an astonishing amount of variability among the individuals. In each species, AN1 of some individuals responded to each pulse, while AN1 of others responded only with one AP/double pulse. This variability was more pronounced in N. triops. The large variability makes it unlikely, that the encoding of double pulses or individual pulses plays an important role in call recognition in either species. In N. robustus, a species with single pulse call with a pulse rate of 200 Hz (= the ancestral state), AN1 responded to each pulse and the variability was much smaller.

Phylogenetic analyses indicate that the double pulse pattern in N. bivocatus evolved only recently, while in N. triops this pattern is much older. We propose here that the ancestral state in Neoconocephalus is the encoding of each pulse; the fast pulse rates typical for this genus select for fast firing rates of AN1. After the evolution of the double pulse pattern and recognition of the double pulse rate, selection on fast firing rates of AN1 was released, as only half the rate (the double pulse rate) is needed for call recognition. As selection does not remove mutations resulting in lower AN1 firing rates, the variability of AN1 response properties should increase in double pulse species. This should result in higher variability in N. triops, where the double pulse pattern is much older than in N. bivocatus.

Our conclusion highlights the importance of the evolutionary context of traits, when inferring their function and adaptive value.
Evolutionary Origins of Vibration Signals in Caterpillars (Drepanidae: Drepanoidea)

J.L. Scott and J. E. Yack

1Carleton University, Department of Biology, Ottawa, ON, Canada
*correspondence with: jyack@connect.carleton.ca

Biologists have long sought explanations for the evolutionary origins of communication signals. It is believed that signals evolved from cues associated with non-signaling behaviours through ritualization. Empirical evidence for ritualization is limited, however. We study the origins of vibratory signals in Drepanidae caterpillars by: (i) characterizing morphological and/or behavioural correlates of signals and cues in 36 species, (ii) mapping characters onto a molecular phylogeny, and (iii) comparing signals, cues and movement patterns between basal and derived conditions. Certain species of larval Drepanidae communicate ownership of a leaf shelter to conspecifics using vibratory signaling. Territorial signals can include ‘anal scraping’ (specialized ‘anal oars’ are dragged across the leaf), mandible drumming, and mandible scraping. Some species also employ physical aggression that involves crawling towards the intruder and pushing, biting or hitting. We propose that vibratory signals originated from cues associated with physical territorial behaviors. We hypothesize that anal scraping evolved from crawling, mandible scraping from hitting, and mandible drumming from pushing and/or biting.

Character mapping shows that the anal scraping features (lack of anal prolegs and presence of anal ‘oars’) derive from a basal condition (abdominal legs used for crawling and non-specialized setae that are homologous to ‘oars’). Mapping head movements shows that hitting is basal to mandible scraping. Comparisons of behaviour sequences during territorial encounters in different species show similar patterns of signaling and non-signaling behaviours. For example, in a basal species (Tethea or) the encounter involves crawling toward the intruder, hitting and biting; corresponding behaviours in the derived species (Drepana arcuata) include anal scraping, drumming and mandible scraping. Further support comes from comparisons between body movement patterns associated with signaling and corresponding non-signaling behaviours. For example, movements associated with both anal signaling and crawling show statistical similarities in timing, duration, distance, velocity and direction of motion. Finally, comparisons of signals and non-signaling vibration cues show that signals are significantly more repetitive, exaggerated and stereotyped, fulfilling criteria for ritualization.

Our results provide evidence for the non-signaling origins and ritualization of communication signals. In the Drepanidae, we propose that vibratory territorial signals evolved to avoid costs associated with physical aggression.

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Vibratory Signals in Pentatomid Bugs (Heteroptera, Pentatomidae) from European Russia
L.S. Shestakov
Institute for Information Transmission Problems, Russian Academy of Sciences,
Moscow, Russia
correspondence with: zicrona@iitp.ru

Pentatomidae is one of the largest families within the Heteroptera, and vibratory signals play an important role in their communications. Both sexes of different bug species communicate with vibratory signals transmitted through the plants. The vibratory signals of 21 species of Pentatomidae (Heteroptera) from European Russia were described. Vibratory communication during mating behaviour was studied in 19 species. The signals of 20 species were recorded from two or more localities. The signals emitted by adult bugs were classified by several types: male rivalry song, male calling song, male courtship song, female calling song, and female protest song. The dominant frequency peak of all recorded signals lied around 100 Hz and harmonics were found below 1000 Hz. Temporal parameters of signals emitted by some species of Pentatomidae were species-specific. Frequency modulation in some signals was also species-specific. Oscillograms and sonograms of vibratory signals are given for all species studied. Taxonomic status and relationships of the studied species are discussed on the basis of the songs characters. Partition of vibration transmission channels between closely related species were investigated in species of genera Carpocoris, Graphosoma and Chlorochroa. It was shown that sympatric species occurring on the same plant species produced signals with different temporal structure. At the same time, sympatric species whose signals had similar temporal characters produced songs on the different plant species.
Signal perception of a tropical katydid in a noisy environment

M. Siegert*, H. Römer, I. Fertschai and M. Hartbauer
Department of Zoology, Karl-Franzens-University, Graz, Austria.
*correspondence with: marian.siegert@uni-graz.at

Ambient background noise can be a limiting factor for the acoustic communication of animals. This is especially true for tropical insects where many simultaneously active signallers contribute to a constant sonic noise band as well as transient ultrasonic noise. Males of the tropical katydid Mecopoda elongata synchronize their chirps in acoustic interactions, an ability that allowed us to investigate the influence of various levels of background noise at the behavioural level.

In a behavioural paradigm periodic conspecific signals were presented together with rainforest noise (either as full-spectrum noise or sonic noise <10 kHz). Without noise males generate chirps in synchrony with a periodic conspecific signal presented at 66 dB SPL (Fig. 1 upper trace). Under noise, however, this ability dropped to 50% when the noise level exceeded signal level by 1 dB (Fig.1 lower trace). The sonic component of the noise on signal detection was less pronounced, allowing males to synchronize about 50% of their chirps at a S/N ratio of -7 dB. The song of a congeneric signaller, however, with trains of broadband syllables strongly affected the successful recognition of conspecific signals (50% synchronized chirps at a S/N ratio of +7 dB).

