**Title**

Substrate-borne Bioacoustics and the Impacts of Anthropogenic Noise

**Author**

Raboin, Maggie J

**Publication Date**

2021

# Substrate-borne Bioacoustics and the Impacts of Anthropogenic Noise

By

Maggie J. Raboin

A dissertation submitted in partial satisfaction of the

requirements for the degree of

Doctor of Philosophy

in

Environmental Science, Policy, and Management

in the

Graduate Division

of the

University of California, Berkeley

Committee in charge:

Professor Damian O. Elias, Chair
Professor Eileen A. Lacey
Professor Justin S. Brashares

Fall 2021

# Abstract

## Substrate-borne Bioacoustics and the Impacts of Anthropogenic Noise

By

Maggie J. Raboin

Doctor of Philosophy in Environmental Science, Policy, and Management

University of California, Berkeley

Professor Damian O. Elias, Chair

Across ecosystems, animals face expanding human populations, transportation networks, and urbanization that threaten their survival. Traditional strategies for conservation often hinge on understanding an animal's habitat and population structure, with less attention is paid to the animal's "habit", their way of being in and sensing the world. However, recent appeals to consider the sensory ecology - the way organisms acquire, process, and share information - of species suggest transitioning away from questions like "What do these organisms eat?" and "Who eats them?" toward questions that ask, "In what ways do these animals find food or avoid being eaten?" For many animals, the ubiquitous answer to questions concerning the mechanism for finding food or mates, avoiding predators, choosing suitable habitats, or communicating with conspecifics is "substrate-borne sound".

Substrate-borne bioacoustics is the subset of bioacoustics that concerns the exchange of information via mechanical waves through substrates such as rock, soil, litter, or plant material. It likely long precedes airborne communication via pressure waves in evolutionary time and is used by the vast majority of terrestrial animals - over 95% of all species. Despite this, substrate-borne bioacoustics have been largely ignored in broad acoustic fields of study. For example, animals sensitive to substrate-borne sounds were long excluded from decades of research attempting to explain the diversity of acoustics across taxa (Chapter 2) and mostly left out of research investigating the impacts of anthropogenic noise on animal behavior (Chapter 3). In this dissertation, my colleagues and I do our best to address these exclusions and examine the impacts of substrate-borne anthropogenic noise on a single species; the mason spider (*Castianeira sp.*) (Chapters 4 & 5).

We found that the exclusion of substrate-borne bioacoustics from major fields of study skewed biophysical explanations of acoustic diversity across taxa and may limit understandings of the reach of anthropogenic noise. In addition, when we narrowed our focus to a single invertebrate species, we found that the impact of substrate-borne anthropogenic noise has profound effects on invertebrate behavior. Our research suggests that understanding substrate-borne bioacoustics and substrate-borne anthropogenic noise may be critically important in conserving species, communities, and ultimately, biodiversity

TABLE OF CONTENTS

# ACKNOWLEDGEMENTS

First, thank you to my advisor Damian Elias. Damian exhibited all of the things I had hoped for in an advisor. He gave me ample space to grow and develop ideas, he provided intellectual and emotional support, and he listened. Most importantly, he taught me how to be open, and even welcoming, to the harshest criticism of ideas. Through his example in humility and vulnerability, Damian showed me what it means to be a great scientist. He fostered a lab environment that was open, supportive, stimulating, exploratory, and aspirational. I thank him for his endless encouragement, steadfast support that went above and beyond, incredible generosity, and invaluable guidance.

Thank you to Berkeley, the University, and the Department of Environmental Science, Policy, and Management for inviting me into their incredibly inspiring and stimulating communities. I am grateful for my committee members, including Eileen Lacey, Neil Tsutsui, Justin Brashares, for their guidance throughout this process.

Thank you to my peers and friends in Berkeley and Wyoming. It is because of you that my years in graduate school were some of the greatest of my life. Thank you to Elias Lab graduate students and postdocs present (Trinity Walls) and past (Ignacio Escalante, Erin Brandt, Benji Kessler, Malcolm Rosenthal, Ambika Kamath, and Ashton Wesner) for your generous feedback and helpful advice, much-needed lunch dates, Arizona field adventures, drop-everything-and-party attitudes, stimulating conversations, and unwavering friendships. Much love to my friends and cohort mates, especially Clay Noss, Katie Kinkopf, Kelsey Scheckel, Matt Libassi, and Allie Byrne, for being constant sources of laughter and support. And to my Jackson family who always encouraged me to prioritize the adventure. Special thanks to Blakeney Spong, Blair Loughrie, Sarah Knight, Kristi Onzik, and Bart Young. This dissertation would not be complete without you.

To the Teton Range and all living things that inhabit them: you have welcomed, comforted, and inspired me. Thank you for sharing your sounds, sights, and smells. Thank you for allowing me glimpses into the small things that make up your mystery. I am forever indebted to you for facilitating the relationships that I most cherish and for teaching me what it means to be patient, compassionate, flexible, and resilient.

To my family, who encouraged me to finish by constantly asking, “Are you done yet?” You have always pushed me to try harder, reach further, and be better, and I love it. My only hope is that in finishing this dissertation, I get to see you more often.

Lastly, to my partner William, who, as I write this is putting our little baby to bed and cooking dinner so that I might finish this dissertation in a timely manner. Seven years ago, you took the chance of moving with me to Berkeley so that I might pursue my dream of attending graduate school. In these years you have provided unwavering support, constructive criticism, inspiration, optimism, and comic relief. I hope that I’ve made you proud. I love you and can’t wait for the next adventure.

# CHAPTER 1 INTRODUCTION

## *Invertebrate Bioacoustics*

In natural history museums, you can find millions of individual invertebrates, from ants and anemones to stoneflies and shrimp. All are collected with care, meticulously analyzed by morphology, labeled, and stored on a shelf. Once there, little attention is paid to the sensory life that defined their day-to-day life. At first glance, invertebrates would appear to be too strange and void of emotion to interact with sound in a meaningful way. Moreover, in contrast to mammals, most invertebrates lack protruding folds that are identifiable as ears. They don't delight us with their audible praise of the morning sun the way that birds do. Their anguish isn't conveyed through familiar bellows. But invertebrates have rich sensory lives that are much different from our own and are often dominated by sound.

Recall the cacophony of crickets singing on a warm summer night. Crickets, like humans and vertebrates, rely on airborne pressure waves (far-field sound) to sense and convey acoustic information. However, the audibility of a cricket's song to human ears is an exception among invertebrates. In fact, most of the invertebrate sounds you know, like those produced by crickets, cicadas, katydids, and grasshoppers, are departures from the invertebrate rules of sound production. Few invertebrates are large enough to efficiently move air (Bennet-Clark, 1998) and thus resort to transmitting information through vibrations of solids (substrate-borne sound), a modalitiy of sound out of the sensory reach of humans.

Substrate-borne communication is the subset of acoustic communication that concerns the exchange of information via mechanical waves through substrates such as rock, soil, litter, or plant material. It likely long precedes airborne communication via pressure waves in evolutionary time (Hoch et al., 2006) and is used by the vast majority of terrestrial animals - over 95% of all species (Cocroft and Rodriguez, 2005). Substrate-borne signalers use a variety of mechanisms to produce sounds with frequencies below about 2,000 Hz because low frequencies experience little attenuation in solids (Bennet- Clark, 1998). As a signaling medium, substrates include many differing physical properties, boundaries, and intersecting surfaces (reviewed in Elias & Mason; 2006). This means that in traveling from sender to receiver, substrate-borne sounds can take many forms and be filtered in unexpected or unpredictable ways (Magal et al., 2000). Natural selection is thought to favor those signals that maximize transmission (Endler, 1992; Boughman, 2002), therefore substrate-borne communication is likely more complex than communication through a homogenous medium like air or water.

Invertebrate bioacoustics suggests, with emphasis, the first step to understanding sound in the natural world: human perceptions are limiting. This is reflected in the omission of substrate-borne communication from broad acoustic fields of study. For example, animals sensitive to substrate-borne sounds have largely been left out of decades of research attempting to explain the diversity of acoustics across taxa (Chapter 2) and were long excluded from research into the impacts of anthropogenic noise on animal behavior (Chapter 3; Raboin & Elias, 2019). In this dissertation, my colleagues and I do our best to address these exclusions and examine the impacts of substrate-borne anthropogenic noise on a single species; the mason spider (Castianeira *sp.*) (Chapters 4 & 5; Raboin & Elias, 2021).

## *Anthropogenic Noise*

Anthropogenic noise is widely recognized as an issue of environmental concern (Shannon et al., 2016). Produced by human activities like those associated with urbanization, economic development, transportation networks, and recreation, anthropogenic noise now penetrates some of the quietest places on Earth (Buxton et al., 2017). In fact, over 60% of US protected lands experience noise levels double those of background noise, despite their distance from major metropolitan areas (Buxton et al., 2017). For vertebrates, the consequences of noise in natural landscapes have been found to be multifaceted, impacting mating, movement, predator-prey dynamics, and physiology (Shannon et al., 2016). However, research has mostly focused on the impacts of pressure waves on vertebrates, with the impact of anthropogenic sound on invertebrates and the acoustic modalities they rely on (mainly particle motion and substrate-borne sound) remaining largely unstudied.

Indeed, when evaluated in 2016, only 4% of the work on the impact of anthropogenic noise on animals had been on invertebrates, despite their comprising 97% of species on Earth (Shannon et al., 2016). However, recent research investigating anthropogenic noise and invertebrates suggests that the impact of noise on invertebrate behavior, physiology, and communities is likely diverse and complicated.

### *Overview of Dissertation*

My dissertation is comprised of four chapters. In Chapter 2, my co-authors and I investigate a biophysical model of the diversity of acoustic signals as it applies to substrate-borne communication. For many decades, scientists have attempted to explain acoustic signal diversity with mathematical models. Recently, patterns of acoustic communication have been attributed to metabolic rate, broadly controlled by body size and temperature. However, it was unclear how well this model applied to substrate-borne communication. We conducted a meta-analysis, including acoustic signals from over 200 species, to examine the relationship between various call characteristics (call frequency and call rate) and body size and temperature. Our results indicate that the diversity of acoustic communication across taxa cannot be attributed solely to metabolic rate, but is likely a result of many factors, including signaling medium and sound-production mechanism.

Chapter 3 provides the framework and impetus for the remaining chapters of this dissertation. Noise created by ever-growing transportation networks and human activities is ubiquitous and has penetrated some of the quietest places on Earth. However, the impact of anthropogenic noise on invertebrates has largely gone unstudied. We aimed to close this knowledge gap by integrating information about invertebrate bioacoustics, characteristics of anthropogenic noise, and the ways in which animals adapt to noise. We propose a general framework and outline predictions for constraints and adaptations specific to invertebrates in responding to anthropogenic noise.

In Chapter 4, my co-authors and I develop a foundation in which to investigate the impacts of anthropogenic substrate-borne noise on invertebrate parental care. We explore spider parental care by quantifying the function and benefits of spider nests built by mason spiders (Castianeira sp.), wandering spiders endemic to the Greater Yellowstone Ecosystem (GYE). While most spiders protect their offspring with silk structures (e.g., egg sacs, webs), mason spiders construct mounds made of hundreds of pebbles and leaves. Through field observations, we described this unique behavior among spiders and found that despite the immense effort of mason spiders to construct nests, they only remain for a small portion of time that offspring occupy nest-sites. Through field experiments, we determined that nests greatly reduce the rate of predation and parasitism of egg sacs and offspring mortality. However, these effects are only present the few days following nest construction. Our study illuminates the idea that durability, the ability to withstand environmental perturbations, is a critical feature to animal structures, expanding how we think about nest evolution.

Chapter 5 builds on Chapter 4 and quantifies the impact of substrate-borne noise on mason spider mound-building behavior. Visitation to the GYE has more than doubled in the last 30 years, and with-it human activities that produce anthropogenic noise. We assessed the consequences of substrate borne noise from roads for mason spider nest building and reproductive success. We compared nest-building behaviors and offspring survival at field sites with high and low substrate-borne noise. We found that in the presence of noise, spiders spent less time building nests and were more likely to “get lost” during building. This study was the first field based empirical study demonstrating that substrate-borne noise from anthropogenic sources has important consequences for parental care behavior and offspring survival.

# CHAPTER 2 IS THERE AN ENERGETIC BASIS TO SUBSTRATE-BORNE ACOUSTIC COMMUNICATION?

Maggie Raboin and Damian O. Elias

Included here with permission from Damian O. Elias

## 2.1 ABSTRACT

Animals communicate with a diversity of sounds that minimally includes the transmission of waves and oscillation of particles in air, water, and solids with an assortment of signal characteristics produced by a range of morphological structures. For many decades, scientists have attempted to explain acoustic signal diversity with mathematical models. Recently, patterns of acoustic communication have been attributed to metabolic rate, broadly determined to be controlled by body size and temperature. However, it was unclear how well this model applies to substrate-borne communication. We conducted a meta-analysis, including acoustic signals from over 300 species, to examine the relationship between various acoustic signal characteristics, like call frequency and call rate, and body size and temperature. Our results indicate that the diversity of acoustic communication across taxa cannot be attributed solely to metabolic rate, but is likely a result of many factors, including signaling medium and sound-production mechanism.

## 2.2 INTRODUCTION

Animals communicate with an incredible diversity of sounds from the head-thumping of termites to the howling of wolves. Acoustic communication includes the transmission of waves and oscillation of particles in air, water, and solids, produced by structures that range from the soft-tissue trachea of humans to the rigid ripples of a spider's exoskeleton (Bradbury & Vehrencamp, 2011). It occurs in oceans and soils, within plant stems and leaves, over grasslands, and through forests. Animals use sound for everything from mating and foraging to caring for young and aiding social relationships (Bradbury & Vehrencamp, 2011). The ubiquity of acoustic communication across taxa exemplifies its importance in carrying out life's basic functions.

For many decades, scientists have sought to explain the diversity of animal acoustics with proximate and ultimate hypotheses (Bradbury & Vehrencamp, 2011; Gerhardt, 1994; James F. Gillooly & Ophir, 2010; Ryan & Brenowitz, 2010; Tonini et al., 2020). Patterns of acoustic communication have been attributed to variation in body size relating to the size of an open mouth or beak (Bradbury & Vehrencamp, 2011; García-Hernández & Machado, 2017; Morton, 1977; Tonini et al., 2020), neurophysiology (Bass & McKibben, 2003), and metabolic rate (James F. Gillooly & Ophir, 2010; Prestwich et al., 1989; Sanborn, 1997). Of particular interest is the hypothesis that metabolic rate, broadly controlled by temperature and body size, is responsible for signal diversity among all animals (Gillooly & Ophir, 2010). Here, the idea is that traits that govern the ability to take up and use energy for survival and reproduction also govern the ability of an animal to produce energetically costly sounds (Oberweger & Goller, 2001; Prestwich, 1994). However, models like this one, aren't often tested with the range of diversity they are trying to explain (Rosenthal et al., 2017), illustrated by the fact that none of these models have been applied to animals that use substrate-borne communication, despite its ubiquity (Cocroft & Rodriguez, 2005).

Substrate-borne communication is the subset of acoustic communication that concerns the exchange of information via mechanical waves through solids such as rock, soil, litter, and plant material. It likely long precedes airborne communication via pressure waves (Hoch et al., 2006) and is by far the most common type of acoustic communication among terrestrial animals, used by over 95% of terrestrial species (Cocroft & Rodriguez, 2005). While the majority of species that communicate with substrate-borne sounds are invertebrates (insects, arachnids, and crustaceans (Cocroft & Rodriguez, 2005; Greenfield, 2016; Hill, 2008), it is also common among mammals, reptiles, and amphibians (Hill, 2008). Recently, birds have been added to the list of potential substrate-borne signalers (Ota, 2020).

Substrates impose different constraints on acoustic communication than air or water. First, solids generally take relatively less force to induce a propagating signal than air and thus, smaller animals can more efficiently produce low frequency substrate-borne sounds than airborne sounds (Bennet-Clark, 1998). Second, solid substrates are inherently more variable than air or water. While air and water tend to be relatively homogeneous mediums, substrates are often made of many solid materials with potentially differing physical properties, architectures, boundaries, and intersecting surfaces (Casas et al., 2007; Markl, 1983). In addition, they have the potential of transmitting vibrations with many different types of waves, including longitudinal, transverse, and/or bending waves (reviewed in Elias & Mason, 2014). This means that in traveling from sender to receiver, substrate-borne sounds can take many forms and be altered, often in unexpected or unpredictable ways (Casas et al., 2007; Magal et al., 2000). Natural selection is thought to favor those signals that maximize transmission and fidelity (Boughman, 2002; Endler, 1992), therefore it is conceivable that the diversity of substrate-borne signals is more constrained by the physics of the medium than airborne or waterborne signals due to the vast forms that solids can take. Finally, animals induce substrate-borne signals in a multitude of ways including vibrating various body parts without contact to the ground or other body parts (tremulation, wing-fanning, tymbal buckling, vocalization), striking the substrate (percussion), or rubbing two body parts together (stridulation) (Hill, 2014). Each mechanism may be differentially influenced by body size, metabolic rate, neurophysiology, or temperature. This lies in stark contrast to airborne acoustic signals, where signal production most often occurs via one mechanism: vibrating membranes driven by airflow (e.g., larynx in mammals and anurans, syrinx in birds) (Bradbury & Vehrencamp, 2011).