We also investigated the detection of conspecific signals in noise in a neurophysiological approach using the response of the omega-neuron and applying signal detection (ROC) analysis.

The presentation of conspecific signals resulted in bursts of action potentials of which 88% could be successfully detected at a signal-to-noise (S/N) ratio of -2 dB. However, under these conditions the false alarm rate increased to 0.24 Hz, which is about half of the rate of signal presentation (0.5 Hz). By contrast, the sonic noise component did not affect the detection of conspecific signals up to a noise level of 76 dB SPL and further, as monitored in the bursting activity of the omega cell. The noise-robustness of encoding conspecific signals was in part the consequence of spike rate adaptations, which maintained bursting fidelity in response to conspecific signals despite the presence of high levels of background noise.
Acoustic Communication in the Pine Engraver Bark Beetle, *Ips pini* (Coleoptera: Scolytinae)

S. Sivalinghem$^1$ and J. E. Yack$^1$

$^1$Carleton University, Department of Biology, Ottawa, Canada, *correspondence with: s.sen24@hotmail.com

Bark beetles (Scolytinae) impose significant threats to forests throughout North America, and management strategists rely heavily upon knowledge of pest species' life history attributes and sensory ecology to develop effective control programs. Most bark beetle species produce acoustic signals, which have been implicated to function in defense, courtship, aggression, and species recognition. However, there is a surprising dearth of information about how acoustic signals are received and transmitted in any bark beetle species. An understanding of signal characteristics allows for developing hypotheses regarding signal function and receptor mechanisms.

Using the pine engraver (*Ips pini*) species as a model, the objectives of this study were to: 1) characterize their sound and vibratory signals; and 2) determine potential receptor mechanisms. Using broadband microphones and laser vibrometry, we recorded and characterized female acoustic signals during pre-mating interactions and tactile disturbance, and compared chirp characteristics between conditions. Females produced low intensity (69 dB SPL; at 1 cm) chirps through a vertex-pronotum stridulatory mechanism (see image). Males do not produce sounds. Signals consisted of multiple tooth-strikes with peak frequencies between 12-25 kHz. Distress chirps had significantly higher peak frequency (24 kHz) and tooth-strike rate than did pre-mating chirps (13 kHz), implying possible differences in signal function. Only signaling females entered male nuptial chambers, and chirp rates significantly decreased after entrance, suggesting that these signals function for species recognition. Also, chirps produced four minutes after entrance had significantly slower tooth-strike rates, indicating that pre-mating signals may serve different functions depending on the stage of the encounter. Females also produced solid-borne vibrations through the phloem layer of pine trees during male-female pre-mating interactions.

Our results contribute novel information on the physical characteristics of sound and vibration signals in bark beetles. These results elucidate possible functions of signaling, and acoustic reception in bark beetle, which is crucial for designing future behavioural and neurophysiological studies, and developing effective pest management strategies.

We would like to thank Dr. Mary L. Reid for collecting and shipping beetles. This project was funded by grants from the National Science and Engineering Research Council (NSERC) Discovery Grant to Dr. Jayne E. Yack, and grants from the Ministry of Research and Innovation (Early Research Award) to Dr. Jayne E. Yack.
Courtship Songs and Female Preferences in a Narrow Hybrid Zone between Grasshopper Species *Stenobothrus rubicundus* and *S. clavatus* in Northern Greece

J. Sradnick\(^2\), V.Yu. Vedenina\(^1\)* and N. Elsner\(^2\)

\(^1\)Institute for Information Transmission Problems, Moscow, Russia, 
\(^2\)Institute for Zoology and Anthropology, Göttingen, Germany

*correspondence with: vedenin@iitp.ru

Two grasshopper species *Stenobothrus rubicundus* and *S. clavatus* (subfamily Gomphocerinae) were shown to hybridize in a very narrow contact zone (16 square km) at the Mt. Tomaros in Northern Greece. These species are remarkably different in several morphological characters, as well as in both calling and courtship songs. We analyzed the courtship songs of natural hybrids between *S. rubicundus* and *S. clavatus* and compared them with the songs of laboratory hybrids. Some hybrid songs were shown to have intermediate features between parental songs, whereas other hybrid songs comprised completely new elements. We also found a dominance of the *clavatus*-like song elements in the hybrid courtship songs. In playback experiments, we investigated female preferences for the courtship songs of *S. rubicundus*, *S. clavatus* and hybrid males. Females of the parental species significantly more often preferred the songs of conspecific males. Comparison of preferences in females from allopatric populations and from parental-like localities of the contact zone showed no evidence for reinforcement. Hybrid females showed lower selectivity than the parental females, responding somewhat equally eager to playback of the songs of *S. clavatus*, *S. rubicundus* and hybrid males. They, however, preferred the songs possessing rather *clavatus*-like than *rubicundus*-like elements. Dominance of song elements of *S. clavatus* in both hybrid songs and female preferences may evidence an ancestral origin of *clavatus* song pattern. Asymmetry found in female preferences may also have implications for a structure of the hybrid zone.
Which information is contained in the songs of *Chorthippus biguttulus*?

N. Stange¹, B. Ronacher¹,²

¹ Humboldt-Universität zu Berlin, Department of Biology, Berlin, Germany
² Bernstein Center for Computational Neuroscience, Berlin, Germany

*correspondence with: nicole.stange@biologie.hu-berlin.de*

Many insect species use acoustic communication signals ("songs") to attract mates. Usually, the females are the more selective gender, because of their higher parental investment. A female should be able to extract three types of information from a male's song: i) whether the sender is of the correct species, ii) whether its gender is matching, and iii) possibly also the quality of the sender.

The grasshopper *Chorthippus biguttulus* is a species with a bidirectional communication system. Males sing spontaneously and a female produces a reply song, if the song appears attractive to her. During this duet the male approaches the female and the mating can occur. The songs are produced by stridulation, i.e. by rubbing the hind legs against the forewings. The songs are species-specific (von Helversen, 1972) and gender-specific (Elsner 1974), and are a major barrier against hybridization (von Helversen and von Helversen, 1975; Gottsberger and Mayer 2007). In addition, songs of *C. biguttulus* males reveal cues about the intactness of the singer (von Helversen, 1972; Kriegbaum, 1989).

We tested the hypotheses that males transmit information about their health, size, age and the origin of their population, and that the females are able to extract this information from the heard signals.

We recorded songs of N = 40 males caught in the field that differed in size, age, and origin of their population. The recorded songs were used in playback-experiments on females to assess their attractiveness. Size parameters of males were correlated with their immunological competence and the attractiveness of the produced songs.

The males of the four tested populations differed significantly in size, for example the length of the femur (Kruskal-Wallis Test: p<0.0001) and in some song features, e.g. the accentuation of syllable onsets (ANOVA: p<0.0001). Females preferred males, which produced higher onsets (Pearson: r=0.721, p=0.019) and had heavier legs (Pearson: r=0.645, p=0.044) and they discriminate males from different populations (ANOVA: p=0.0018).
Selective Processing of Calling Songs by AN2 Interneurons of Female *Gryllus bimaculatus*: Roles in a Temporally Selective Neuronal Network

J. Stout*, L. Samuel and G. Atkins

Andrews University, Department of Biology, Berrien Springs, MI, USA
*correspondence with: stout@andrews.edu

Like several other species of gryllids, the phonotactic responses of female *Gryllus bimaculatus* to models of the male’s calling songs (CSs) exhibit substantial plasticity. Individual virgin females choose to respond phonotactically to different ranges of syllable periods (SPs), which usually include the SPs produced by conspecific males but are very commonly broader than the males produce. Individual females, when tested sequentially over periods of several hours or days, also commonly respond to different ranges of SPs. These results indicate that the underlying processing of these auditory signals by interneurons is also quite plastic. Several different manipulations of the prothoracic ganglion, including the nanoinjection of juvenile hormone III (JHIII) narrow the range of SPs female *Acheta domesticus* and *G. bimaculatus* respond to phonotactically. For individual female *G. bimaculatus*, SP-selective phonotaxis is paralleled by, and significantly correlated with, SP-selective processing by their prothoracic auditory AN2 interneurons. Nanoinjection of JHIII into the prothoracic ganglion also changes and narrows the ranges of SPs that the AN2 neurons respond to selectively. The changes in AN2’s SP-selective processing, induced by JHIII injection, include reduced contralateral inhibition. This suggests that the inhibitory synaptic input provided by the contralateral ON1 neuron is at least partially uncoupled by JHIII. JHIII also reduces the inhibitory coupling between the paired ON1 neurons. Ongoing work with the interaction of AN2 and ON1 neurons suggests that the range of responses that the ON1s can make to model CSs is more dynamic than currently suggested by the relevant literature and is influenced by the female’s social environment.
Males increase the efficacy of courtship signaling in response to female receptivity cues:
A test with puppet females

L. Sullivan-Beckers and E. Hebets
University of Nebraska-Lincoln,
School of Biological Sciences, Lincoln, NE, USA,
*correspondence with: LSB@unlserve.unl.edu

A male displaying to attract a mate faces the problem of effectively communicating through a complex and variable signal environment. A common solution to this problem is for males to position themselves to increase signal transmission, yet in many cases, the mechanism(s) underlying this solution remains unknown.

We propose that males optimize signal transmission by attending to female feedback cues and adjusting their signaling position accordingly. We test this hypothesis with males of the wolf spider *Schizocosa rovneri*, which court females with seismic signals transmitted through substrates on the forest floor. In response, receptive *S. rovneri* females perform a slow pivot display, producing visual and seismic cues. We mimic female receptivity using puppets, manipulated remotely, and ask whether males alter their signaling position, in terms of substrate use, with female feedback. We further ask if adjustment depends upon receiving cues in particular sensory modalities.

We found that males receiving visual and/or seismic feedback cues from puppet females increased signaling effort. However, only males that received seismic feedback cues altered substrate use when signaling. Ultimately, males optimized their signal transmission by altering their use of signaling substrate in response to seismic female receptivity cues. Our results present a previously undocumented behavioral mechanism for how males effectively position themselves in the signaling environment—learning through female feedback.

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Use of amplitude cues during vibration localization by a small plant-dwelling insect
Caitlin A. Swatek, Jeremy S. Gibson and Reginald B. Cocroft
Division of Biological Sciences, University of Missouri

“For many small insects that communicate using plant-borne vibrations, finding the vibration source is often necessary during mate searching or recruitment to a feeding site. However, determining the direction of a substrate-borne wave is challenging for small species, because time and amplitude differences are minimal between vibration receptors in different legs. An alternative solution for small species is to compare sequential samples along an amplitude gradient. We tested the role of amplitude cues in mate searching in the thornbug treehopper, *Umbonia crassicornis*. In this species, mate-searching males home in on the vibrational signals of stationary females by sampling at multiple locations along host plant stems. We used vibrational playback to create two contrasting amplitude 'landscapes' on a 1-m tall potted host plant (*Albizia julibrissin*). In one treatment, playback amplitude was increased as the male moved closer to the source (by 3 dB every 4 cm). In the other the pattern was reversed, and playback amplitude was increased as the male moved farther from the source; in each case the amplitude experienced by the male at a given location depended on the interaction of the source amplitude and the plant substrate. All males (n=20) located the source when amplitude was increased with proximity, and failed to locate the source when the pattern was reversed. Future research will investigate the conditions under which natural amplitude gradients occur on plants, and how changes in amplitude interact with other potential cues during vibration localization.”