Here, we test a general model of acoustic signaling based on principles of animal energetics, outlined by Gillooly and Ophir (2010), with a diversity of substrate-borne signals. The model predictions stem from the presumptive dependence of metabolic rate on body size and temperature for ectotherms and endotherms, alike (J. F. Gillooly et al., 2001). It supposes that a whole organism's metabolic rate per unit mass, B/M, is related to body mass M (in grams) and shows exponential temperature dependence ($e^{-E/kT}$) such that

(1.1) $\frac{B}{M} = b_0 M^{-1/4} e^{-E/kT}$,

where $b_0$ is a normalization constant specific to taxa ($W g^{-3/4}$), E is the average activation energy of the respiratory complex (approx. 0.6–0.7 eV), k is Boltzmann's constant (8.62 x $10^{-5}$ eV$K^{-1}$), and T is the absolute temperature in degrees Kelvin (K) (See Gillooly et al., 2001; Allen & Gillooly 2007; and Gillooly & Ophir 2010 for further descriptions of this equation).

Building on equation 1.1 and operating under two main assumptions concerning call frequency and call rate, Gillooly and Ophir (2010) developed model predictions relating to the dependence of acoustic communication on metabolic rate and thus, body mass and temperature. They assumed (1) that call frequency and call rate are driven primarily by the muscular activity of sound producing structures rather than by the morphological features of those structures, and (2) that muscular activity of an individual is proportional to that individual's metabolic rate. Given these assumptions, they predicted that call frequency (i.e., pitch), f (cycles $s^{-1}$), and call rate (inverse of call period), r (call $s^{-1}$), should show the same body mass and temperature dependence as metabolic rate such that

(1.2) $f = \frac{f_0 B}{M} = f_0 b_0 M^{-1/4} e^{-E/kT}$

and

(1.3) $r = \frac{r_0 B}{M} = r_0 b_0 M^{-1/4} e^{-E/kT}$,

where $f_0$ and $r_0$ are normalization constants that represent the number of cycles per joule of metabolic energy flux through a gram of tissue (cycle $J^{-1}$ g) and calls per joule of metabolic energy flux through a gram of tissue (call $J^{-1}$ g), respectively. These equations predict that the relationships between the natural logarithms of temperature-corrected call frequency or call rate (i.e., ln ($f e^{E/kT}$) and ln ($r e^{E/kT}$)) and the natural logarithm of body mass are linear with slopes of -0.25. Additionally, they predict that the relationships between the natural logarithms of mass-corrected call frequency or call rate (i.e., ln ($fM^{1/4}$) and ln ($rM^{1/4}$)) and inverse absolute temperature (i.e., 1/kT) will be linear with slopes of -0.65 (average of 0.6–0.7 range).

Gillooly and Ophir (2010) originally tested this model for animals that signal using airborne and waterborne signals, almost all of which use air or water flow to produce signals (~89% of species in dataset). For this study, we tested the generality of the Gillooly and Ophir (2010) model using animals that communicate via substrate-borne signals and examined whether it is applicable across different sound production mechanisms.

## 2.3 METHODS

We collected from the literature field and laboratory data across a diversity of animals (n = 313 species) that communicate with substrate-borne signals, including insects = 281, arachnids = 15, mammals = 8, amphibians = 4, malacostracans= 4, and Squamata = 1. Species varied in the mechanisms they used to produce substrate-borne sounds including percussion = 128, stridulation = 58, tremulation = 87, tymbalation = 10, wing-fanning = 13, mandible scraping = 1, web-shaking = 1, and vocalizations = 1. Of the species included in our dataset, 25 of them used a mechanism that was unknown. Species varied in size from about $10^{-4}$g for the plant lice *Aacanthocnema dobsoni* to $10^{6}$g for the African elephant *Loxodonta africana* and in temperature from 18℃ for the plant lice *Cacopsylla picta* to 37℃ for various mammals (e.g., African elephant *Loxodonta africana*, Grey seal *Halichoerus grypus*, etc.). Most of the calls considered in our dataset were for the purpose of courtship (n = 234), however some calls were for facilitating social relationships = 38, agonistic interactions = 14, distress = 12, alarm calling = 7, foraging = 4, predator avoidance = 2, territoriality = 1, or the context was unknown = 3. We excluded taxa data that was pre-corrected for temperature (following Gillooly & Ophir, 2010).

We defined call frequency in cycles s$^{-1}$, (Hz) in the medium in which communication is likely taking place. For example, call frequency is the vibration of a substrate induced by one strike of a drumming series or one strike of file and plectrum in a stridulatory call. Call frequency was taken from the reported “dominant’ frequency or the frequency with the highest amplitude. We defined call rate as the rate at which vibration was induced in a substrate (cycles s$^{-1}$, also defined as the inverse of call period). For example, the rate of strikes to a substrate during drumming or between file and plectrum in a stridulatory call. We did not include measures of call power (dB) in our dataset as this is highly variable in recordings of substrate-borne sounds and often not reported.

Ectotherm body temperatures were estimated based on ambient temperature recordings and were assumed to be 20℃ if the study was done in a lab setting and no temperature measure was otherwise recorded. Temperatures of mammals were considered to be 37℃ unless otherwise recorded (Gillooly et al., 2001). Mean temperature values were included in the analyses when a range of temperature values were reported. We did not include studies where temperature values ranged greater than 10℃. For invertebrates, body length rather than weight is often recorded. Therefore, we applied body-weight regressions to get an estimate of wet body weight for these taxa (Sage, 1982). We tested model predictions by conducting linear models in RStudio v. 1.3.1056 (R Core Team, 2020).

## 2.4 RESULTS AND DISCUSSION

Overall, our data on substrate-borne acoustic signaling did not support the general model put forth by Gillooly and Ophir (2010) that predicted a negative relationship between signaling frequency and mass/temperature with a slope of -0.25 and signaling rate and mass/temperature with a slope of -0.65. Instead, we found (1) no relationship between the natural logarithm of temperature-corrected call frequency and the natural logarithm of body mass (Figure 2.1a; slope: -0.10; $r^2$= 0.03; 95% CI: -0.21 to 0.01), (2) no relationship between the natural logarithm of mass-corrected call frequency and inverse absolute temperature (Figure 2.2a; 0.32 eV; $r^2$: 0.01; 95% CI: --0.46 to 1.11), (3) no relationship between the natural logarithm of temperature-corrected call rate and the natural logarithm of body mass (Figure 2.3a; slope: -0.03; $r^2$: 0.00; 95% CI: -0.12 to 0.05), and (4) no relationship between the natural logarithm of mass-corrected call rate and inverse absolute temperature (Figure 2.4a; -0.55 eV; $r^2$: 0.01; 95% CI: -1.24 to 0.13). Note that for all of these relationships, the confidence intervals included a slope of 0. The original predictions were based on the hypothesis that metabolic rate is the primary driver of acoustic signaling diversity among all animals (Gillooly et al., 2001; Gillooly & Ophir, 2010). Our data demonstrates that this is not the case for substrate-borne signals and suggests that other drivers are responsible for signal diversity in substrate-borne communication.

Substrate-borne signaling differs from airborne and waterborne signaling in several key ways including (1) the energetics of wave propagation and (2) the variation in mechanisms used to produce substrate-borne signals. One of the key differences between air- and substrate-borne signaling is the energy required to create a propagating wave. For small animals, producing low frequency signals in air is much less efficient than coupling them with substrates (Bennet-Clark, 1998). For example, an Asian elephant (*Elephas maximus*) and a jumping spider (*Habronattus doessenus*) that is less than 1/3000000 its size, produce airborne and substrate-borne signals of the same frequency (65 Hz), respectively (Elias et al., 2003; O'Connell-Rodwell et al., 2000). Comparing our data with Gillooly and Ophir (2010), we see that after controlling for size and temperature, animals that signal at low frequencies (<1000 Hz) were rare in the Gillooly and Ophir (2010) dataset but common in ours. We suggest that higher signaling efficiency at lower frequencies in substrate-borne signalers, which may decouple muscular activity from an individual's metabolic rate in a way that is not the case with airborne signalers, is one of the primary reasons that our data fail to meet model predictions (Gillooly & Ophir, 2010). This pattern also holds broadly for call rate suggesting that the relaxation of the constraints governing the production of low frequencies also affects low-rate callers. Comparing our call rate data with Gillooly and Ophir (2010), we find that our data set includes a much wider range of body mass and calling rates (Figure 2.3a).

Substrate-borne signalers have evolved a variety of sound production mechanism relative to airborne signalers (Hill, 2008) giving us the opportunity to test the predictions of Gillooly and Ophir (2010) as they relate to sound production mechanism. Gillooly and Ophir (2010) based their model on a main assumption that across acoustic signals, signal frequency and rate are more strongly dependent on muscle activity and therefore, metabolic rate, than on morphological features. However, the muscle activity necessary to produce substrate-borne signals of a given spectral frequency differ substantially if signals are being produced via mechanisms with frequency multipliers (e.g., stridulation, tymbalation) or those without (e.g., tremulation, percussion) (Bennet-Clark, 1999; Hill, 2008). Because our data seems to violate the main assumption of the Gillooly & Ohpir (2010) model, we predicted that different sound production mechanisms would show different patterns in the dependence of signal characteristics on metabolic rate (temperature and mass).

We found that when grouped by sound-production mechanism, the relationship between the natural logarithm of temperature-corrected call frequency and the natural logarithm of body mass came close to the predicted negative slope of -0.25 for sounds produced by tremulation (slope: -0.24; $r^2$= 0.26; 95% CI: -0.37 to -0.11) (Figure 2.1b) and that this relationship for sounds produced by tymbalation had a significantly negative slope (slope: -0.54; $r^2$= 0.68; 95% CI: -0.96 to -0.12). However, we did not find a significant linear relationship for any of the other sound production mechanisms examined (Figure 2.1b). We did not find a linear relationship between the natural logarithm of mass-corrected call frequency and inverse absolute temperature for any sound production mechanism (Figure 2.2b). When grouped by sound-production mechanism, we found a negative linear relationship between the natural logarithm of temperature-corrected call rate and the natural logarithm of body mass for calls produced by wing-fanning (-1.50 eV; $r^2$: 0.93; 95% CI: -2.28 to -0.71) that was different from the predicted slope of -0.25 (Gillooly & Ophir, 2010). For all other sound-production mechanisms, this relationship was not statistically different from zero (Figure 2.3b). Finally, when grouped by mechanism, we found a negative linear relationship between the natural logarithm of mass-corrected call rate and inverse absolute temperature for percussive signals (-1.42 eV; $r^2$: 0.16; 95% CI: -2.13 to -0.71) although this was far from the predicted value of -0.65 (Gillooly & Ophir, 2010). All other sound-production mechanisms were not statistically different from zero (Figure 2.4b).

For animals that produce calls via tremulation, we found that the relationship between mass and call frequency was consistent with the relationship predicted by Gillooly and Ophir (2010). Tremulation produces an acoustic signal when an animal rapidly vibrates their muscles of a body part at a given frequency that is directly transmitted to the substrate. Therefore, it is not a surprise that signals produced by tremulation are influenced by metabolic rate. In contrast, stridulatory mechanisms have accessory morphological structures that determine the frequencies of calls (i.e., frequency multipliers) (Bennet-Clark, 1999) and thus it is not surprising that we did not find a relationship between call frequency and body mass and temperature for these species. While call frequencies produced via tymbalation failed to meet model predictions, we did find a significant negative relationship between call frequency and body mass. In this case, we predict that surface of the tymbal (which is correlated with size) constrains call frequency such that larger animals are able to produce lower frequency calls. Interestingly, the slope for tymbalation is much greater than that of other mechanisms (including the predicted slope from Gillooly and Ophir (2010)) suggesting that signals produced via tymbalation experience more extreme size constraints on call frequency. Much more work is needed to examine these patterns.

Our findings included additional findings that were striking. First, we found that the relationship between calling frequency and body mass and calling rate and body mass is not equivalent, as predicted by the model (Gillooly & Ophir, 2010). This suggests that the energetics behind calling at low frequencies and calling at low rates are different for substrate-borne signalers than airborne signalers. Second, we found negative relationships between signal characteristics and body mass/temperature for some signal production mechanisms and not for others. Negative relationships between body mass/temperature and signal characteristics are thought to reflect intrinsic trade-offs that are used by choosers to select high quality mates (Bradbury & Vehrencamp, 2011; Gerhardt & Huber, 2002; McLean et al., 2012). A classic example is the oft-cited negative relationship between body mass and call frequency - considered to be a major "rule" in animal communication (Bradbury & Vehrencamp, 2011; Gerhardt & Huber, 2002; McLean et al., 2012; but see Rodríguez et al., 2015). Our results suggest that this is not a broad rule across substrate-borne acoustic communication but is only relevant for signals produced via tremulation and tymbalation.

We would be remiss to ignore the fact that biotremology, the study of substrate-borne communication, is a relatively new field of study with little consistency in the way that terms associated with call characteristics are applied across taxa and sound production mechanisms (Hill & Wessel, 2016). It is a great challenge to identify analogous components of calls produced with the same mechanism but by different species, let alone calls that are produced by different sound-production mechanisms. What distinguishes call frequency and call rate from one another, but also from other characteristics of calls (i.e., syllables, transients, trains, bouts, etc.)? For example, species that produce calls with stridulation may produce a single coherent sound or a series of sounds based on how fast or slow their file teeth impact the plectrum (Bennet-Clark, 1998). In this scenario, without knowing the specific motions that produce each sound component, call frequency and call rate can easily be confused. Additionally, new substrate-borne signalers are being found each day (Benediktov et al., 2020; Quiroga et al., 2020), many of which the mechanism of sound production is unknown, and best-practices for recording and analyzing substrate-borne communication among them is constantly evolving (Raboin & Elias, 2019; Stritih-Peljhan & Virant-Doberlet, 2021). All of which makes for a field of study that is exciting, progressing, and full of discovery, but difficult to generalize across. Moving forward, it will be important to standardize terminology to better understand the broad principles governing substrate-borne communication.

Our findings suggest that the diversity of acoustic communication across taxa is likely a result of many important factors, of which metabolism is one. Substrate-borne signals are less dependent on energetics than airborne signals and the degree to which call frequency or call rate is influenced by metabolic rate depends on the mechanism of sound production. In considering a broad theoretical framework that attempts to explain the diversity of all acoustic communication, including substrate-borne communication, we recommend a theoretical framework contrary to Gillooly and Ophir (2010), one that is more complex and incorporates medium, mechanism, and metabolism. However, standardized terminology of signal characteristics across acoustic communication and a better understanding of substrate-borne communication, in general, is necessary. Over 200,000 described insect species are estimated to use substrate-borne signals (Cocroft & Rodriguez, 2005; Hill & Wessel, 2016), not to mention the many arachnid, crustacean, amphibian, and mammalian species that do the same. However, only a vanishingly small fraction of these species has been studied. Only with these data can we begin to understand general principles governing acoustic communication.

*Acknowledgements*

We are grateful to E. Brandt, I. Escalante, A. Kamath, M. Rosenthal and the Elias lab members for their helpful comments that contributed to this manuscript. We also thank the many authors and researchers that collected the data that contributed to this study.

## 2.5 FIGURES

Figure 2.1a

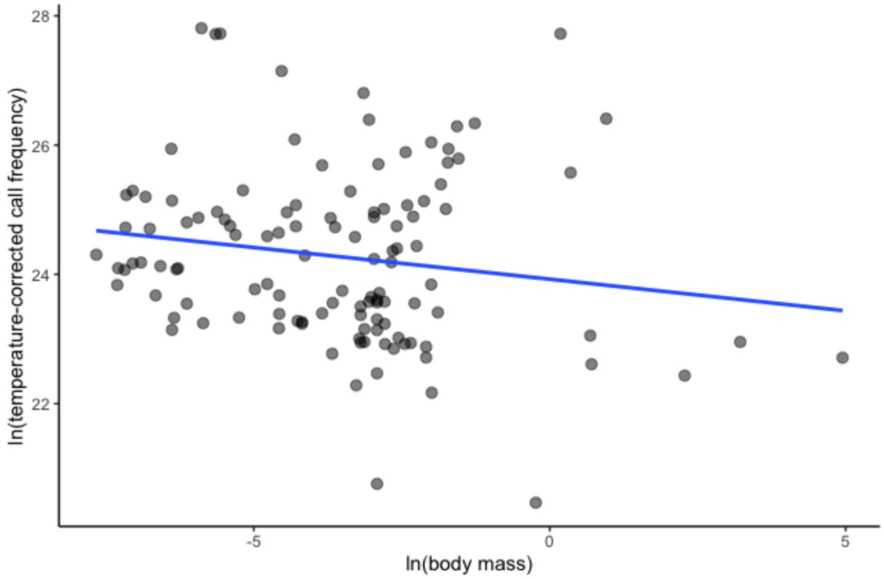

Figure 2.1b

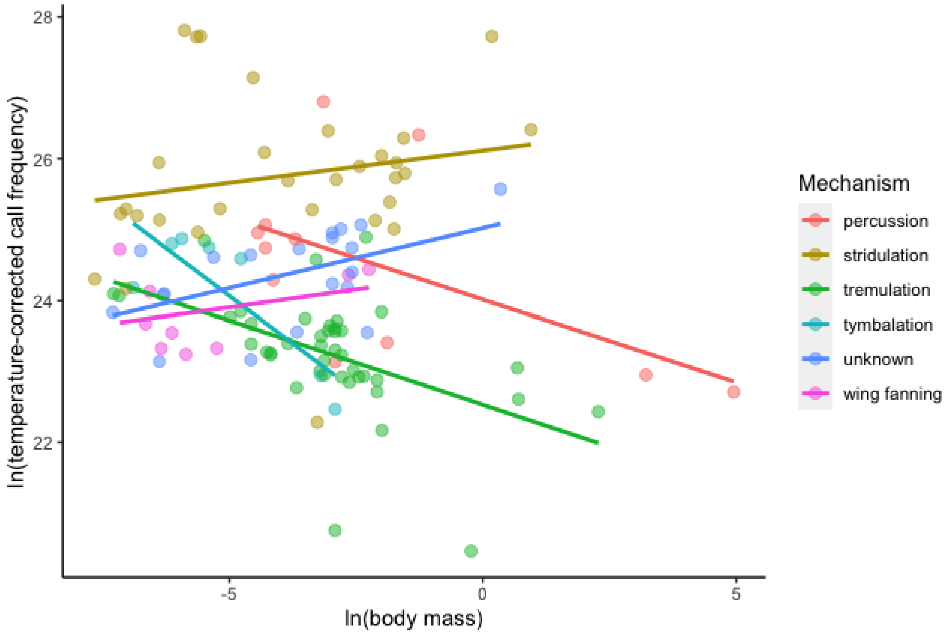

**Figure 2.1.** Relationship between the natural logarithm of temperature-corrected call frequency (cycles $s^{-1}$ • $e^{E/kT}$; equation (1.2)) and the natural logarithm of body mass (in grams) (a) across all substrate-borne signals (y = -0.10x + 23.93; $r^2$ = 0.03; *n* = 119) and (b) when grouped by sound production mechanism. Note that equation (1.2) predicts a slope of -0.25. Percussion, y = -0.23x + 24.02; $r^2$ = 0.31; *n* = 11; stridulation, y = 0.09x + 26.13; $r^2$ = 0.03; *n* = 30; tremulation, y = -0.24x + 22.53; $r^2$ = 0.26; *n* = 42; tymbalation, y = -0.54x + 21.38; $r^2$ = 0.68; *n* = 7; unknown, y = 0.17x + 25.03; $r^2$ = 0.25; *n* = 20; wing fanning, y = 0.10x + 24.41; $r^2$ = 0.10; n = 10.