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The role of acoustic and seismic communication in *Gladicosa gulosa*: complex vibration signals in a wolf spider

A. L. Sweger¹, G. W. Uetz¹

¹University of Cincinnati, Cincinnati, OH

*correspondence with: swegeral@mail.uc.edu

Many wolf spiders (Lycosidae) produce complex multimodal signals, making them excellent models for testing hypotheses about the evolution of signaling behavior. This research examines acoustic/vibratory communication in the “purring” wolf spider *Gladicosa gulosa*, and the use of a vibration playback device in demonstrating social facilitation of courtship. Only minimal research has been conducted on *G. gulosa*, but early studies describe the loud volume of its acoustic/vibratory courtship, suggesting that signaling in this species may be energetically costly and vulnerable to eavesdropping, making it a potential model for studies of condition-dependent signaling, eavesdropping behavior, and male-male competition. Research objectives are to (1) characterize the signals of courting males, (2) determine which (if any) components of a complex signal may reflect an energetic cost and (3) examine whether eavesdropping and social facilitation of signaling occur in this species. Using Laser Doppler Vibrometry and sensitive microphones, we recorded and characterized the components of male courtship. Preliminary analyses of results suggest that courtship displays by males of this species produce both airborne (acoustic) and seismic (vibration) signals (using stridulation and percussion) and that the components of courtship may be affected differently by varying ecological conditions. We also used a “spiderphone” apparatus to transmit vibration recordings back into the substrate and document male response. There appears to be some evidence that males can detect and respond to the courtship vibrations of other conspecific males. These results suggest the potential for male eavesdropping, which could lead to male competitive behavior in the form of social facilitation of courtship.

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**Variation in Courtship Ultrasounds of Moths with Reference to Sex Pheromones**

T. Takanashi\(^1,2,\*\), N. Skals\(^3\), A. Surlykke\(^3\), H. Tatsuta\(^4\), Y. Ishikawa\(^5\), and R. Nakano\(^2,6\)

\(^1\)Forestry and Forest Products Research Institute, Ibaraki, Japan, \(2\)Neurosensing and Bionavigation Research Center, Doshisha University, Kyoto, Japan, \(3\)Institute of Biology, University of Southern Denmark, Odense, Denmark, \(4\)Graduate School of Agriculture, University of the Ryukyus, Okinawa, Japan, \(5\)Graduate School of Agricultural and Life Sciences, The University of Tokyo, Tokyo, Japan, \(6\)National Institute of Fruit Tree Science, Ibaraki, Japan, *correspondence with: takanasi@affrc.go.jp

Moths use ultrasounds as well as pheromones for sexual communication. The European corn borer, *Ostrinia nubilalis* (Crambidae: Lepidoptera), and its Asian congeners, *Ostrinia furnacalis* and *Ostrinia scapulalis*, exhibit within-species and between-species variation in their pheromone communication. Recently, we reported ultrasound communication in *O. furnacalis*; however, variations in ultrasounds in the three congeners have not been addressed to date. Here we investigated features of ultrasound production and hearing in *O. nubilalis* and *O. scapulalis*, and compared them with those of *O. furnacalis*. As in *O. furnacalis*, males of *O. nubilalis* and *O. scapulalis* produced ultrasounds during courtship by rubbing specialized scales on the wings against scales on the thorax. The covering of these scales muffled the sounds and significantly reduced mating success in *O. nubilalis*, showing the importance of ultrasound signaling in mating. The ultrasounds produced by *O. nubilalis* and *O. scapulalis* were similar, consisting of long trains of pairs of pulses with a main energy at 40 kHz, but distinctly different from the ultrasound produced by *O. furnacalis*, consisting of groups of pulses peaking at 50 kHz and with substantially more energy up to 80 kHz. There was no significant difference in hearing among the three species with regard to the most sensitive frequencies and hearing threshold levels. Despite overall similarities, temporal and amplitude features of the sounds produced by *O. nubilalis* (and *O. scapulalis*) of different pheromone type differed significantly. The patterns of variations in the songs and pheromones well reflected those of the phylogenetic relationships, implying that ultrasound and pheromone communications have diverged concordantly.

In order to widely explore acoustic communication in moths, we recorded and analyzed courtship ultrasounds of 13 moth species from Noctuidae, Arctiidae, Geometridae and Crambidae, which are distantly related to *Ostrinia*. Males of nine species produced broadband ultrasounds with a peak power frequency ranging from 38 to >100 kHz. Courtship ultrasounds appear to be widespread among phylogenetically distant groups of hearing moths that utilize sex pheromones.

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Cellular mechanisms underlying stimulus-specific adaptation in the tettigoniid TN-1 neuron

J. D. Triblehorn\(^1\), J. Pre\v{s}ern\(^2\), and J. Schul\(^3\)

\(^1\)College of Charleston, Department of Biology, Charleston, SC, USA, \(^2\)National Institute for Biology, Department of Entomology, Ljubljana, Slovenia, \(^3\)University of Missouri, Department of Biology, Columbia, MO, USA

*correspondence with: triblehornj@cofc.edu

The tettigoniid TN-1 auditory neuron detects novel or transient sounds. TN-1 adapts rapidly to fast pulse rates, but responds to transient sound pulses presented during fast pulse rate stimulation if the carrier frequencies are sufficiently different. This phenomenon has been termed stimulus-specific adaptation (SSA) in the vertebrate literature. In tettigoniids, auditory afferents project to the TN-1 dendritic field in a tonotopic manner; therefore, different stimulus frequencies activate different TN-1 dendritic regions. Our dynamic dendritic hypothesis proposes that SSA in TN-1 can be explained by limiting adaptation neural mechanisms to dendritic regions activated by the acoustic frequencies comprising the fast pulse rates, leaving the other, unstimulated dendritic regions free to respond to novel input.