Figure 2.2a

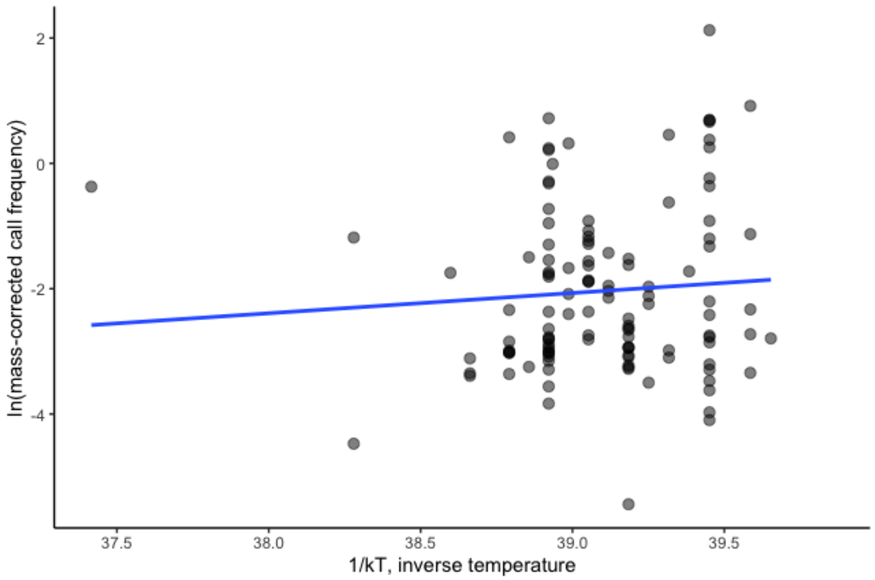

Figure 2.2b

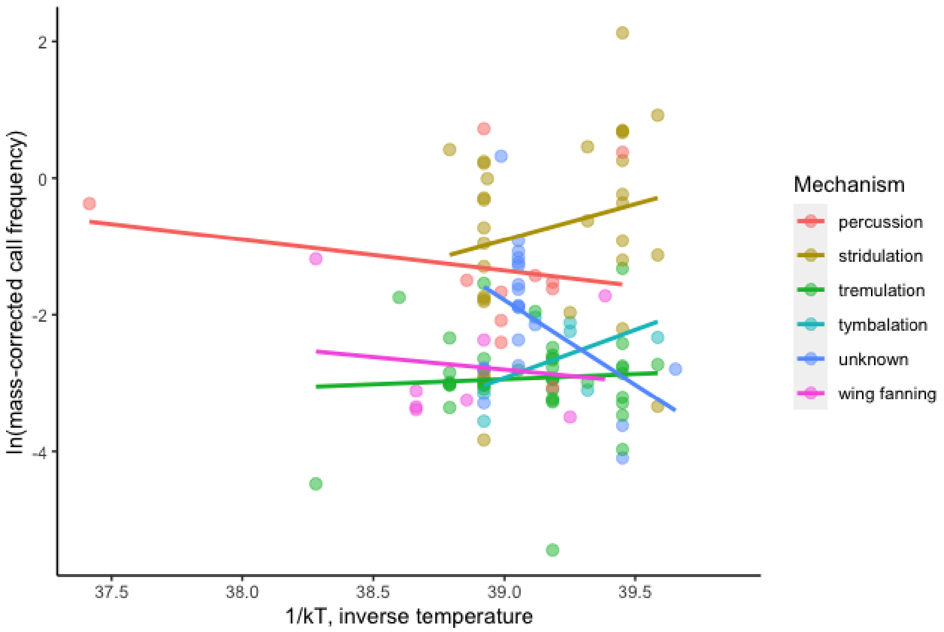

**Figure 2.2.** Relationship between the natural logarithm of mass-corrected call frequency (cycles $s^{-1} \cdot M^{1/4}$; equation (1.2)) and inverse absolute temperature, $1/kT$, where $k$ is Boltzmann's constant and $T$ is the absolute temperature in degrees Kelvin, (a) across all substrate-borne signals ($y = 0.32x - 14.68$; $r^2 = 0.01$; $n = 119$) and (b) when grouped by sound production mechanism. Note that equation (1.2) predicts a slope of -0.65. Percussion, $y = -0.45x + 16.32$; $r^2 = 0.04$; $n = 11$; stridulation, $y = 1.05x - 42.05$; $r^2 = 0.05$; $n = 30$; tremulation, $y = 0.15x - 8.81$; $r^2 = 0.00$; $n = 42$; tymbalation, $y = 1.40x - 57.58$; $r^2 = 0.29$; $n = 7$; unknown, $y = -2.48x + 94.79$; $r^2 = 0.20$; $n = 20$; wing fanning, $y = -0.37x + 11.50$; $r^2 = 0.02$; n = 9.

Figure 2.3a

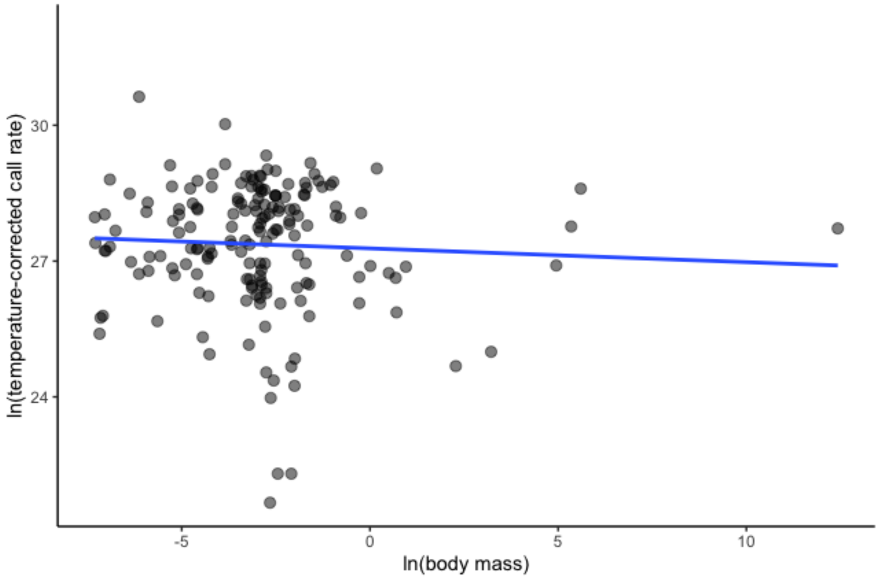

Figure 2.3b

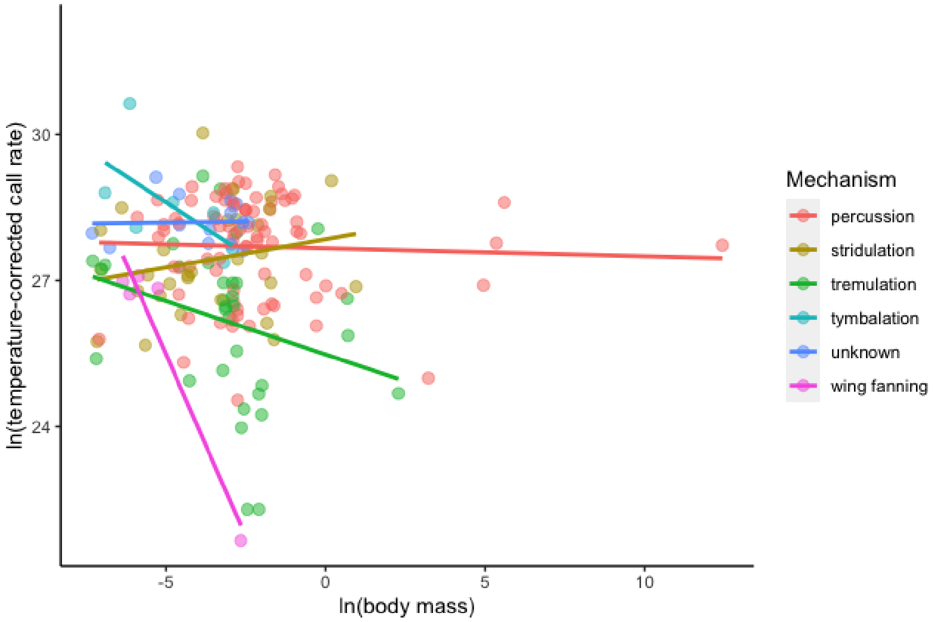

**Figure 2.3.** Relationship between the natural logarithm of temperature-corrected call rate (calls $s^{-1}$ • $e^{E/kT}$; equation (1.3)) and the natural logarithm of body mass (in grams) (a) across all substrate-borne signals ($y = -0.03x + 27.28$; $r^2 = 0.00$; $n = 171$) and (b) when grouped by sound production mechanism. Note that equation (1.3) predicts a slope of -0.25. Percussion, $y = -0.02x + 27.66$; $r^2 = 0.00$; $n = 83$; stridulation, $y = 0.12x + 27.84$; $r^2 = 0.05$; $n = 29$; tremulation, $y = -0.22x + 25.48$; $r^2 = 0.08$; $n = 33$; tymbalation, $y = -0.43x + 26.46$; $r^2 = 0.41$; $n = 7$; unknown, $y = 0.01x + 28.23$; $r^2 = 0.00$; $n = 14$; wing fanning, $y = -1.50x + 17.99$; $r^2 = 0.93$; n = 5.

Figure 2.4a

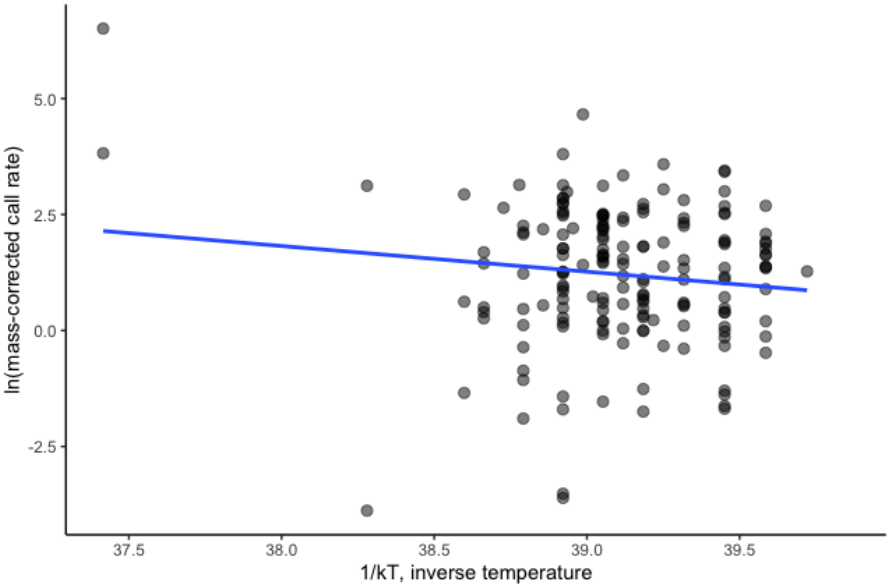

Figure 2.4b

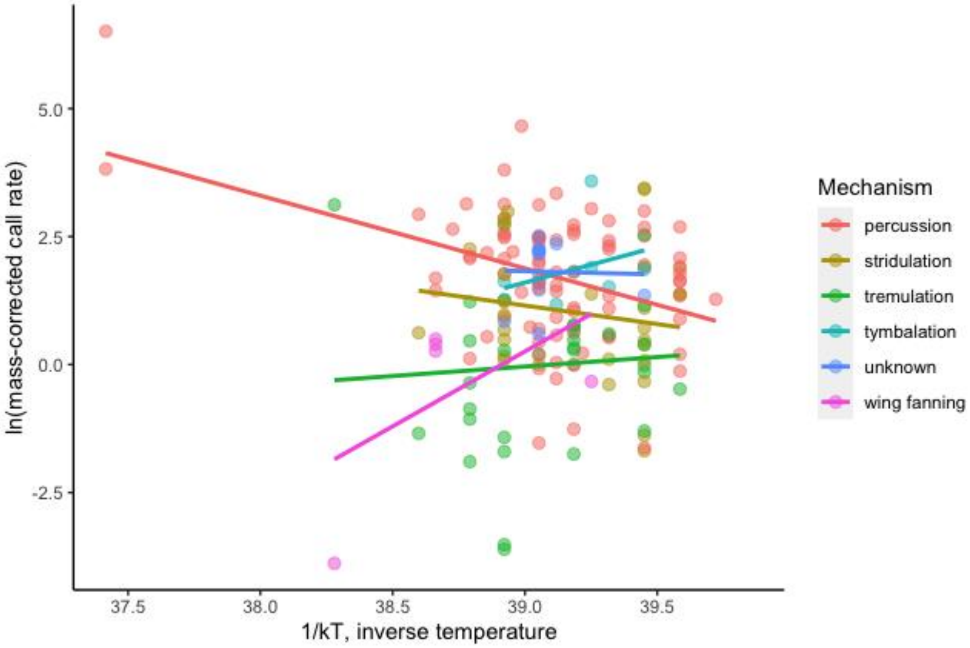

**Figure 2.4.** Relationship between the natural logarithm of mass-corrected call rate (calls $s^{-1}$ • $M^{1/4}$; equation (1.3)) and inverse absolute temperature, $1/kT$, where $k$ is Boltzmann's constant and $T$ is the absolute temperature in degrees Kelvin, (a) across all substrate-borne signals ($y = -0.55x + 22.86$; $r^2 = 0.01$; $n = 171$) and (b) when grouped by sound production mechanism. Note that equation (1.3) predicts a slope of -0.65. Percussion, $y = -1.42x + 57.34$; $r^2 = 0.16$; $n = 83$; stridulation, $y = -0.72x + 29.40$; $r^2 = 0.03$; $n = 29$; tremulation, $y = 0.37x – 14.48$; $r^2 = 0.00$; $n = 33$; tymbalation, $y = 1.39x – 52.74$; $r^2 = 0.12$; $n = 7$; unknown, $y = -0.13x + 6.81$; $r^2 = 0.00$; $n = 14$; wing fanning, $y = 2.93x – 113.85$; $r^2 = 0.30$; n = 5.

# CHAPTER 3 ANTHROPOGENIC NOISE AND THE BIOACOUSTICS OF TERRESTRIAL INVERTEBRATES

Maggie Raboin and Damian O. Elias

Originally published in the *Journal of Experimental Biology* (2019; **222**, 12) and reproduced here with the permission of Damian O. Elias

## 3.1 ABSTRACT

Anthropogenic noise is an important issue of environmental concern owing to its wide-ranging effects on the physiology, behavior and ecology of animals. To date, research has focused on the impacts of far-field airborne noise (i.e., pressure waves) on vertebrates, with few exceptions. However, invertebrates and the other acoustic modalities they rely on, primarily near-field airborne and substrate-borne sound (i.e., particle motion and vibrations, respectively) have received little attention. Here, we review the literature on the impacts of different types of anthropogenic noise (airborne far-field, airborne near-field, substrate-borne) on terrestrial invertebrates. Using literature on invertebrate bioacoustics, we propose a framework for understanding the potential impact of anthropogenic noise on invertebrates and outline predictions of possible constraints and adaptations for invertebrates in responding to anthropogenic noise. We argue that understanding the impacts of anthropogenic noise requires us to consider multiple modalities of sound and to cultivate a broader understanding of invertebrate bioacoustics.

## 3.2 INTRODUCTION

Anthropogenic acoustic noise (see Glossary, Table 3.1.) is widely recognized as an issue of environmental concern (Barber et al., 2011b; Shannon et al., 2016). Noise created by ever growing transportation networks and human activities associated with economic development has become so prevalent that it has penetrated some of the quietest places on Earth. For example, 63% of US protected public lands have background noise levels double that of environmental background noise levels (Buxton, McKenna, et al., 2017). Importantly, the acoustic characteristics of anthropogenic noise differ from those of environmental noise (e.g., sound produced by wind, rain, conspecifics, heterospecifics); thus, it represents a novel challenge for animals. For vertebrates, the impact of noise is multifaceted. It has been found to have negative consequences for mating and courtship behavior, predator–prey dynamics, movement, habitat selection and physiology (Shannon et al., 2016).