Pharmacological studies revealed two post-synaptic adaptation mechanisms: a transient calcium-mediated mechanism and a slow, tonic sodium-mediated mechanism. BAPTA injected into TN-1’s main dendrite increased the duration of spiking activity to fast pulse rates, but did not completely eliminate SSA or TN-1’s ability to detect transient sounds. This indicated a second mechanism was involved. Replacing normal saline with low sodium saline eliminated SSA as TN-1 responded to fast pulse rates for the stimulus duration. Based on these results, we hypothesized that: 1) a sodium-mediated mechanism occurs within the dendritic regions stimulated by fast pulse rates and reduces current enough to keep TN-1 from reaching threshold and, 2) a calcium-mediated mechanism occurs within TN-1’s axonal region activated by spiking activity. To test these hypotheses, we used intracellular calcium and sodium imaging. Our results confirmed that: 1) fast pulse rates evoke transient calcium concentration increases in both dendritic and axonal regions and slow pulse rates led to a gradual accumulation of calcium in both regions; 2) fast pulse rates tonically increased the sodium concentration within TN-1 dendritic regions only; slow pulse rates did not result in a significant increase in sodium concentration; and 3) increases in sodium concentration were restricted to those dendritic regions stimulated by the acoustic frequencies contained in the fast pulse rates, consistent with the tonotopic organization of the auditory afferent projections onto TN-1’s dendrites.

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Present status of mountain cicadas
(*Cicadetta montana s. lato*) in Europe

Tomi Trilar¹ and Matija Gogala²

¹ Slovenian Museum of Natural History, Prešernova 20, 1000 Ljubljana, Slovenia
² Slovenian Academy of Sciences and Arts, Novi trg 3, 1000 Ljubljana, Slovenia
*correspondence with: t.trilar@pms-lj.si, matija.gogala@guest.arnes.si

The Palearctic mountain cicadas were considered as one and the same species, *Cicadetta montana Scopoli*, 1772. Small differences in the form of the wings, the colour of venation and patterns on the thorax were considered to be characteristics of local forms or subspecies. Bioacoustic investigations during the last fifteen years shown than this taxon is actually a complex of sibling species, which can be best distinguished by their calling song structures. At present time in Europe is described 12 species and at least for two more enough material and recordings is available. This bioacoustic data are supported also by molecular analysis. Therefore a distribution of various species of this complex should be determined again. This has been done till now for some regions or countries like Slovenia, France, Switzerland, Austria (partly), Italy (partly), Poland, Montenegro, Romania, Macedonia, Bulgaria and Greece. A good example for this is a distribution of species of this complex in S.E. Europe, where sudden change from sympatric occurrence of a few species changes to alopaticy in other endemic ones.

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Parallel changes in mate-attracting calls and female preferences due to auto-polyploidy.
Mitch Tucker, H. Carl Gerhardt
University of Missouri, Columbia, Missouri, USA
*correspondence with: GerhardtH@missouri.edu

Polyploidy (genome duplication or fusion) has generated enormous organismal diversity in plants and played a role in the early evolution of vertebrates. Among modern vertebrates, polyploid speciation has occurred relatively recently in diverse groups of sexually reproducing fish and anuran amphibians. Polyploid individuals face the daunting task of surviving in competition with individuals of their diploid parental species and remaining reproductively isolated from them.

In frogs, cryptic species pairs with different ploidy levels often cannot be distinguished by external morphology but differ in the structure of the male advertisement (mate-attracting) call. Differences in such calls first led to the discovery of a diploid-tetraploid complex of North American gray treefrogs. Moreover, a previous study found that the pulse rate of the calls of artificially produced autotriploids of the diploid (*H. chrysoscelis*) in this complex shifted to lower values, in the direction of the pulse rate of the tetraploid species (*H. versicolor*). In this study, we investigated other fine-scale properties (pulse duration, interpulse interval, pulse shape) of auto-triploid males’ mate-attracting call that are used by females to select mates. We found that pulse and inter-pulse duration increased as pulse rate decreases, a finding similar to the characteristics of *H. versicolor*. The fine-scale changes which result from auto-triploidy may be behaviorally relevant to auto-triploid females.

In order to investigate the selectivity of auto-triploid females, we used two-choice experiments to estimate a preference function for pulse-repetition rate, the property used by wild-type diploids. We show here that polyploidy per se also results in a parallel shift in pulse-rate selectivity in artificially produced autotriploid females of *H. chrysoscelis*. Such a parallel "pleiotropic" effect of polyploidy is almost certainly a large part of the explanation for the origin of reproductive isolation of wild-type individuals of the two species. Our new result is also consistent with the observation that wild-type tetraploids with different, independent origins have similar calls and interbreed when their ranges of distribution overlap.

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Active space of multimodal signaling in a complex environment.

G.W. Uetz\textsuperscript{1}, J. S. Gibson\textsuperscript{1,2}, S. D. Gordon\textsuperscript{1,3}, J. A. Roberts\textsuperscript{4}, D.L. Clark\textsuperscript{5}

\textsuperscript{1}University of Cincinnati, Cincinnati, OH, \textsuperscript{2}University of Missouri, Columbia, MO, \textsuperscript{3}University of Strathclyde, Glasgow, UK, \textsuperscript{4}The Ohio State University, Newark, OH, \textsuperscript{5}Alma College, Alma, MI

*correspondence with: george.uetz@uc.edu

Multimodal signals may have evolved to compensate for constraints of complex environments on transmission and perception, as signals in different modalities may vary in efficacy. Male \textit{Schizocosa ocreata} (Hentz) wolf spiders (Araneae: Lycosidae) court females using seismic signals (stridulation and percussion) and visual cues (leg tapping, waving). However, the complex structure of forest floor habitats may interfere with transmission of individual signal modes.

We examined the influence of complex leaf litter microhabitats on transmission of both seismic and visual signals of courting male \textit{S. ocreata} by measuring the “active space” of signals in the field and lab. We used Laser Doppler vibrometry to record the seismic component of male courtship in the laboratory on natural substrata typical for the habitat (leaves, bark/wood, soil, and rock) and to measure seismic vanishing point distances \textit{in situ} in the field. We also measured maximum visual detection range of courting males by females in laboratory studies, and used laser distance measures to determine effective line-of-sight visual detection distance in the field.

Laser vibrometry revealed that leaves are highly conductive substrates for seismic signals compared to others (soil, wood, rock), but that signal amplitude attenuates with distance in leaf litter. While detection distance of visual and seismic signals is similar, visual signals exhibit greater variation, and the visual range of spiders is greater than the active space of seismic signals. Behavioral studies demonstrate that mating success is greater on leaf litter, and that spiders spend more time on leaf litter substrates. However, when confined to substrates that attenuate seismic signals, spiders may compensate by increasing visual signals. Overlapping active space of multimodal signals in forest leaf litter suggests \textit{S. ocreata} signaling takes place within a communication network, and may be perceived by both intended receivers (females) and eavesdroppers (competitor males, predators). As a consequence, multimodal signaling behavior may be subject to selection from multiple opposing forces.

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Speciation in Gomphocerine Grasshoppers: Molecular Phylogeny vs. Bioacoustics and Courtship Behavior
V.Yu. Vedenina\textsuperscript{1} and N.S. Mugue\textsuperscript{2}
\textsuperscript{1}Institute for Information Transmission Problems, Moscow, Russia, \textsuperscript{2}Vavilov Institute of Developmental Biology, Moscow, Russia
*correspondence with: vedenin@iitp.ru

To understand the driving forces of speciation in grasshoppers of the subfamily Gomphocerinae, we compared the molecular phylogenetic tree with the distribution of the song pattern complexity and courtship behavior. In 51 grasshopper species of Gomphocerinae, a barcoding region of mitochondrial gene COI was sequenced and analyzed. A plesiomorphic pattern of calling song was shown to be predominant in the species of the most basal cluster including the tribes Chrysochraontini, Dociostaurini and Arcypterini. In the tribes Stenobothrini and Gomphocerini, plesiomorphic pattern of the calling song was found in less than half of the species studied; others demonstrated the increasing song complexity. The species of the basal cluster of the phylogenetic tree did not show complex courtship songs. Courtship songs that are different and more complex than the calling songs were only found in about half of species belonging to the tribes Stenobothrini and Gomphocerini. Most species with complex courtship (species of Stenobothrus genus, of Chorthippus albomarginatus-group) were shown to be recently diverged species. Comparison of visual display accompanying complex courtship song revealed similarities between the species from different groups. According to the molecular phylogeny, complex courtship behavior in Gomphocerinae evolved independently and convergently. Since the courtship song can be used by a female to judge the mate quality, sexual selection is suggested to be the main driving force of rapid speciation in these young species.
In the current study, we recorded and analyzed the courtship song in the field cricket *Gryllus assimilis*, and investigated the importance of different parameters of the courtship song for mating success in playback experiments. Males that were rendered mute by removing their forewings had little mating success (28% of females responded by mounting the male) in comparison to the intact males (90% mounting frequency). Normal courtship song consists of low-carrier (ca. 3.5 kHz) chirps punctuated by pairs of high-carrier (ca. 17 kHz) ticks. Replacing a muted male's song with a model based on these parameters resulted in a mounting frequency similar to that of intact males (83%). Playback of model songs containing only one element (chirps or ticks) resulted in slightly lower response rates (66-70%), however, the difference was non-significant from positive control. *G. assimilis* is the only known North-American species of *Gryllus* that produces double ticks during courtship. To test whether the tick number might be subject to directional selection by females, we played back model song containing the chirps alternating with four ticks (instead of double ticks); this model song was almost as effective as courtship of intact males (83%). Other model songs containing both courtship elements, but with one of these being different from the natural element either in frequency or temporal parameters, were significantly less effective (33-60%) than the natural courtship song. Least effective (33-37%) were two model songs containing the chirps with the high-frequency pulses. We suggest that an “incorrect” element in the courtship song may be inhibitory.
1 pulse, 2 pulse, 3 pulse, 4: Acoustic communication in a dueting katydid, *Scudderia pistillata*

S.M. Villarreal* and C. Gilbert

1Cornell University, Department of Entomology, Ithaca, NY, USA

*correspondence with: smv32@cornell.edu

The Broad-Winged Bush katydid, *Scudderia pistillata*, is a dueting katydid, meaning both sexes produce sounds. Analysis of the male call demonstrates that males produce a counting series, in which 1-2 pulses are added to each phrase of the bout. Males are stereotypic in the pulse sequence they produce, and their call shows some association with their overall size. Female *S. pistillata* were subjected to various playbacks of male calls in which the pulse sequence was altered. Females produce multiple ticks in response to each male phrase, and the number of ticks a female produces is dependent on the number of pulses in the phrase. Females however are unaffected by the sequence in which the pulses arrive. Females do not show an acoustic preference to bouts of consistent counters, calls with n+1 pulses added to each phrase, compared to inconsistent counters. They also do not show a change in acoustic preference to a bout with a counting sequence versus a bout of phrases with equal numbers of pulses. Further analysis of both female acoustic response and phonotaxis response to manipulated male bouts is currently underway to determine what effect adding pulses to each phrase has on female mating decisions.

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Extremely high sound pressure level from a pygmy aquatic insect

J.F.C. Windmill\textsuperscript{1}, D. Mackie\textsuperscript{1}, and J. Sueur\textsuperscript{2}

\textsuperscript{1}University of Strathclyde, Department of Electronic & Electrical Engineering, Glasgow, UK,

\textsuperscript{2}Muséum national d'Histoire naturelle, Département Systématique et Evolution, Paris, France

*correspondence with: james.windmill@eee.strath.ac.uk

To communicate at long range, animals have to produce intense but intelligible signals. This task might be difficult to achieve due to mechanical constraints; in particular relating to body size. Whilst the acoustic behavior of large marine and terrestrial animals has been thoroughly studied, very little is known about the sound produced by small arthropods living in freshwater habitats. Here we analyze for the first time the calling song produced by the male of a small insect, the water boatman \textit{Micronecta scholtzi}, shown in the figure to the right (scale bar = 0.5 mm).