However, the impact of anthropogenic noise on invertebrates has largely gone unstudied (Morley et al., 2014; Shannon et al., 2016). Although invertebrates comprise 97% of animal species on Earth, and are important in most ecological processes, only 4% of the work on noise and wildlife has been on invertebrates (Shannon et al., 2016). Viewed with an evolutionary history perspective, this skew becomes even more dramatic. The ability to hear, which requires a specialized organ or organs, evolved from a single ancestor in vertebrates (Manley, 2012), whereas the ability to hear far-field airborne sounds (see Glossary, Table 3.1.) evolved independently at least 24 times in insects alone (Greenfield, 2016), and likely many more times in invertebrates. Invertebrates send and receive sound in highly diverse ways; thus, the ways in which anthropogenic noise affects invertebrate behavior are likely vast and complicated.

In this Review, we focus on the effects of anthropogenic noise on acoustically mediated behaviors in terrestrial invertebrates. We define acoustics in the broad sense, as any exchange of information that occurs via mechanical waves propagating in a medium (Fig. 3.1.). Acoustics in terrestrial environments are extensive and their simplest configuration includes airborne far-field sound (pressure waves), as well as airborne near-field sound (particle motion; see Glossary) and substrate-borne sound (see Glossary, Table 3.1.).

For sounds transmitted through air, the power produced via waves is a product of pressure and particle velocity (Kinsler et al., 1999). Close to the sound source (or in the near-field), particle velocity dominates, whereas further from the sound source (or far-field), pressure waves dominate (Kinsler et al., 1999). This physical phenomenon is partially driven by the fact that pressure attenuates less with distance (1/r, where r is the distance from the source) than do particle movements ($1/r^2$) (Jacobsen, 2007; Kinsler et al., 1999). In a general sense, the near-field only occurs at a distance of approximately 0.5–1 wavelength from the source (Jacobsen, 2007; Kinsler et al., 1999), whereas far-field sound waves (pressure waves) can travel many meters, thus dominating long-range airborne communication in animals.

Substrate-borne sounds are waves transmitted through or on the surface of a solid substrate. Solid substrates are an inherently more complex medium for transmission than air or water. Contrary to airborne or waterborne signals (see Glossary, Table 3.1.) that travel through a single medium, substrate-borne signals often travel through multiple media with differing properties and many articulating surfaces and boundaries (Elias & Mason, 2014). Additionally, substrate-borne waves can take multiple forms beyond longitudinal waves, depending on the material, geometry and/or size of the medium (Elias & Mason, 2014). The nature of a substrate (e.g., plants, rocks, soil, litter, wood) has major implications for the types of waves transmitted (e.g., longitudinal, transverse, bending, Rayleigh), the distance sound travels, the speed at which different frequencies travel and the optimal frequencies for transmission (Aicher & Tautz, 1990; Brownell, 1977; Hill, 2008b; Michelsen et al., 1982). The diversity of possible substrates introduces many possibilities regarding distortion in the spectral and temporal domain of signals.

The study of the interplay between the acoustics of terrestrial vertebrates and anthropogenic noise has been dominated by animals using pressure waves in air (airborne far-field) with few, but notable, exceptions (Mortimer et al., 2018; Narins, 1990, 2001; Shier et al., 2012). However, terrestrial invertebrates routinely use all three types of sound. At the same time, anthropogenic activities are known to produce noise in each modality. Here, we attempt to bridge the gap between two fields of study: invertebrate bioacoustics and anthropogenic noise. By mining known information (or current understandings) about the mechanisms of invertebrate bioacoustics, the characteristics of anthropogenic noise and the ways in which animals adapt to noise, we have come up with a framework for investigating and understanding the potential impact of anthropogenic noise on invertebrates.

We have organized our discussion into three main categories that correspond to three interrelated types of sound: far-field pressure waves, near-field particle motion and substrate-borne waves. For each category, we present what little information is known about the impact of anthropogenic noise on invertebrates. In addition, we make predictions about the ways in which noise can affect communication, including detection, by focusing on the mechanisms invertebrates use for sending and receiving acoustic information. We also discuss how invertebrates might adapt to anthropogenic noise in each acoustic modality and the various constraints inherent to each sound type. In Fig. 3.2, we lay out hypotheses on how invertebrates may adjust signal characteristics in order to avoid the impacts of anthropogenic noise if there is substantial overlap between noise and communication signals (masking; see Glossary, Table 3.1.). Finally, with the goal of more broadly understanding anthropogenic noise as an environmental issue, we outline our thoughts on the most pressing lines of inquiry for research in each modality.

## 3.3 AIRBORNE SOUND

### Far-field

Of the modalities of sound that invertebrates use, airborne sound has by far received the most attention, despite the fact that it is the least common modality for acoustic communication. Seven orders of insects (Coleoptera, Diptera, Hemiptera, Lepidoptera, Mantodea, Neuroptera and Orthoptera; Greenfield, 2016) are known to use far-field sound (600 to >130,000 Hz; Schmidt & Balakrishnan, 2015). Their calls can contain information about species identity (Hoy et al., 1982), the caller's location (Cade, 1975; Doherty, 1985) and different aspects of mate quality (Tuckerman et al., 1993; Wagner & Reiser, 2000), as well as fighting ability (Brown et al., 2006). In addition, some species of flies eavesdrop on calling Orthoptera to locate and parasitize them (Cade, 1975). Finally, many species use far-field sounds to detect, avoid or deter predators. For example, some species rely on far-field ultrasound to detect and avoid echolocating bat predators when they are being pursued, whereas others produce defensive acoustic signals to ward off predators (ter Hofstede & Ratcliffe, 2016).

Thanks to a great effort to understand the impact of specific noise sources on vertebrates that use far-field sounds (Shannon et al., 2016), we have a good understanding of the noise sources likely to impact invertebrates that communicate in the far-field. Anthropogenic noise sources such as traffic on roads and railways (10–10,000 Hz up to 50,000 Hz; Hayek, 1990; Talotte et al., 2003), oil, gas and wind development (compressor noise <20–5000 Hz, wind turbines <50,000 Hz; Barber et al., 2011; Bunkley et al., 2017; Long et al., 2011), military activities (Larkin et al., 1996) and general urban environments (0–22,0000 Hz; Wood & Yezerinac, 2006) create noise that overlaps with the frequency ranges of signals and cues (see Glossary, Table 3.1.) used by invertebrates. Anthropogenic noise sources either produce intermittent noise (traffic on roads and railways, military activities, oil and gas development) or continuous noise (wind turbines, general urban environments); the constancy of the noise can have implications for masking, as well as other impacts (i.e., distraction; Table 3.2.), and likely has implications for the ability of invertebrates to habituate to particular sources of anthropogenic noise (Barber et al., 2009).

### *Impacts of airborne noise*

One of the most common and likely consequences of noise from anthropogenic activities for far-field communication is masking. Masking happens when noise co-occurs with an acoustic signal or cue, thus making it difficult or impossible for animals to assess the information encoded therein. For invertebrates where males use far-field sounds to call to females, such as field crickets and katydids, masking by road noise renders females unable to detect or locate males for mating (Bailey & Morris, 1986; Bent et al., 2018; R. Schmidt et al., 2014). Similarly, male grasshoppers that locate females by their calls are less responsive to calling females in the presence of noise but are nonetheless accurate when turning in their direction (Reichert, 2015). Masking noise also decreases the ability of the parasitoid fly *Ormea ochracea* to localize calls of their host cricket (N. Lee & Mason, 2017). For some animals, masking of courtship songs may change the preference functions of choosers. For example, in the grasshopper *Chorthippus biguttulus*, masking noise significantly increases female preference for some traits and decreases it for others, leading to a decreased overall responsiveness of females to male signals (Reichert & Ronacher, 2015). However, masking noise does not always change a chooser's preference. For example, Einhäupl et al., (2011) found that individual male songs preferred by female grasshoppers (*C. biguttulus*) without noise present also elicited responses by females at higher amplitudes of white noise than songs that were not preferred. Finally, rather than suffering the consequences of their signals being masked in the presence of noise, some invertebrates put less energy into calling by shortening calls (which likely diminishes their effectiveness) (Orci et al., 2016) or by stopping calls altogether (Costello & Symes, 2014).

Masking by anthropogenic noise might impact invertebrate predator–prey dynamics, especially between some invertebrate species and their bat predators. Recent studies have found that some bat species alter their foraging patterns (Bunkley et al., 2015; Schaub et al., 2008) or are less efficient foragers in the presence of anthropogenic noise (Siemers & Schaub, 2011a). Although this evidence suggests invertebrates experience predation relief when noise is present, the signals and cues used by invertebrates to hear and flee approaching predators may also be masked. For example, most flying insects use acoustic cues to detect predators, and some produce defensive signals to avoid or deter predators (ter Hofstede & Ratcliffe, 2016). Masking of these signals and cues might increase predation pressure on invertebrates where noise is present; however, these dynamics have yet to be tested.

### *Strategies to avoid masking*

Invertebrates that transmit far-field sounds in noisy environments have multiple ways of overcoming the challenges associated with anthropogenic noise. First, they can avoid noise spatially by moving away from areas heavily impacted by human activities. Although there is no direct evidence of this in invertebrates, Bunkley et al. (2017) found that grasshoppers and camel crickets were less abundant at gas drilling sites with noise than those without. Second, animals may avoid anthropogenic noise temporally, by calling at times when noise is absent or reduced. However, one source of noise, road traffic, is predictably most intense during dawn and dusk (rush hour), times when many invertebrates concentrate their calling activity (Luther & Gentry, 2013). Researchers have suggested that it is unlikely that invertebrates will be able to temporally shift calling because there are increased costs to calling at other times of day, owing to suboptimal atmospheric conditions, particularly at sunset (Van Staaden & Römer, 1997). In addition, short-term temporal activities for some invertebrates might be constrained by phylogenetic history (Bao-sen Shieh et al., 2015). Third, like some vertebrates, invertebrates could increase the amplitude of their calls (Lombard effect) (Nemeth & Brumm, 2010). However, to date, there is no evidence that this occurs. Finally, animals can alter their signals to avoid calling in masked frequencies or, alternatively, increase the intensity of masked frequencies. This has been found to be the case for some invertebrate species. For example, male grasshoppers and cicadas shift their songs to higher frequencies in the presence of noise (Lampe et al., 2012, 2014; Shieh et al., 2012).

On the receiving end, listening animals may be able to overcome masking by anthropogenic noise using a variety of neurological mechanisms, including frequency tuning, where receivers are most sensitive to the call frequencies that contain the most energy (Schmidt & Römer, 2011). Receivers might also use spatial release from masking (see Glossary, Table 3.1.) and/or active amplification mechanisms (Mhatre & Robert, 2013; Morley & Mason, 2015; Romer, 2013; Schmidt & Balakrishnan, 2015). All of these strategies have been demonstrated in invertebrates that contend with environmental noise, but they have yet to be found in response to anthropogenic noise. It is critical that future work seeks to understand neurological strategies for avoiding or compensating for anthropogenic noise.

### *Constraints to plasticity*

Most invertebrates produce far-field sound with hardened sclerotized structures. For example, many invertebrates produce calls by rubbing together structures on their forewings, or tegminal stridulation (see Glossary, Table 3.1.), coupled with a resonating structure. This sound-production mechanism requires a hardened file of teeth and a scraper that is dragged across the teeth to produce vibrations (see Glossary, Table 3.1.; Bennet-Clark, 1999; Koch et al., 1988; Montealegre-Z & Mason, 2005). For species that use this mechanism, the frequencies they can produce are driven by the shape of the hardened structures as well as the speed of the scraper movement (Bennet-Clark, 1999; Chivers et al., 2017; Koch et al., 1988). Song frequency is also highly dependent on resonator geometry, with some tree crickets able to produce different frequencies using multiple resonant modes of their wings (Mhatre et al., 2012). Regardless, it is likely that most invertebrate species are constrained in their ability to plastically adjust the spectral properties of signals. Interestingly, Lampe et al., (2014) found developmental plasticity in response to anthropogenic noise, whereby grasshoppers raised under noisy conditions produce higher-frequency songs as adults. Similar predictions can also be made for invertebrates that use other sound-producing mechanisms such as tymbalation, percussion, fluid compression and aerodynamic sound, as these also use sclerotized structures to produce sound (Chapman, 1998).

Across and within invertebrate species that produce far-field sound, active plasticity in response to noise may be partly limited by constraints resulting from their small body sizes. The frequency and intensity of far-field calls that insects can produce is highly correlated with size (Bennet-Clark, 1998; Simmons, 1995). In general, larger individuals can produce louder, lower-frequency sounds and receive lower-frequency sounds than smaller invertebrates (Bennet-Clark, 1998); thus, call frequency is often an honest signal of size in insects (Simmons, 1995). These dynamics will likely limit the use of frequency-shift mechanisms in response to anthropogenic noise by some insects.

Finally, it is important to consider the environment and ecological community in which invertebrates are calling when evaluating the potential impacts of, and adaptations to, masking by anthropogenic noise. Invertebrates face constraints to the frequencies and timing of their calling brought on by habitat structure (attenuation and distortion), masking by other calling animals and predation (Romer, 2013; Schmidt & Balakrishnan, 2015). For example, many crickets and katydids live in assemblages where they are already partitioning the spectral or temporal aspects of their calls so that they do not overlap with one another (Gogala & Riede, 1995; Jain et al., 2014; Schmidt et al., 2011). In these communities, it is unlikely that all species will be able to avoid masking by anthropogenic noise while maintaining their spectral or temporal partitioning.

### Near-field

Near-field sound attenuates quickly relative to far-field sound, and conventional thought has been that its detection by terrestrial invertebrates is physiologically limited to less than a wavelength from the source (Kinsler et al., 1999). Thus, research on near-field communication among terrestrial invertebrates has primarily focused on a limited number of animals that communicate at close range and detect near-field sound via the Johnston's organ (see Glossary, Table 3.1.; flies, mosquitoes, bees; Gibson & Russell, 2006; Göpfert & Robert, 2002; Tsujiuchi et al., 2007) or filiform hairs (e.g., trichobothria) sensitive to particle motion (crickets, spiders; Barth, 2000; Kämper & Kleindienst, 1990). However, many terrestrial invertebrates are covered in innervated hairs, and particle motion is a rich source of information; therefore, many invertebrates are likely to have some capacity for detecting particle motion that has been underappreciated. This hypothesis, however, needs to be assessed further.

Near-field receptors are exquisitely sensitive, with deflections as small as 1 Å triggering neural responses (Humphrey & Barth, 2008; Shimozawa & Kanou, 1984). These receptors are generally tuned to low frequencies (<500 Hz) (Shamble et al., 2016; Wang et al., 2000). The tuning of each receptor depends primarily on its length, diameter and mass (Barth et al., 1993). Invertebrates use near-field receptors in mating interactions (Lapshin & Vorontsov, 2017; Tauber & Eberl, 2003), to forage (Barth & Höller, 1999; Kirchner, 1994), to detect incoming predators (Tautz & Markl, 1978) and during antagonistic interactions (Santer & Hebets, 2008).

Near-field anthropogenic noise has been overlooked in the literature thus far. However, all sources of airborne anthropogenic noise produce particle motion, as it is inherent to the production of airborne sound (Kinsler et al., 1999). Thus, in the presence of noise, invertebrates that communicate with near-field sound may be subject to a host of consequences, from masking to injury. Noise sources that have a large amount of energy in frequencies below 500 Hz, such as noise from roads (Hayek, 1990), railways (Talotte et al., 2003), and oil and gas development (Barber et al., 2011b), are the most likely candidates to produce near-field noise relevant to invertebrates.

At present, no direct evidence exists to support the idea that anthropogenic noise impacts near-field communication. However, one study by Samarra et al., (2009) found that near-field white noise hinders the ability of female *Drosophila montana* to detect and recognize male courtship song when it falls within the same frequency bands. In addition, a host of studies contain new information that expands our understanding of near-field communication in ways that suggest invertebrates may be less robust to the effects of anthropogenic near-field noise than previously thought.

First, near-field communication may take place at much longer distances than once suspected. Previous physical modeling and measurements suggested that near-field communication could only occur across small distances (1–70 cm), such as when animals are flying next to each other in a swarm (Aldersley et al., 2017) or interacting at close distances (Santer & Hebets, 2008; Tauber & Eberl, 2003). However, Shamble et al. (2016) demonstrated with behavioral and physiological data that jumping spiders can detect acoustic energy at distances of at least 3 m using near-field receptors. Similarly, Menda et al., (2019) demonstrated that mosquitoes can detect sound up to 10 m away using their antennae. Furthermore, Zhou & Miles (2017) presented models showing that small fibers (>1 μm), such as those used as near-field receptors, move with the surrounding medium. This scenario suggests that thin hairs will move in response to a large range of stimuli, even those produced at long distances. Additionally, some invertebrates, such as mosquitoes and flies, employ near-field receptor organs that actively amplify quiet signals and provide directional sensitivity (Gopfert et al., 2005; Göpfert & Robert, 2001; Morley et al., 2018). Together, these pieces of evidence extend the effective range of anthropogenic near-field noise to at least 10 m and potentially much further.

Second, invertebrate near-field receptors are likely able to detect a much wider range of frequencies than previously thought. In the past, research mainly focused on the detection of low frequency particle motion, because it was thought that biologically relevant cues such as wind and predator/prey movements are also dominated by low frequencies (Barth & Höller, 1999). More recent work, however, has demonstrated that near-field receptors can respond to a wider range of frequencies than previously thought (Bathellier et al., 2012; Zhou & Miles, 2017), and that biologically relevant stimuli also likely contain a broad range of frequencies (Casas et al., 2008). Zhou and Miles (2017), for example, suggested that thin fibers move in response to a large range of frequencies. For example, spider silk, an important near-field detector for many spiders, could measurably capture airflow over frequency ranges spanning infrasound to ultrasound (1–50,000 Hz) (Zhou and Miles, 2017). In another study, Bathellier et al. (2012) used particle image velocimetry (PIV) to demonstrate that spider and cricket filiform hairs are extremely sensitive at much higher frequencies than previously suspected.