The song is made of three distinct parts differing in their temporal and amplitude parameters, but not in their frequency content. Surprisingly, sound is produced at 78.9 (63.6 – 82.2) SPL rms \textit{re} $2 \times 10^{-5}$ Pa with a peak at 99.2 (85.7 – 104.6) SPL \textit{re} $2 \times 10^{-5}$ Pa measured at a distance of 1 metre. This energy output is significant considering the small size of the insect.

When scaled to body length and compared to 227 other acoustic species, \textit{M. scholtzi} can be considered the loudest animal ever recorded, with the highest ratio dB/body size, outperforming all marine and terrestrial mammal vocalizations. This water bug is clearly the exception that proves the rule that stipulates that the size and the intensity of a source are positively related. Such an extreme display is interpreted as an exaggerated secondary sexual trait resulting from a runaway sexual selection without predation pressure.

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Near-field Hearing in Monarch Butterfly Caterpillars (Nymphalidae: Danaus plexippus)

J.E. Yack and C. Taylor

Department of Biology, Carleton University, Ottawa, ON, Canada, K1S 5B6
*correspondence with: jyack@connect.carleton.ca

Many species of larval Lepidoptera have been observed to respond to sound, but there has been limited formal study of this phenomenon. Our study focuses on the behavioural responses to sound and identification of receptor mechanisms in late instar larvae of Monarch butterflies (Danaus plexippus). Using high-speed videography caterpillars were shown to respond to sounds by freezing, contracting their heads, and vigorously flicking their thorax in a vertical direction. Behavioural responses occur at latencies between 50 and 800 ms (mean 290 ms) to sound frequencies ranging between 50 and 900 Hz, with a best frequency of 150 Hz. Using ablation studies, sensory receptors were identified as 3 pairs of elongated trichoid sensillae located on the prothorax and last abdominal segments. The most important of these are 2 setae (an upper and lower pair) located on each side of the prothorax (figure shows one of these setae). The upper and lower thoracic setae are on average 410 and 340 microns long respectively, and each is innervated by a single bipolar sensory neuron. Ablations of all three pairs of setae (thoracic and abdominal) in individuals previously demonstrated to respond to sound, resulted in all individuals losing their ability to detect the sound (n=27), while (non-ablated) sham control individuals responded in 95% of the post-operation trials (n =15). Ablation of either the upper or lower setae resulted in a significant decrease in sound reception, but ablation of only the abdominal receptors resulted only in a non-significant decrease in sensitivity. Ablations of other putative structures, including anterior and posterior tubercles and an anterior hair plate structure demonstrated that these structures were not involved in sound reception. We suggest that the unique orientations and lengths of different setae contribute to increasing the caterpillar’s receptive field. Behavioural responses to near-field sounds are discussed in terms of their importance in the insect’s defense against natural predators and parasitoids. A survey of other caterpillar species that were tested and shown to respond to sounds will also be discussed.
The mating behavior of *Psalmocharias alhageos* (Hemiptera: Cicadidae)

Hossein Zamanian¹, Maedeh Mehdipour²*

¹Islamic Azad University Yazd branch, Iran, Member of Young researchers club
²Department of Plant Protection, College of Agriculture, University of Guilan, Rasht, Iran
*correspondence with: Maede.mehdipour@gmail.com

The cicada *Psalmocharias alhageos* is an important pest of vine. The damage on vine products is very much and one of the most important factors in product reduction in vineyard. So, for identifying their mating behavior will help us to find different ways for controlling them. It was conducted for the first time to study the behaviors of the mating of *P. alhageos*. The research was surveyed in Iran in the summer of 2007. It was observed that these cicadas prefer weeds to grapevine for mating. Most sound producing activities of male cicadas was in the warmest hours of the day. The male cicada starts his calling song after sitting on a plant and recognizing his environment and feeling no fear. The female approaches to males by their calling song. Calling song includes two parts: 1- Start sound, 2-Continued sound. Continued sound follows the Start sound. Continued sound has the highest frequency of 10.2 kHz. As soon as the female entrance into male's territory causes the change of calling song into Reply sound. Reply sound attracts the female and this is continued until female go out of the area or they start mating. The dominant frequency of Reply sound is 8 kHz. After the acceptance of the male's sound by the female, the female sits near the male (on the same branch). At this time, the male produces a sound like click and the female replies alternately. Then, the male insect approaches the female which leads to mating. Otherwise if the female leaves territory, the sound of male would change from Reply to Continued sound. And this cycle will be continued.

Key words: *Psalmocharias alhageos*, cicada, mating behavior, calling song.

Note: the presenter (Maedeh Mehdipour) was not able to attend the meeting, due to difficulties with acquiring a visa for the USA.
Insect sound application in identification, classification using ARMA model based on machine learning and pest control

Hossein Zamanian1*, Maedeh Mehdipour2, Klaus Riede3

1 Member of Young Researchers club, Islamic Azad University, Yazd branch, Iran,
2 Department of Plant Protection, College of Agriculture, University of Guilan, Rasht, Iran
3 Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany
*correspondence with: Avrhossein@gmail.com

Many insects (e.g. Diptera, Orthoptera and Hemiptera) generate sounds audible to humans. With the advancement of bioacoustics recording and analyzing tools, species-specific sound features can be identified and used in taxonomy. Consequently, automatic classification based on acoustical signals can be used as a new approach for insect classification, providing rapid tools for species identification and complementing taxonomy based on morphology, eventually supported by DNA analysis. The autoregressive moving average (ARMA) is the most general and widely spread tool for modelling a signal. It provides coefficients improving understanding and even predicting future values of the signal. Based on sound recordings in Iran, two cicada species were analysed: *Lyristes plebejus* and *Psalmocharias alhageos* (Hemiptera: Auchenorhyncha: Cicadidae). Their songs were analysed by ARMA, and identified features were used as inputs into an SVM (support vector machine) classifier. Training the SVM not only allowed to identify the respective species, but also modelled the song and allowed to measure population density and distances among individual species. Moreover, the analysis of insect’s sounds can support behavioural control of insect pests by trapping, repelling, attraction of natural enemies or disruption of mating communication. Therefore, acoustic control methods can indeed be regarded as a new set of methods in Integrated Pest Management.

Key words: insects, bioacoustics, classification, ARMA model, SVM, control.

Note: the presenter (Hossein Zamanian) was not able to attend the meeting, due to difficulties with acquiring a visa for the USA.
Effect of mating-disrupt electronic system on vine cicada control, *Psalmocharias alhageos* (Hom.:Cicadidae)

Hossein Zamanian1*, Hossein Farazmand2

1 Member of Young Researchers club, Islamic Azad University, Yazd branch, Iran,
2 Iranian Research Institute of Plant Protection, Tehran, Iran,
*correspondence with: Avrhossein@gmail.com

One of way for pest controlling through biological control is making disruption. Disruption usually made in communication channel. For example it is made pheromone disruption for insects that use pheromone for their communication. Because of some insects communicate by sound signals, Therefore, sound signals can be used in controlling these pests. Vine cicada, *Psalmocharias alhageos* (Hom.: Cicadidae), is one of the most important pests of grape vine in Iran, which generates sound for it’s communication. Main damage of vine cicada is caused by long feeding of nymphs on vine roots and oviposition inside shoots. For controlling this pest, sound traps which mimic the adult cicada sound are used to lure and kill the opposite sex. However, it is hard to mimic the exact sound signal produced by an insect. This problem makes sound traps less efficient. In this research, a new electronic system was designed and tested which disrupted in sound signal communication of adult cicadas. As female cicadas search for the sound signals produced by male cicada, our system was producing a sound signal which had a frequency close to what is produced by male cicada, disrupting on mating behavior of female cicada. In this research, the number of shoots receiving eggs was counted in the area that the sound signals of the designed device were applied. The results showed that this system can disrupt in mating behavior of female cicada resulting in oviposition reduction.

Key words: vine cicada, *Psalmocharias alhageos*, mating behavior, disruptive signals, pest control.

Note: the presenter (H. Zamanian) was not able to attend the meeting, due to difficulties with acquiring a visa for the USA.
Triggers of the male and female calling and courtship song in southern green stink bug *(Nezara viridula)*

V. Zgonik and A. Čolk

National Institute of Biology, Ljubljana, Slovenia

*correspondence with: vera.zgonik@nib.si

Pheromones produced by males play an important role in aggregation of southern green stink bugs (*Nezara viridula*, L.) on host plants. However once they are on the same plant they also communicate with vibratory signals to locate and recognize each other. Relation between pheromone production and substrate-born vibrations has been shown in males which increased pheromone production when stimulated with the female calling song (Miklas et al. 2002). Pheromone compounds ratio time and spectral characteristics of vibrational songs differ among different *N. viridula* populations. The aim of this study was to identify factors that trigger female and male emission of the calling and courtship song. All the experiments have been conducted in the simulated natural conditions on a bean plant. Signals of only one modality have been applied in each test. Females called spontaneously less often than males. Experiments with male odor on filter paper, synthetic pheromone and live male under a red light showed that the male pheromone triggers the emission of the female calling song. Females did not answer to a model (a body of a dead green stink bug or a live female). Males did not start to sing when a female was approached in the dark (under a red light) but they did when approached in the light. A live female was more effective than a model. In our experimental conditions all visual and chemical stimuli were most effective at close range (2-4 cm). Experiments with a pair of bugs on a plant revealed that a male or a female started to call in the same percentage when a female was placed on a fresh plant 5 minutes before the male. In the opposite case the female was the first singer in about 70%. Male started to emit the calling song when close to a female within their visual range. Female courtship song was emitted after male/female physical contact. Our experiments indicate that male emitted pheromone triggers female calling and that male calling is not just a response to female signaling but in many cases represents the first song in a male/female duet.

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Temporal processing of vibrational communication signals

M. Zorovich

National Institute of Biology, Dept. of Entomology, Ljubljana, SLOVENIA
correspondence: maja.zorovic@nib.si

Substrate-borne vibrational communication plays an important role during long-range calling and short-range courtship communication in many small plant dwelling insects. The frequency spectra of the signals are tuned to the resonant frequencies of the host plants, ensuring maximum efficiency of signal transmission. Consequently, in most Heteroptera and Auchenorrhyncha species, the dominant frequency of signals produced by the vibratory mechanism lies below 200 Hz and above 50 Hz. Recognition of a conspecific signal is mainly based on temporal pattern, i.e. the amplitude modulation, while the spectrum of the signals normally only plays a minor role. This is reflected in the enormous diversity of species-specific and stereotype song patterns found in most vibrationally and/or acoustically communicating insects, whereas the spectra, especially of related species, usually differ much less from each other, as the sound producing systems are usually very similar.

During mating, males and females of *N. viridula* produce sex- and species-specific calling and courtship songs. We examined temporal processing of their communication signals by first order vibratory interneurons, which ascend from the central ganglion towards the brain. The stimulus sequence consisted of 54 pulse duration/interval duration (PD/ID) combinations. Four sine wave pulses of 105 Hz and 20 cm/s were played for each PD/ID combination. The neurons’ responses elicited by the 2nd, 3rd and 4th pulse of each PD/ID sequence were analyzed and two response arrays were created for each neuron, showing the intensity of the response either as mean or as peak instantaneous spike rate.

Mean spike rate response arrays mostly show preference for short pulse durations (below 500 ms) and no selectivity towards interval duration, while the peak spike rate response arrays exhibit either short pulse duration/long interval duration selectivity or no selectivity at all. The long pulse/short interval stimulus combinations elicited the weakest responses in all neurons tested. None of the response arrays show receiver preference for either constant period or duty cycle. The data gathered so far matches the temporal characteristics of *N. viridula* male calling songs and points to temporal filtering of the vibrational signals already at lower levels of signal processing.

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