### *Strategies to avoid masking*

Although more research is needed, new understandings of near-field sound and receptors suggest that terrestrial invertebrates are likely to be vulnerable to near-field noise in very fundamental ways. Nevertheless, invertebrates that experience negative impacts of anthropogenic noise have a few important tools for avoiding or mitigating these impacts. First, relative to avoiding other types of acoustic noise, it could be especially effective for invertebrates to move a few meters away from the sound source when possible. Second, some species have shown the physical ability to adjust the frequencies of their signals. For example, male and female mosquitoes modulate near-field flight frequencies during courtship (Cator et al., 2009; Gibson & Russell, 2006). Third, some invertebrates use behavioral strategies, such as clustering flight tones in swarms during mating, to reduce acoustic interference to near-field signals (Aldersley et al., 2017). And fourth, near-field receptors of some invertebrates may have the capacity to avoid harmful effects of noise. For example, some invertebrates have nearfield receptors with active, non-linear tuning, where the tuning of receptors is amplitude dependent (Albert & Kozlov, 2016; Göpfert & Robert, 2002). In these cases, animals may use non-linear tuning to avoid injury to their receptors when noise is loud. Additionally, there is some evidence that this mechanism may be useful for spatial release from masking (see Glossary, Table 3.1.; Morley et al., 2018). These examples likely represent just a small sample of the potential strategies available to invertebrates for avoiding near-field noise. Much more research is needed to understand the prevalence of near-field communication and how it is affected by anthropogenic noise.

## 3.4 SUBSTRATE-BORNE SOUND

Substrate-borne acoustics have largely been left out of the study of anthropogenic noise and its impacts on animals. This is despite the fact that anthropogenic sources create substrate-borne noise (Dowding, 1996; Forman, 2000; Heckl et al., 1996), and over 90% of all animals use some type of substrate-borne sound (R B Cocroft & Rodriguez, 2005). Invertebrates rely on substrate-borne sounds for many important aspects of their lives, including as a way to collect information about their environment (T. A. Evans et al., 2005), to communicate with conspecifics during courtship (Elias et al., 2003; D. Ota & Čokl, 1991), in competition (De Souza et al., 2011; Elias et al., 2008; Yack et al., 2001) and cooperation (Baroni-Urbani et al., 1988; Endo et al., 2019; Michelsen et al., 1986), to detect prey during foraging (Fertin & Casas, 2007; Klärner & Barth, 1982; Pfannenstiel et al., 1995), to avoid predators (Castellanos & Barbosa, 2006; Rohrig et al., 1999) and to facilitate symbiotic relationships (DeVries, 1990).

Invertebrates that communicate with substrate-borne sound most often use frequencies <1000 Hz, because low frequencies experience little attenuation in substrates (Bennet-Clark, 1998; Čokl & Virant-Doberlet, 2003). At the same time, human activities such as airport traffic (Fidell et al., 2002), construction (Dowding, 1996) and use of railroads (Heckl et al., 1996), are known to produce low-frequency vibrations (<1000 Hz). Previous work also suggests that because the majority of spectral energy of road noise is in low frequencies (<2000 Hz), roads are likely to represent significant sources of substrate-borne noise (Forman, 2000). Substrate-borne vibrations do not attenuate quickly and can be detected up to 3000 m from the source (Mortimer et al., 2018). Given that many animals have such sensitive receptors of substrate-borne sound, they are likely to detect anthropogenic sources from even longer distances (Barth & Geethabali, 1982; Mortimer et al., 2018; Shaw, 1994). Anthropogenic sources can produce substrate-borne noise in two ways. First, sources can directly vibrate the earth, producing waves that travel through or on its surface. Second, sources may produce airborne noise that secondarily induces vibrations in substrates (sympathetic vibrations; see Glossary, Table 3.1.). In general, the former produces vibrations that are louder and will travel further than the latter, because sound loses energy at any substrate boundary (Caldwell, 2014). However, invertebrate receptors are likely to be sensitive to both types of substrate-borne sound.

Variation in the types and structures of substrates is likely to influence how, or whether, anthropogenic noise affects invertebrates that communicate with substrate-borne sound. First, the material properties and dimensions of a substrate determine the likelihood that airborne noise will produce sympathetic vibrations (Press & Ewing, 1951), the propagation of vibratory noise

(Elias & Mason, 2011) and its intensity (Hill, 2008b). For instance, substrate-borne vibrations do not propagate as well through materials such as sand as they do through plant material (Elias & Mason, 2011), so invertebrates that live on plants or leaf litter might contend with a noisier signaling environment in the presence of human activities than those that live on sand. Second, material properties and dimensions determine the resonance, attenuation and filtering of a given substrate (Kinsler et al., 1999). Invertebrates often take advantage of substrate properties to enhance the efficacy of their signaling by preferentially signaling with frequencies that transmit well through the substrate (Cocroft et al., 2010; Cokl et al., 2005; Elias et al., 2004, 2010). In some cases, vibratory noise from anthropogenic sources could stimulate the resonant characteristics of substrates and mask the frequencies used by invertebrates for communication. Complicating matters further, some substrates reflect sound waves (i.e., echoes and reverberations). For example, noise propagated through rod-like substrates (e.g., stems) could drive the production of standing and/or reflected waves that would distort the properties of signals (Michelsen et al., 1982; Miklas et al., 2001). Third, the boundary conditions of the substrates in question (i.e., substrate shape, articulating surfaces, heterogeneities in surface) can be complex and affect transmission in important ways (Magal et al., 2000). Finally, an individual's signaling environment can include a diversity of substrates, including combinations of natural or human-made materials, all of which differently influence how sound propagates (C. Wu & Elias, 2014). Currently, it is difficult to make predictions about the ways in which invertebrates will be affected by anthropogenic noise because little is known about the details of substrate-borne sound propagation in natural signaling environments (Elias & Mason, 2014).

*Impact of substrate-borne noise*

For the most part, researchers have investigated the impact of general substrate-borne noise disturbance (rather than anthropogenic noise) on communication by experimentally inducing white noise. Substrate-borne noise has been found to disrupt mating in a variety of contexts. For example, female stink bugs adjust the frequency of their signal in response to noise of similar frequencies but do not adjust temporal aspects of their signal when this is masked by noise (Polajnar & Čokl, 2008). In the presence of temporally disruptive substrate-borne noise, male stink bugs respond less frequently to female signals (Polajnar & Čokl, 2008). Wolf spiders that rely on substrate-borne signals for courtship are less likely to mate in the presence of white noise (Gordon & Uetz, 2012). Finally, male black-faced leafhoppers (which produce substrate-borne courtship signals with three distinct sections) cease signaling when white noise is played during the initial phase but not latter phases (Hunt & Morton, 2001). Interestingly, a handful of studies on substrate-borne noise and mating were motivated by the potential to use noise for pest management in agriculture (Polajnar et al., 2015). For example, researchers found that playing substrate-borne noise to mask the mating calls of leafhoppers results in reduced mating (Eriksson et al., 2012; Mazzoni et al., 2009; Nieri & Mazzoni, 2018). In addition, Hofstetter et al., (2014) reported reduced reproductive success, movement and survival of pine bark beetles in the presence of substrate-borne noise that spectrally overlapped with beetle signals.

Masking by anthropogenic noise is also likely to impact foraging and predator–prey relationships of invertebrates, as many animals use substrate-borne sound for finding prey or avoiding predators (Castellanos & Barbosa, 2006; Fertin & Casas, 2007). To date, no evidence exists that this is the case and only one study has investigated this dynamic. Wu & Elias (2014) experimentally induced vibratory white noise of different intensities in webs of European garden spiders and did not find a consistent decrease in prey-detection sensitivities. By contrast, studies investigating substrate-borne noise induced by wind indicate that some invertebrates exploit substrate-borne noise when hunting prey. The salticid spider (*Portia*) and the assassin bug (*Stenolemus bituberus*) are more likely to successfully hunt web-spiders in the presence of wind (Wignall et al., 2011; Wilcox et al., 1996). In these cases, substrate-borne noise is likely to mask vibrations that the predators produce during their approach.

### *Strategies to avoid masking*

Substrate-borne noise may be especially difficult for invertebrates to spatially avoid owing to the fact that it does not attenuate quickly (Kinsler et al., 1999). However, evidence exists that some species may be able to exploit gaps in noise and temporally avoid masking. Wind produces intermittent substrate-borne noise similar to anthropogenic noise sources such as traffic. Researchers found that male treehoppers (which produce substrate-borne courtship signals) preferentially signal during wind-free gaps rather than during experimentally induced wind gusts; females are less likely to respond to male signals during induced wind gusts, and natural treehopper populations are more likely to signal during times of day with less wind (McNett et al., 2010).

Invertebrates produce substrate-borne sound with a diverse array of mechanisms (e.g., percussion, stridulation; see Glossary), and the mechanism an animal uses is likely to affect the extent to which they will be able to shift their signaling frequency in the presence of noise. For example, Bunkley et al. (2017) found differential impacts of noise on the abundances of arthropod families that communicate with substrate-borne sound, potentially owing to the fact that a range of signaling mechanisms is used across families. Terrestrial arthropods use four major mechanisms to produce substrate-borne sound: percussion, stridulation, tymbalation and tremulation (see Glossary). Percussive sound is produced by collisions between parts of the body or between a part of the body and the substrate. These sounds are broadband at the source and the spectral information that arrives at the receiver is solely a result of filtering properties of the substrate (Elias & Mason, 2011). Thus, it is hypothesized that receivers are more likely to use information contained in the timing and/or amplitude of percussive signals than frequency (Elias & Mason, 2011). In the presence of substrate-borne noise, invertebrates that communicate with percussion are unlikely to be able to use frequency-shift mechanisms, such as narrowing the spectrum of signals, to overcome masking.

By contrast, tremulation mechanisms use simple muscular movements of the body and appendages to produce narrowband signals. The ability to shift the spectral properties of tremulation signals depends solely on muscle properties, suggesting that invertebrates that use tremulation will be able to modify the spectral content of their signals in the presence of noise. For example, female southern green stink bugs change the frequency of their tremulations in the presence of frequency-overlapping noise (Polajnar & Čokl, 2008). As mentioned above, invertebrates can also produce substrate-borne signals with stridulation and tymbalation. These mechanisms require specialized exoskeletal structures; when the individual produces vibrations, these structures concentrate acoustic energy to specific bandwidths. In this way, animals can maximize their signal efficacy in particular substrates. The ability of invertebrates to shift the frequency characteristics of signals when using stridulation and tymbalation is likely constrained by muscular physiology (how fast can muscles twitch) and the particular details of their sclerotized sound-producing structures. We do not yet know the extent to which these animals are able to shift the frequencies of their signals in the presence of noise. However, for all invertebrates that communicate with substrate-borne sound, spectral or temporal components of signals are often species- and plant-host specific (Cocroft et al., 2006; Cokl et al., 2005; McNett & Cocroft, 2008). Thus, even if senders can adjust these components to avoid masking by noise, receivers may not respond to the new signals.

## 3.5 FUTURE DIRECTIONS

Across the different communication modalities discussed in this Review, some common research needs have emerged that will need to be addressed to allow us to understand the potential impacts of anthropogenic noise on invertebrate communication. First, it is vital that noise from anthropogenic sources is adequately quantified. In the past, recording equipment developed to record sound that is audible to humans has been sufficient for recording sound relevant to most vertebrates. In order to record sound that is relevant to a broader taxonomic range, many have argued for recording far-field sound without the use of recording filters designed for human hearing (Francis & Barber, 2013a; Morley et al., 2014; Shannon et al., 2016). We echo that suggestion here. In addition, there is presently no straightforward method for measuring near-field anthropogenic noise. Although technologies such as PIV and hot wire anemometers have potential applications in this context (Bomphrey et al., 2005; Sane & Jacobson, 2006), PIV is expensive and has not been easily adapted for field applications, and hot wire anemometers do not have fine enough resolution to record particle motion relevant to invertebrates. Similarly, the recording of substrate-borne sound currently requires expensive laser vibrometer technology. This technology has only been employed once for measuring noise from anthropogenic activities (C. Wu & Elias, 2014), and it is not accessible to many researchers. Accelerometers are potentially low-cost alternatives to measure substrate-borne noise, although they are unsuitable for recording sound through many substrates given their weight (Cocroft et al., 2014). All in all, recording and quantifying near-field and substrate-borne anthropogenic noise is a major challenge, but with increased attention and focused effort, existing technologies could be adapted to fit this purpose.

Second, future research should seek to understand the variety of impacts that anthropogenic noise in each modality has on a diversity of invertebrate species. Studies should make sure to report the noise source, characteristics of the noise, the signaling environment (e.g., substrate type), signaling mechanisms and type of acoustic receivers of the animals of interest. Additionally, research should establish patterns of constraints and adaptations to noise in each modality and should address whether adaptations result in differential reproductive success.

Finally, it is pivotal that research seeks to understand how noise affects invertebrates under natural field conditions, particularly for invertebrates that use near-field and substrate-borne modalities. While laboratory studies are important, especially for isolating and manipulating sounds, it is difficult to extract meaningful information about the ecological implications of noise from their results. So far, the best studies in this regard combine data from field and laboratory settings (Lampe et al., 2012, 2014), or take advantage of heterogeneous noise in the landscape (Bunkley et al., 2017). For example, Bunkley et al. (2017) compared arthropod communities at sites developed for gas extraction that had gas compressors (noise) with those that did not have compressors (no noise). Results from these types of studies are critically important for understanding the impact of anthropogenic noise on invertebrates.

## 3.6 CONCLUSIONS

Anthropogenic noise is an issue of critical environmental concern, predicted to become an even greater problem with increasing population growth and land-use change. At the same time, invertebrates are experiencing major declines across ecosystems (Hallmann et al., 2017; Potts et al., 2010). The evidence presented in this Review, although limited, suggests that anthropogenic noise is likely to impact invertebrate communication in significant ways. Over the past decades, researchers have conducted important work to understand how anthropogenic noise affects vertebrate species (for excellent reviews, see Barber et al., 2011a; Brumm & Slabbekoorn, 2005; Francis & Barber, 2013; Ortega, 2012; Patricelli & Blickley, 2006; Radford et al., 2014; Shannon et al., 2016; Slabbekoorn & Ripmeester, 2008), but investigation into the ways it affects invertebrate life is incomplete. Vertebrates and invertebrates differ in substantive ways, including in the mechanisms they use for producing and receiving sound; critically, this informs how they can respond to noise and the constraints in doing so.

Throughout this Review, we have discussed the sound-producing mechanisms used by invertebrates and their respective vulnerabilities to anthropogenic noise for three types of sound – far-field, near-field and substrate-borne. For the most part, we have focused on how anthropogenic noise might affect the individual interactions of animals, but these dynamics are also important to understand for their bearing on communities and ecosystems (Francis et al., 2012). The majority of species on Earth are invertebrates; they are critical parts of ecosystems (Mulder et al., 1999; Yang & Gratton, 2014) and are food for many species (Morse, 1971). They also provide ecosystem services important for human life, such as pollination, nutrient cycling and waste removal (Losey & Vaughan, 2006; Noriega et al., 2018). The ways in which invertebrates are affected by and adapt to anthropogenic noise could have great implications for ecosystems and ecosystem services. We argue for the expansion of the focus of anthropogenic noise to include noise in near-field and substrate-borne modalities. Expanding our definition of anthropogenic noise and our focus of research will create a more holistic understanding of the potential reach of anthropogenic noise as a pollutant and will potentially lead to effective and efficient mitigation strategies.

## *Acknowledgements*

We thank Sarah Allen and Jim Wiegand for providing the initial inspiration for the formation of these ideas. We are grateful to all members of the Elias lab, Alexander Stubbs, Jesse Barber, Andrew Mason and three anonymous reviewers for their helpful comments on this manuscript. This work was supported by the University of Wyoming-National Park Service small grants program.

## 3.7 FIGURES

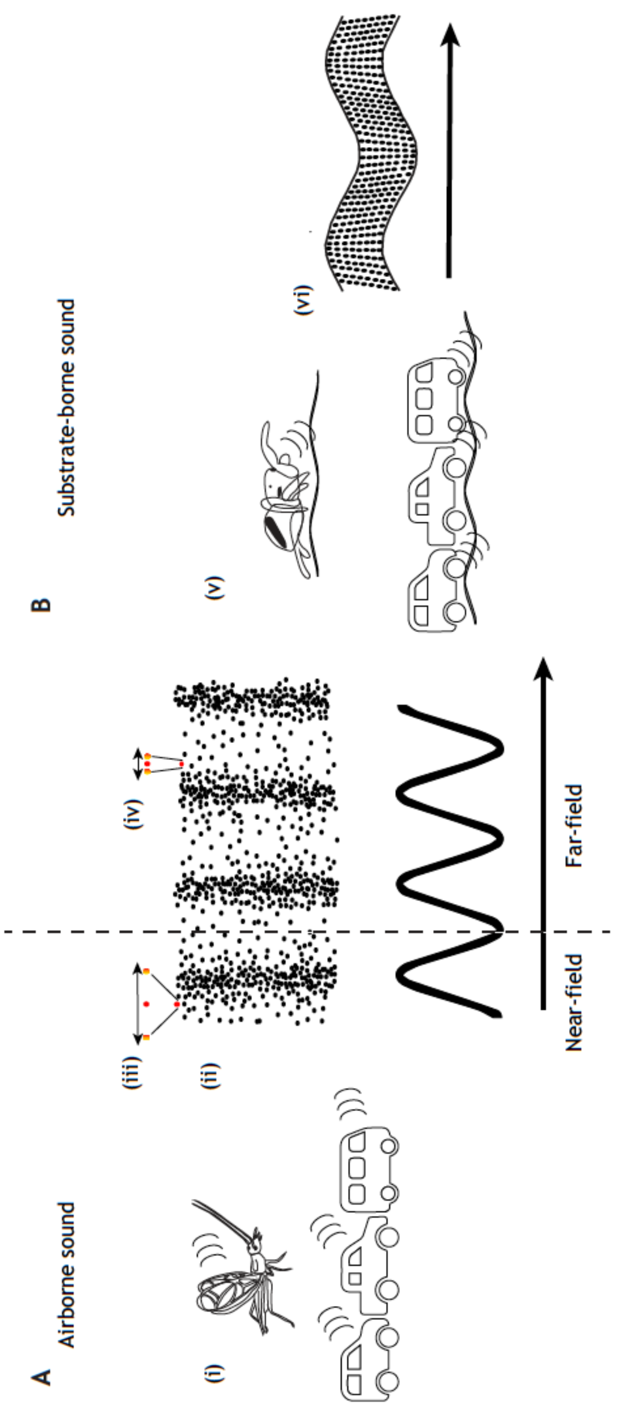

**Figure. 3.1**. Acoustic properties of airborne and substrate-borne sound. (A) (i) Both biotic and anthropogenic sources can produce airborne sound. (ii) Airborne sound waves are produced by air particle movements (movement of one air particle highlighted in red with double-headed arrows denoting amplitude of movement), and the resultant changes in air pressure (air pressure amplitude denoted by spacing of air particles shown in black) based on those particle movements are shown. Airborne sound waves can be categorized as either near-field or far-field depending on the distance from the sound source and the relative differences between particle motion or air pressure amplitude. Arrow denotes the direction of a propagating airborne sound wave (iii). In the near-field, air particle movement dominates relative to air pressure differences. Near-field sound occurs within one wavelength of the sound source. (iv) In the far-field, air pressure differences dominate over air particle movements. Far-field sound occurs at a distance of greater than one wavelength from the sound source. (B) (v) Both biotic and anthropogenic sources can produce substrate-borne sound. (vi) Substrate-borne waves are complex and can occur within or on the surface of a solid substrate (solid lines denote outline of solid surface). Arrow denotes the direction of a propagating substrate-borne sound wave.

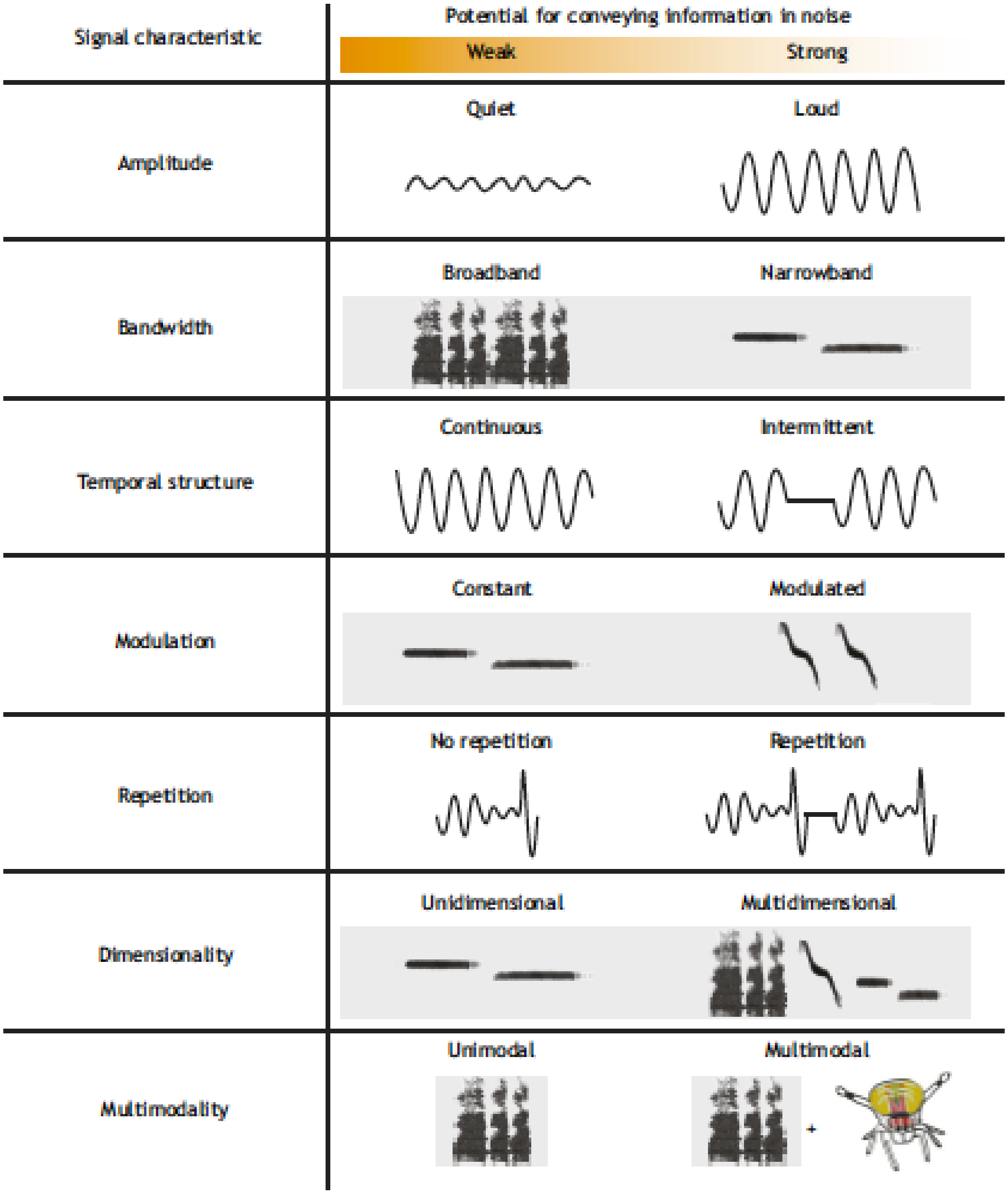

**Figure. 3.2.** Signal characteristics and their hypothesized robustness to masking noise. Column 1: signal information can be conveyed across multiple acoustic characteristics. Column 2: certain variations of each characteristic are predicted to be better at conveying information in the presence of masking noise than others (right to left, respectively). Information can be conveyed using temporal, amplitudinal (white box– wave form) and spectral (grey box– spectrogram) properties.

## 3.8 TABLES AND GLOSSARY

**Table 3.1.** Glossary

**Aerodynamic sound:** Sound production mechanism where the flow of fluid over a structure excites resonance properties of the structure.

**Airborne far-field sound:** Vibration propagating in air at a distance where sound pressure dominates, and sound particle velocity and sound pressure are in phase.

**Airborne near-field sound:** Vibration propagating in air at a distance where air particle velocity dominates and sound particle velocity and sound pressure are not in phase.

**Cue:** Act or structure produced by a sender that has information but has not evolved to elicit a response in a receiver.

**Fluid compression:** Sound-production mechanism where animals produce rapid changes in the local pressure of the medium (e.g. cavitation, ‘sonic boom’).

**Johnston’s organ:** Sensory organ found in the antennae of insects that can detect vibrations in the air.

**Masking:** Situation where a signal/cue co-occurs with noise thereby increasing the threshold for detection by the receiver.

**Noise:** Mechanical waves uncorrelated with any acoustic feature of interest to a receiver. May be anthropogenic (e.g. traffic, industry) or environmental (e.g. heterospecifics, rain, water, wind).

**Percussion:** Sound-production mechanism whereby animals produce vibrations using transient impacts of an appendage against another appendage or against the substrate.

**Signal:** Act or structure produced by a sender that has evolved to elicit a response in a receiver.

**Spatial release from masking:** A phenomenon whereby a signal/cue is more easily detected when spatially separated from noise.

**Substrate-borne sound:** Vibration propagating in a solid.

**Stridulation:** Sound-production mechanism whereby animals produce vibrations using two rigid structures that are rubbed against each other. At least one of the structures (the file) is ridged.

**Sympathetic vibrations:** Phenomenon whereby an airborne sound causes vibrations in a solid that was previously not moving.

**Tremulation:** Sound-production mechanism whereby animals produce vibrations using oscillations of a body part.

**Tymbalation:** Sound-production mechanism whereby animals produce vibrations using a tymbal, a corrugated structure on the exoskeleton.

**Vibration:** Mechanical waves propagating in a solid or fluid medium.

| Consequence | Invertebrate | Sound modality | Source |
|---|---|---|---|
| Distraction | Caribbean hermit crab (*Coenobita clypeatus*) | Airborne far-field | Chan et al., 2010; Walsh et al., 2017 |
| Processing errors | Earthworm | Substrate-borne | Darwin, 1892; Mitra et al., 2009 |
| Increased stress | Monarch butterfly larvae (*Danaus plexippus*) | Unclear, likely substrate-borne | Davis et al., 2018 |
| Developmental changes | Indian meal moth larvae (*Plodia interpunctell*a)<br>Field cricket (*Teleogryllus oceanicus*) | Airborne far-field | Huang et al., 2003; Gurule-Small and Tingnitella, 2018; 2019 |
| Decreased life span | Field cricket (*Teleogryllus oceanicus*) | Airborne far-field | Gurule-Small and Tingnitella, 2019 |

**Table 3.2.** Summary of literature examining the consequences of anthropogenic noise beyond masking for invertebrates

# CHAPTER 4 BUILT TO LAST A DAY: THE FUNCTION AND BENEFITS OF SPIDER MOUND NESTS

Maggie Raboin and Damian O. Elias

Originally published in the *Journal of Ethology* (2021; **127**) and reproduced here with the permission of Damian O. Elias

## 4.1 ABSTRACT

Nests are crucial to the survival of offspring and reproductive success of the animals that build them. These benefits are subject to change over time due to fluctuating conditions inside and outside of nests. For many species, nests are assumed to benefit offspring until they disperse and therefore, nest destruction prior to offspring dispersal results in reduced reproductive success for parents. However, the consequences of nest destruction to reproductive success, or lack thereof, remain largely unstudied across diverse taxa. Here, we experimentally investigate the function and benefits of nests of a mound-building spider. Mason spiders (*Castianeira* sp.) are wandering spiders that build intricate nests (mounds) on top of their egg sacs. Their offspring inhabit egg sacs at nest-sites for up to 7 months, including through winter. We find that despite requiring hundreds of collecting trips and many hours to construct, mason spider nests remain for a small portion of time that offspring occupy nest-sites. Our study finds that nest benefits change over time, likely explaining this dynamic. Nests greatly reduce the rate of predation and parasitism of egg sacs by 19.1% and offspring mortality within egg sacs due to abiotic factors by 19.9%. These effects are only present the few days following nest construction. Our study illuminates the idea that nest destruction does not always result in reduced reproductive success for nest builders. We suggest that nest durability, the ability of a nest to withstand environmental conditions, may be subject to natural selection and a critical, yet understudied, aspect of parental care.

## 4.2 INTRODUCTION

For many animals, early life stages are at higher risk of mortality from sources like predation, disease, and environmental fluctuations than other life stages (Clutton-Brock, 2001). To increase their reproductive success, some parents invest time and energy into protecting offspring by building protective structures. Benefits of protective structures like nests have been found across species. For example, nests increase reproductive success for many mammals (Reichman & Smith, 1990), birds (Mainwaring et al., 2014), reptiles (Angilletta et al., 2009), fish (Ishimatsu et al., 2007; Takegaki & Nakazono, 2000), and arthropods (Hieber, 1992b; Wyatt, 1986). However, the benefits of nests are unlikely to be static through time. From the day they are constructed, conditions outside of the nest like environmental conditions and predator dynamics, are constantly fluctuating and threatening to damage the nest and/or harm offspring.

The dynamic nature of nest benefits through time has great implications for how much parents invest in building and/or maintaining nests. Across species, this varies greatly. For example, some nests are actively maintained for years like those belonging to social animals that use nests for generations, including some termite mounds that are occupied for centuries (Erens et al., 2015). In contrast, many songbirds build nests are made to last one breeding season (Mainwaring et al., 2014), and still others, like some amphibians (Giaretta & Menin, 2004) and army ants (Schneirla et al., 1954), construct nests that only need to remain intact for hours to days.

Outside nests, the intensity, frequency, and predictability of environmental conditions may impact the length of time that nests benefit offspring. For example, rainfall has been implicated in nest destruction of vertebrate and invertebrate nests, sometimes zeroing the benefits of nests and leading to their abandonment by parents (Thompson & Furness, 1991; Rojas *et al.*, 2019). In other well-known cases, the presence of predators induces accelerated hatching or fledging of offspring. In these situations, the benefits of nests for aggregated, stationary life stages rapidly decrease as the risk of predation increases (Martin et al., 2018; Warkentin, 1995).

Inside nests, life history traits of species, like how much parental care early life stages require and the length of time that care is necessary, impact the rate that nest benefits decrease over time. For example, scientists have long recognized that the young of most species can be placed along an altricial to precocial spectrum (Augustine et al., 2019). Nests of altricial animals (species where young are born at earlier stages of development) need to stay in nests longer and the benefits of nests decay slowly, whereas many precocial animals do not need nests at all (Starck & Ricklefs, 1998). Over time and as offspring develop, the benefits of nests decrease until they are no longer necessary.

For most species, the length of time that nests benefit offspring and the amount of time that offspring occupy nest-sites are assumed to be inextricably linked. In fact, examples of nest-destruction prior to offspring dispersal are almost always reported to result in reduced reproductive success for nest-builders (Thompson & Furness, 1991; Rojas *et al.*, 2019). However, the consequences of nest destruction to reproductive success, or lack thereof, remains largely unstudied across diverse taxa. We investigate the consequences of nest destruction on reproductive success by untangling the length of time that offspring occupy nest-sites, the benefits of nest presence, and how those benefits change over time.

Our study focuses on the mason spider, *Castianeira* sp., wandering spiders of the northern Rocky Mountains, USA that cover their eggs with elaborate mound nests, protective structures that include both an egg sac and elaborate mound. While most spiders protect their eggs and young with protective structures that minimally involve investment in silk for egg sacs or webs (Hieber, 1992; Toyama, 1999), mason spiders construct mounds made of hundreds of pebbles, leaves and sticks, held together with silk. Our preliminary observations indicated that despite a large investment in parental care and the fact that offspring persisted at nest sites for many months, mason spider mounds are regularly destroyed. Why do mason spiders go through such effort to build a mound nest that only remains intact for a small portion of the time that offspring inhabit nest sites? We sought to answer this question by describing the details of parental care and life history of a mound-building spider for the first time. We then experimentally investigated the function of mason spider mound nests and how the benefits of mounds change over time. Finally, we discuss why nest duration is an important, yet understudied aspect of parental care.

## 4.3 MATERIALS AND METHODS

### *Study Site and Data Collection*

The mason spider studied here is an undescribed species in the *descripta* group of the genus *Castianeira* (Corrinidae) (Reiskind, 1969). The necessary taxonomic work for species determination of mason spiders is outside the scope of this study. Mason spider specimens have been deposited in UC Berkeley's Essig Museum (EMEC 1199520 – EMEC 1199527).

We studied mason spiders along the Snake River in Bridger-Teton National Forest, WY, USA, unceded lands of the Cheyenne, Eastern Shoshone, and Shoshone-Bannock nations (43°18'10.3"N 110°46'27.6"W; altitude 1800 m) in open habitats dominated by sage, alfalfa, and various grasses. These habitats have gravel soil with large rocks scattered throughout. Mason spiders lay egg sacs in the crevices of rocks and build their mounds on top (see Figure 4.1A, B; *Behavioral description*). We observed 1,368 mounds (June – September 2015-2018 and in the winter of 2017/18) and filmed the construction of 14 mounds using GoPro (HERO 4) cameras across 4 mound-building seasons. Each day, we deployed 3-4 GoPro cameras that were mounted on tripods and positioned one meter from nest sites so as not to disrupt mason spiders during mound construction. We describe mason spider mound-building behavior using observational data collected at field sites in combination with videos of mound construction. We analyzed the videos of mound construction using BORIS (Behavioral Observation Research Interactive Software) (Friard & Gamba, 2016) and ImageJ (MtrackJ) software (Schneider et al., 2012) to collect data on the number of collecting trips per hour and length of collecting trips.

### *Mound removal experiment*

We experimentally tested the impact of mason spider mounds on offspring survival over time. In 2017, we identified 188 egg sacs under construction and randomly assigned them to one of four treatment groups. For each treatment, we removed mounds (1) immediately following their completion (N=50), (2) 24 hours post-construction (N=51), and (3) 10 days post-construction (N=42). Control mounds (4) were never removed (N=45). All egg sacs remained in place until they were collected (range 24-109 days). Mound construction was determined to be completed when mason spiders did not return to the mound for 1 hour. We put a small dab of super glue on top of all mounds to ensure that they remained in place for duration of the treatment. The super glue was superficial; structurally reinforcing a few pieces of the mound and did not touch the egg sac. Treatment time intervals were chosen haphazardly based on field observations.

Egg sacs were randomly chosen to be collected in August (N=84) or October (N=104) of 2017. Egg sacs collected in August remained in place for 24 - 45 days (31.23 ± 5.08, mean ± SD) and egg sacs collected in October remained in place for 84 - 109 days (94.44 ± 5.00) before they were collected. Once collected, egg sacs were transported to UC Berkeley and dissected to determine offspring mortality in each egg sac (presented as a proportion - number of dead spiderlings and/or eggs divided by total offspring in egg sac), life stage (egg or spiderling), presence of mold or desiccation, and evidence of parasitism or predation (Figure 4.1C-E). Eggs were determined to be dead if they were desiccated or covered in mold. Egg sacs were determined to be parasitized if wasps or wasp larva were found in egg sacs and predated if egg sac had a large hole and was empty. Dissections were done blind to any information about treatment.

### *Statistical analyses*

All statistical tests were performed in R v.3.6.2 (R Core Team, 2020). We performed generalized linear models to assess the effect of mounds on mortality in mason spider egg sacs overtime. Egg sacs that were predated/parasitized resulted in 100% mortality of eggs. Therefore, we analyzed mortality due to predation or parasitism (biotic mortality) and desiccation or mold (abiotic mortality) separately. We first assessed the effect of mounds on predation/parasitism of mason spider egg sacs over time by using a generalized linear model with a binomial distribution and assigned presence/absence of biotic mortality as our response variable and treatment as our predictor variable.

Next, we assessed the effect of mounds on abiotic mortality in mason spider egg sacs over time. In our model, we assigned dead/live offspring as our response variable with the *cbind* function in R and treatment as our predictor variable. We accounted for overdispersion in our data by using a quasibinomial distribution.

## 4.4 RESULTS

### *Behavioral description: Mound-building*

Female mason spiders lay eggs and construct mound nests at field sites mid-July through the beginning of September (Figure 4.2A). To begin, a female constructs an egg sac in a small indentation in a rock by laying silk flush with the rock. The female then lays 8 - 36 orange eggs (18 ± 5.1, mean ± SD, N=151) and covers them with another layer of silk (Figure 4.1A). This layer of silk is tough and papery, with an opaque pearl color, much like those described in other *Castianeira* species (Montgomery, 1909; Reiskind, 1969). Often, this is the final layer of silk in egg sac construction, however some females will construct a third, thin layer of silk with an empty space (~2-4 mm) between the second and third layers of silk.

Following completion of the egg sac, the female constructs a mound (Figure 4.2B). To build mounds, she gathers items (e.g. pebbles, dried leaves, seeds, small sticks, arthropod parts, bird feathers) in individual collecting trips traveling between 1.25 - 80.66 cm (15.34 ± 11.75, N=462 observed in 14 females), and returning to assemble the items into a mound held together by silk (Figure 4.1A,B). Shorter collecting trips were often due to females stealing material from nearby mounds rather than collecting their own. The number of collecting trips conducted by individual females to construct a mound varies. Females conduct 36 - 174 collecting trips per hour (102.43 ± 44.31, N=14) until the mound is finished, which can take anywhere from 6 to 13 hours (Figure 4.2B). Based on this, female mason spiders likely conduct ~ 500 - 2,000 collecting trips to complete a mound. During all observations, we never witnessed a female spider returning to her mound following its completion. Eggs remain in the egg sac for ~ 2 - 4 weeks before they hatch into spiderlings and overwinter as 1st or 2nd instar spiderlings in the egg sac for ~ 7 months. In May, mason spiders hatch out of egg sacs as 2nd instar spiderlings, leaving a molt behind in the egg sac (Figure 4.2A).

In our observations, mounds were regularly destroyed likely by weather events. Egg sacs visited one month or more following their completion were never observed with a mound. However, egg sacs remained in place through winter until spiderlings dispersed in spring (Figure 4.2A).

*Mound removal experiment*

Mason spider egg sacs were most often predated on by field crickets (*Gryllus sp.*) and parasitized by parasitoid wasps (*Gelis spp.*). We found that mounds significantly decreased predation/parasitism. Overall, 20.2% of egg sacs (N = 188) were predated/parasitized and these rates differed across the four treatments. Egg sacs whose mounds were removed immediately following completion and 1 day later were the most heavily predated and parasitized (28% (N=50) and 29.4% (N=51), respectively) as compared to egg sacs whose mounds were removed at 10 days and >24 days (11.9% (N=42) and 8.9% (N=45), respectively). We found significant differences between predation/parasitism of egg sacs with mounds removed immediately and those that were never removed (control) (Table 4.1, Figure 4.3). In addition, we found that the difference between egg sacs where mounds were removed immediately and at 10 days approached significance (Table 4.1).

We also found that mounds significantly decrease mortality due to abiotic factors. The proportion of offspring mortality in egg sacs showed a negative relationship with the number of days mounds were present (Table 4.2, Figure 4.4). The proportion of offspring mortality in egg sacs where mounds were removed at 1 day (0.12 ± 0.23 mean ± SD:) and never removed (control) (0.11 ± 0.25) were significantly lower than mortality in egg sacs where mounds were removed immediately, 0.30 ± 0.35 (Table 4.2, Figure 4.4).

## 4.5 DISCUSSION

Mason spiders construct elaborate mound nests by building mounds on top of their egg sacs, a parental care behavior that involves hundreds of collecting trips over many hours. We found that mounds are instrumental in reducing offspring mortality only for a short period of time following nest construction. This effect decreases throughout the first 10 days following construction, at which point egg sacs with and without mounds experience the same amount of offspring mortality. Additionally, we found that mounds protect offspring from mortality due to abiotic and biotic factors and that these benefits change differently over time.

Despite requiring a large investment of energy, we observed that mounds only remain on egg sacs for a small portion of the time that offspring inhabit nest-sites. This finding contrasts with other animals that similarly invest in building protective structures but whose nests are durable enough to protect offspring throughout development and/or until they leave the nest-site (Mainwaring *et al.*, 2014). Our study suggests that mason spider mound destruction after a short critical period (~ 10 days) does not result in reduced fitness for mason spiders due to the rapidly decreasing benefits of mounds over time.

*Benefits of mounds against abiotic factors*

The benefits of mason spider mounds are large early on, reducing the rate of predation/parasitism by 19.1% and abiotic mortality within egg sacs by 19.9%. Our experiment suggests the existence of a critical period early in offspring development where mason spider eggs are not able to survive without a mound. Across species, early development is often the period when offspring are most vulnerable to a variety of factors, including fluctuating environmental conditions, parasites and predation (Clutton-Brock, 2001). We found that for the most part, mounds protect offspring from mortality due to abiotic factors in the first 24 hours following construction. Abiotic mortality in mason spider egg sacs may be due to a variety of factors including fluctuating temperatures, humidity, or exposure to UV radiation (UVR) when mounds are not present. In other spider species, eggs have been found to be especially sensitive to temperature and humidity (Hieber, 1992b; Li & Jackson, 1996; Pike et al., 2012). Mounds may provide insulation from fluctuating temperatures or humidity, which can be dramatic in alpine habitats during summer months. Additionally, mason spider eggs are laid on the tops of rocks in exposed alpine habitats with direct UVR exposure. UVR exposure can cause mortality and sub-lethal damage in the early life stages of arthropods and amphibians (Blaustein & Belden, 2003; Bothwel et al., 1994). Mason spider mounds may reduce UVR exposure of eggs early in development and could be one driver of mound-building behavior.

Interestingly, mounds do not protect mason spider offspring during arguably the most dramatic environmental conditions that they encounter, winter. In the eight months that follow mound construction, mason spider offspring remain inside egg sacs at nest-sites as spiderlings and without mounds. They experience dramatic fluctuations in environmental conditions, including rain, snow, freezing temperatures, and snow melt. For arthropods, cold tolerance has been described as a critical component of their biology (Brandt et al., 2020; R. E. Lee, 2010). Future research should seek to understand aspects influencing mason spiderling overwintering, including their cold tolerance strategy, the insulating role of silk and egg sac construction, the conditions that cue diapause and the resumption of development in the spring, and the metabolic characteristics necessary for overwintering.

*Benefits of mounds against biotic factors*

In addition to their abiotic benefits, mounds also protected mason spider egg sacs from predation and parasitism, however this benefit was only present in the first 10 days following construction. Our observations suggest that egg sacs were most often predated on by crickets, although one predation event by a grouse was captured on film. Crickets have been found to be the primary predators of eggs of other arachnid species and may drive the evolution of active defense strategies of a cave-dwelling species of harvestmen (García-Hernández & Machado, 2017). The parasitoids of mason spider egg sacs were wasps in the genus *Gelis* — ichneumonids commonly known to parasitize a variety of silk covered masses including spider egg sacs and cocoons (Harvey, 2008). One hypothesis as to the mechanisms of mound protection is that mounds camouflage egg sacs from predators. To human eyes, mason spider mounds are visually conspicuous. However, *Gelis* parasitoid wasps and crickets likely detect their hosts/prey via olfactory cues (Matsumoto & Mizunami, 2000; Van Baarlen et al., 1996). In the initial days following construction, mounds might camouflage the scent of silk or eggs rendering them undetectable or increase the amount of time parasitoid wasps and other predators need to find eggs. Similarly, some birds are known to include green plant material in their nest construction, and it is thought that compounds in these materials serve as olfactory camouflage (Mainwaring et al., 2014).

### *Costs of mound-building*

Although this study did not explicitly evaluate costs, our observations of mound-building point to a variety of costs that should be assessed in the future. First, building a mound is likely an energetically expensive activity. During mound-building, mason spiders are regularly observed stealing material from nearby mounds rather than collecting their own. Similar behaviors have been witnessed among a variety of bird species and used as indicators that nest-building is energetically costly (Mainwaring & Hartley, 2013). Additionally, direct measurements indicate that birds use vast amounts of energy when transporting nesting material (Mainwaring & Hartley, 2013). Second, increased predation risk is a common cost of parental care and likely applies in this case (Ghalambor & Martin, 2002; Magnhagen, 1992; Reguera & Gomendio, 1999). Mason spiders build mounds and conduct collecting trips in mid-day in exposed areas making them and their nest location conspicuous to visual predators. One hypothesis as to the reason that mason spiders lay eggs at night is that by performing the most vulnerable and exposed parental behaviors in the dark, they reduce their risk of predation by visually oriented predators. Finally, energy spent on the current reproductive event, laying eggs and building mounds, reduces the time and energy that could be spent on future reproductive events (Alonso-Alvarez & Velando, 2012).

### *Nest Durability*

Our study points to multiple proximate reasons as to why mound destruction does not result in reduced reproductive success for mound builders. However, our findings also hint toward ultimate reasons for this dynamic that should be investigated further. Previous research suggests that nests that last longer are more costly to build and maintain (Abé et al., 2017). Therefore, mason spider nest durability, defined as the amount of time that a nest is able to withstand environmental conditions, may be a trait adapted to predictable environmental conditions that cause nest destruction. Similar traits of extended phenotypes, like the materials of bird bowers constructed for signaling or the shape of spider webs constructed for prey capture, have been shown to evolve or plastically respond to changing environments (Blamires, 2010; Schaedelin & Taborsky, 2009). We suggest that nest durability is also subject to selection. Nest durability may be driven by (1) the ability of young to survive independent of nests, (2) the frequency, intensity, and predictability of environmental conditions, (3) nest-site selection, and (4) nest shape and structure, including the costs and benefits of its construction and maintenance. Future work should examine these hypotheses in mason spiders but also across taxa in order to understand the different factors influencing the evolution of parental care strategies and animal architecture.

### *Acknowledgements*

This work was supported by the Meg and Bert Raynes Wildlife Fund, the Boyd Evison Graduate Research Fellowship sponsored by the Grand Teton Association, and the Margaret C. Walker Fund for teaching and research in systematic entomology from UC Berkeley.

We are grateful to S. J. Karikó for the use of her photos (Figure 4.1A, B). S. J. Karikó was generously supported by Canon USA and used a Canon EOS 5D Mark IV camera, EF 100-400mm f/4.5-5.6L IS II USM lens, Canon Extension Tube EF25 II, and Canon Extension Tube EF12 II for field photographs. In addition, we thank Blakeney Spong, Blair Loughrie, Sarah Knight, Daniel Stelling, Hayes McCord, and Rip Lambert for provided housing and support during the field seasons in which this work was conducted. Finally, we thank the Drew Hart of the D-Lab at UC Berkeley for help with statistical analyses and Elias lab members for their many helpful comments on this manuscript.

## 4.6 FIGURES

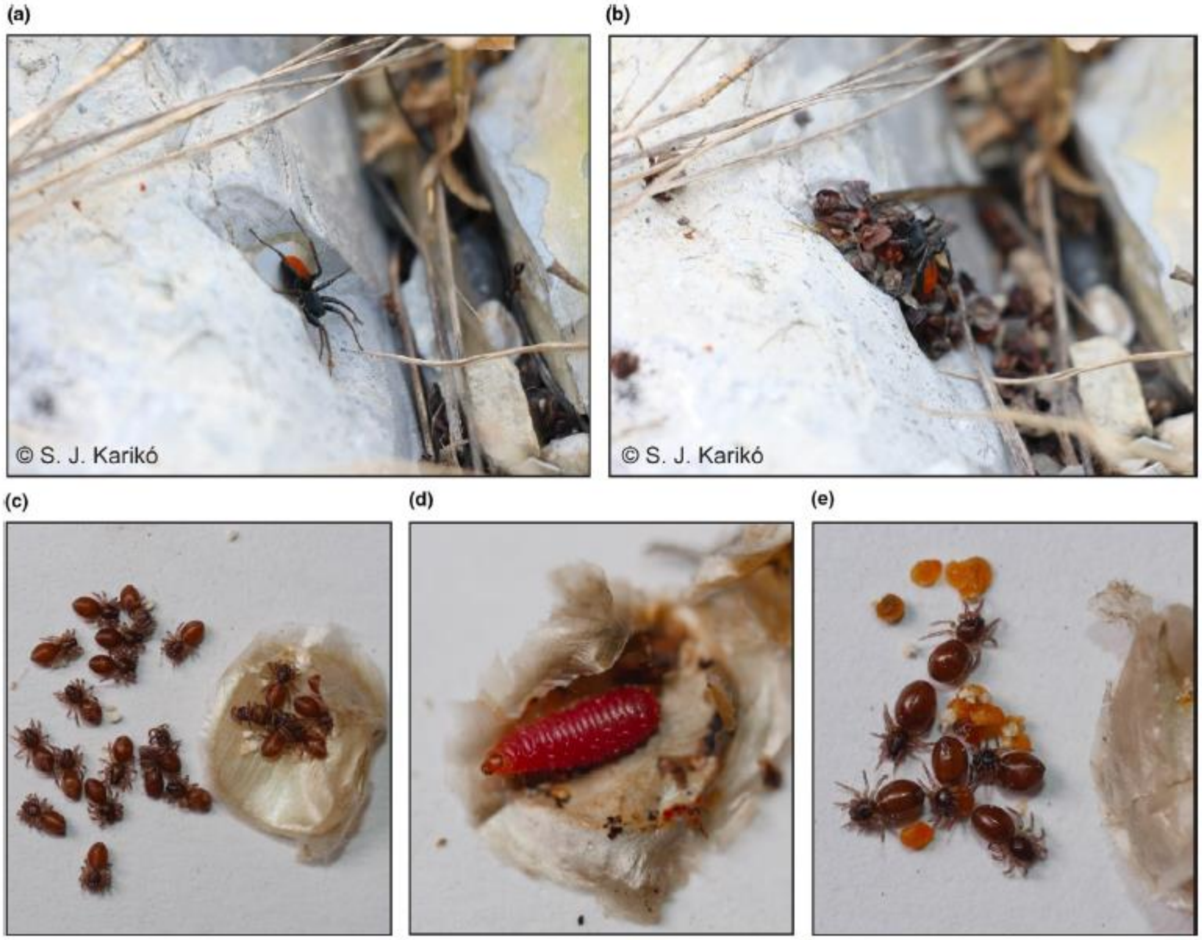

**Figure 4.1.** Mason spider constructing an egg sac and mound in the field and examples of egg sac contents. Mason spider constructing (a) egg sac and (b) mound at a single nest site. (c) Egg sac with healthy spiderlings. (d) Egg sac with wasp larva and total mortality of mason spider offspring. (d) Egg sac with healthy spiderlings and desiccated eggs.

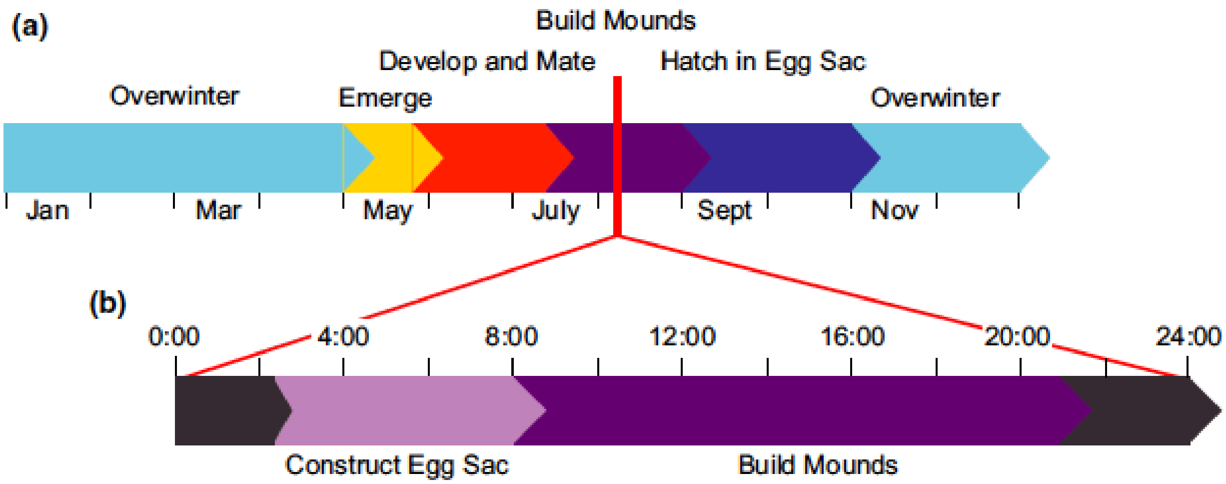

**Figure 4.2.** Timelines of mason spider life history and mound-building. (a) Mason spider stages of development throughout one year. Mason spiders lay eggs and build mounds in July and August. Eggs hatch into spiderlings and remain in egg sac throughout winter. In May, spiderlings emerge from egg sacs and develop into adults in early July. (b) Timeline of the building of one mason spider mound over 24 hr. Information included in timelines is generalizations based on hundreds of observations of individual spiders and egg sacs. However, variation exists in and around each stage of development.

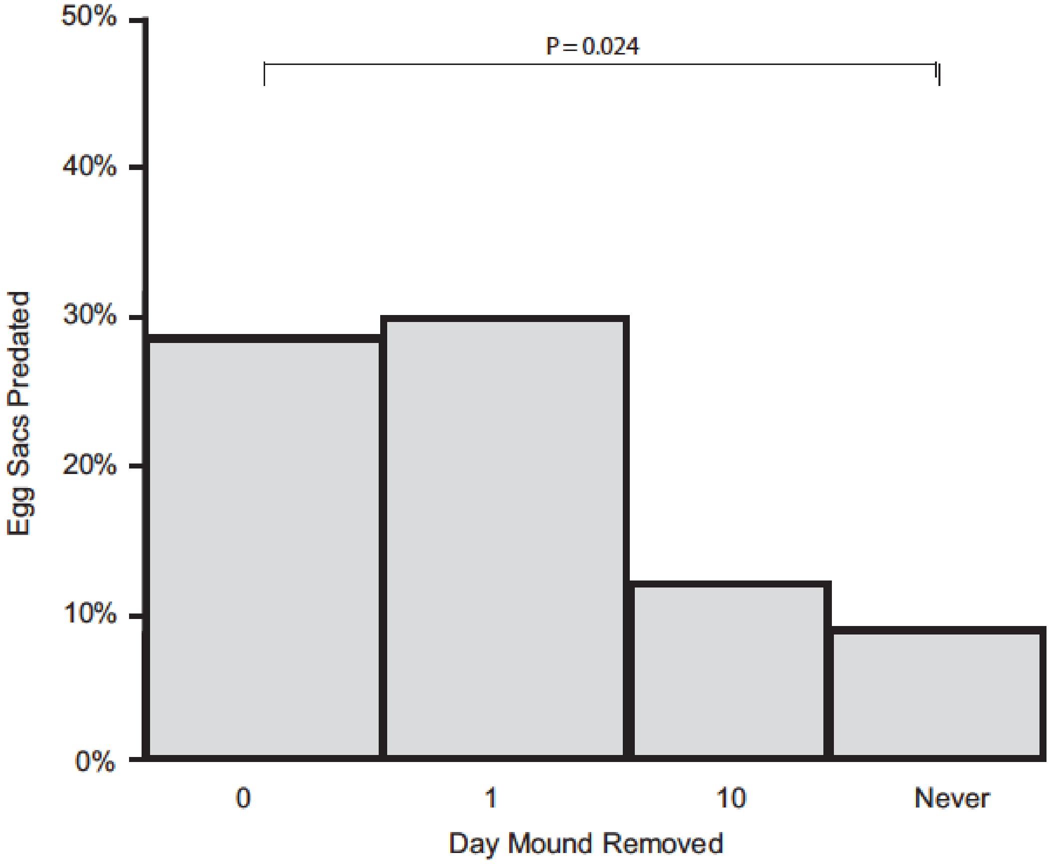

**Figure 4.3.** Predation/parasitism rate of egg sacs when mounds were removed from egg sacs at different time intervals following construction.

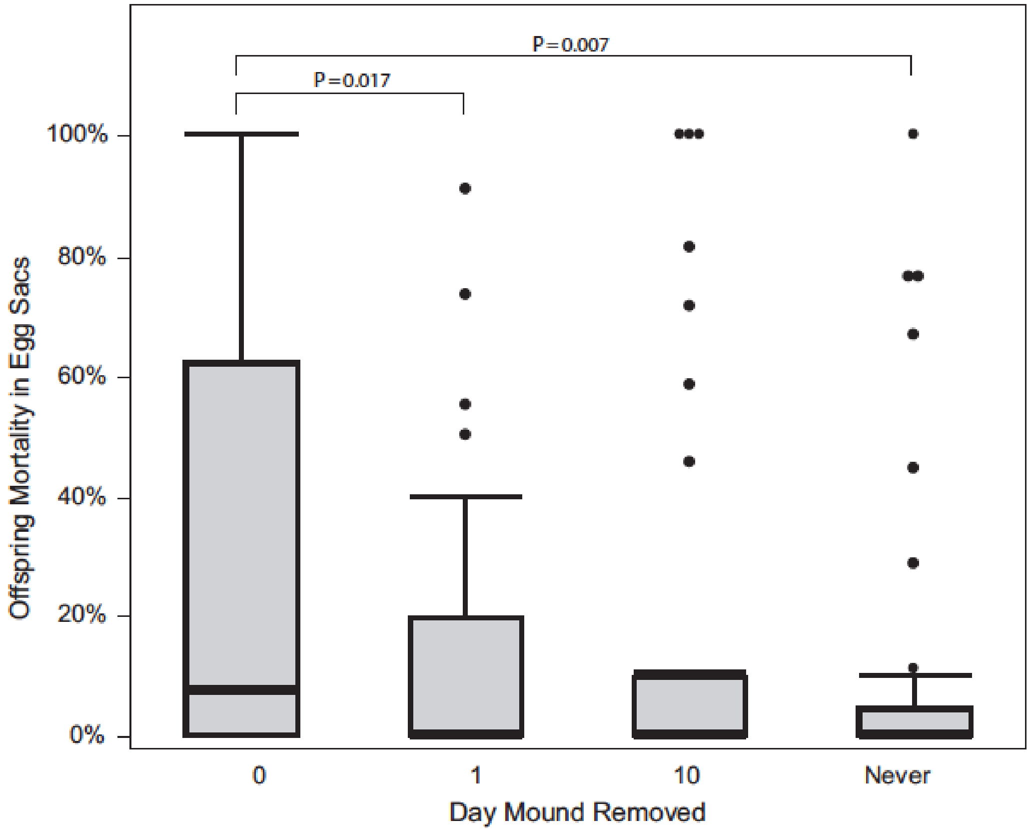

**Figure 4.4.** Box plot representing the percentage of abiotic mortality in egg sacs when mounds were removed at different time intervals following construction.

## 4.7 TABLES

| Parameter | Estimate | Std. Error | *t* | *p* |
|---|---|---|---|---|
| Intercept | -0.944 | 0.315 | -2.999 | **0.003** |
| Day 1 | 0.069 | 0.440 | 0.157 | 0.875 |
| Day 10 | -1.057 | 0.571 | -1.851 | 0.064 |
| Day >24-100 | -1.383 | 0.611 | -2.263 | **0.024** |

**Table 4.1.** Summary of results for generalized linear model assessing the effects of mound removal over time on the presence of predation/parasitism in egg sacs. Bolded values indicate statistical significance.

| Parameter | Estimate | Std. Error | *t* | *p* |
|---|---|---|---|---|
| Intercept | -0.770 | 0.305 | -2.520 | **0.013** |
| Day 1 | -1.264 | 0.524 | -2.411 | **0.017** |
| Day 10 | -0.769 | 0.467 | -1.646 | 0.102 |
| Day >24-100 | -1.384 | 0.505 | -2.739 | **0.007** |

**Table 4.2.** Summary of results for generalized linear model assessing the effects of mound removal over time on the proportion of abiotic mortality in mason spider egg sacs. Bolded values indicate statistical significance.

# CHAPTER 5 SUBSTRATE-BORNE NOISE DISTRACTS FROM PARENTAL CARE

Maggie Raboin and Damian O. Elias

Included here with permission from Damian. O. Elias

## 5.1 ABSTRACT

Caring for young often requires sustained attention that when disrupted can have consequences for offspring survival. Through distraction, extraneous stimuli occupy the limited attention of animals and divert their attention away from important tasks, like parental care. One potential distracting stimulus, anthropogenic noise, has become widespread across ecosystems. Anthropogenic substrate-borne noise, although often overlooked, is thought to be as prevalent as airborne noise and could greatly impact the many animals sensitive to substrate-borne sounds. Here, we record anthropogenic substrate-borne noise at sites with differing road traffic in the Greater Yellowstone Ecosystem – an area with some of the most protected land in the world. We investigate the potential of substrate-borne noise from roads to alter parental care behavior and offspring survival of mason spiders (*Castianeira* sp.), a species that builds elaborate nests to protect offspring from predators and fluctuating environmental conditions. We found that mason spiders spent significantly less time building nests, made fewer nest-building collecting trips per hour, and were more likely to get lost while navigating to and from their nests in the presence of greater substrate-borne noise. However, we did not find an effect of noise on offspring survival. These results suggest that substrate-borne noise distracts mason spiders from providing parental care. Our study provides field-based empirical evidence that substrate-borne noise from an anthropogenic source is present in ecosystems and can impact the parental care of animals.

## 5.2 INTRODUCTION

Many animal parents must perform behaviors that are critical for offspring success but that often require their sustained attention. Attention occurs through neural processes that organize and filter many environmental sensory stimuli to just a few and, in doing so, allows animals to coordinate an appropriate behavioral response to a given stimulus (Bushnell, 1998; Chan et al., 2010). Parental care behaviors like nest-building, brooding, and feeding require attention to the extent that parents will forgo foraging (Sabat, 1994; Weimerskirch, 1995) or investment in future reproduction (Golet et al., 2004; Hanssen et al., 2005) while caring for young. In some cases, extraneous stimuli may occupy the limited attention of animals, thereby involuntarily diverting their attention away from essential tasks – a process called distraction (Chan et al., 2010). Through distraction, stimuli have been found to interrupt behavioral and cognitive processes of animals, like risk assessment (Chan et al., 2010; Morris-Drake et al., 2016), mate assessment (Evans et al., 2006), and food localization and discrimination (Purser & Radford, 2011; Riffell et al., 2014). However, little is known about how distraction can impact parental care behaviors and ultimately, offspring success including survival.

Across environments, animals contend with extraneous stimuli introduced by human activities associated with urbanization, economic development, and transportation networks (Halfwerk & Slabbekoorn, 2015). One such stimulus, anthropogenic noise, is widespread and has been demonstrated to impact animal behavior in a multitude of ways (reviewed in Shannon et al., 2016). For example, anthropogenic noise can alter parental care behaviors like nest maintenance (Picciulin et al., 2010), feeding (Injaian, Taff, & Patricelli, 2018; Nedelec et al., 2017; Ng et al., 2019), and offspring defense (Injaian, Poon, et al., 2018; Nedelec et al., 2017), sometimes impacting offspring growth and survival. Altered behavioral responses are driven by the tendency of anthropogenic noise to mask important sounds, introduce misleading information, or distract animals from processing information appropriately (Dominoni et al., 2020). Through distraction, noise has been shown to affect the cognitive processing of diverse taxa leading to altered perceived predation risk (Chan et al., 2010; Morris-Drake et al., 2016) and decreased foraging efficiency (Halfwerk & Van Oers, 2020; Purser & Radford, 2011).

To date, most research on the impact of anthropogenic noise on animal behavior has focused on airborne and waterborne sound (Hawkins et al., 2021; Raboin & Elias, 2019). However, most terrestrial animals lack the ability to directly detect airborne sound and instead have highly sensitive organs for detecting substrate-borne sound (Cocroft & Rodriguez, 2005; Raboin & Elias, 2019). Spiders, in particular, are well-known for their use of substrate-borne sound in courtship and mating (Elias et al., 2003; Rosenthal & Hebets, 2012), foraging (Klärner & Barth, 1982; Wignall & Taylor, 2011) and avoiding predators (Lohrey et al., 2009; Riechert & Hedrick, 1990). Human activities are thought to produce substrate-borne noise as readily as airborne noise (Lecocq et al., 2020; Riahi & Gerstoft, 2015) and emerging evidence suggests that it has the ability to alter the behavior of animals sensitive to substrate-borne sounds. Substrate-borne noise is known to impact earthworm density (Velilla, Collinson, et al., 2021) and disrupt courtship and mating in stinkbugs, leafhoppers, beetles, and spiders (reviewed in Raboin & Elias, 2019). In addition, Phillips et al. (2020) showed that substrate-borne noise significantly impacted burying beetle brood size, likely through altered parental care behaviors.

In this study we examined mason spiders (Araneae, Corinnidae, *Castianeira* sp.) and the impact of substrate-borne noise on their parental care behavior. The behavioral ecology of mason spiders suggests that anthropogenic substrate-borne noise may impact parental care and the survival of offspring in keyways. Mason spiders are wandering spiders that often live along roadsides in the Greater Yellowstone Ecosystem - an area with some of the most protected land in the world (Lynch et al., 2008) that draws increasing amounts of visitors and human activity every year (NPS, 2021). Mason spiders provide care for young by constructing mound nests to protect their egg sacs from parasitoid wasps and fluctuating environmental conditions (Raboin & Elias, 2021). Mound-building involves focused attention over at least 12 hours to collect nest material and is instrumental in reducing offspring mortality (Raboin & Elias, 2021). Like the majority of spiders, species in the family Corinnidae lack tympanal ears to detect airborne sound (Haddad, 2012; 2013). Instead, they have well developed lyriform organs suggesting that they rely on substrate-borne vibrations for collecting information about the environment (Haddad, 2012; 2013). If human activity produces substrate-borne noise that mason spiders' sense, then it may occupy their limited attention and alter parental care behaviors critical for offspring survival.

Here, we investigate anthropogenic substrate-borne noise and the parental care of two populations of mason spiders in areas of high and low road traffic in the GYE. We first record substrate-borne noise produced by road traffic and test the hypothesis that areas of high traffic will have higher levels of substrate borne noise than areas of low traffic. Next, we investigate the behavioral responses of mason spiders to anthropogenic noise while providing parental care. We measured substrate-borne noise and parental care behaviors associated with building nests including the amount of time spent building nests, the ability of female mason spiders to navigate while building nests, and the directness of collecting trips to and from nests. Finally, we examine if altered parental care behaviors result in reduced offspring survival by measuring the mortality of mason spider offspring at sites with high and low road traffic. We predict that parents distracted by substrate-borne noise spend less time constructing nests resulting in a reduction of resources allocated to offspring protection, and ultimately, in increased offspring mortality.

## 5.3 MATERIALS AND METHODS

### *Study sites and substrate-borne noise*

We studied mason spiders at two sites in Bridger-Teton National Forest, WY, USA in open habitats dominated by sage, alfalfa, and various grasses. Sites were chosen because of their abundance of mason spider nests and proximity to roads. Site A was adjacent to a high traffic paved road and Site B was adjacent to a low traffic dirt road. Sites were 13 miles apart and similar in habitat and elevation. At each site, we identified mason spiders building nests within 25 meters of the road and measured the amount of substrate-borne noise with a portable laser Doppler vibrometer (Polytec PDV 100) connected to a digital recorder (Olympus VN-721PC). To measure substrate-borne noise, we focused the laser on a piece of reflective tape adhered to nylon that was stretched across a metal ring and placed on the ground 25 meters from each road. We made two recordings at each site that were five minutes in length. We analyzed recordings for vehicles passing per minute using Audacity 3.0.0 ® recording and editing software (Audacity Team, 2021). Next, we took three different pseudo-random samples from each recording of five seconds in duration and measured maximum and RMS amplitude using MATLAB (The Mathworks, Natick, MA, USA). Samples were evaluated to ensure stability within the five second period. We report differences in overall maximum and RMS amplitude in dB with the softest measurement across all recordings as the reference.

### *Behavioral responses to substrate-borne noise*

Adult female mason spiders were identified at field sites during egg sac construction. Once identified, a female was monitored every 15 minutes until it began collecting items to build a nest at which point, we began filming. We filmed the construction of 52 nests using GoPro (HERO 4) cameras across 30 days (July 17th - August 16th, 2018). GoPro cameras were mounted on tripods and positioned one meter from each egg sacs so as not to disrupt mason spiders during nest construction. Each nest-building bout was filmed for a total of 3-4 hours. Egg sacs were collected November 4th, 2018. Once collected, egg sacs were transported to UC Berkeley and dissected to determine offspring mortality in each egg sac, life stage (egg or spiderling), presence of mold or desiccation, and evidence of parasitism or predation. Eggs were determined to be dead if they were desiccated or covered in mold. Egg sacs were determined to be parasitized if wasps or wasp larva were present and predated if the egg sac had a large hole and was empty. Dissections were done blind to any information about treatment.

We analyzed videos of mason spider nest-building behavior using BORIS (Behavioral Observation Research Interactive Software) (Friard & Gamba, 2016). We analyzed the second hour of nest-building of each female for the following behaviors: amount of time spent on the nest vs. away from the nest, number of collecting trips per hour, and miss rate (Figure 5.1). The amount of time spent on the nest was analyzed as a proportion of the total time analyzed. Mason spiders were considered to "miss" the nest if they overshot it and had to loop back to find it or if they did at least one 360 degree turn prior to arriving at the nest (Figure 5.1B). We then calculated the miss rate by dividing the number of times a spider missed the nest by the total number of collecting trips made in an hour. Additionally, we used ImageJ (MtrackJ) software (Schneider et al., 2012) to find an average length of collecting trips for each mason spider by measuring the length of 15 consecutive outgoing trips for each spider, beginning with the first collecting trip of the second hour. We also analyzed the average "straightness" of collecting trips by calculating the ratio of the Euclidean distance to a collected item and the actual path length the spider used to get there.

### *Statistical analyses*

All statistical tests were performed in R v. 4.0.2 (R Core Team, 2020). We performed generalized linear models to assess the effect of site and treatment on nest-building behavior and offspring mortality. First, we analyzed the effect of site (predictor variable) on collecting trip length, proportion of time spent building, number of collecting trips per hour, miss rate, and average straightness (response variables) using generalized linear models with normal distributions. We found that the length of collecting trips was significantly different between sites, with spiders at Site A conducting longer collecting trips than those at Site B. To test the hypothesis that distraction rather than differences in collecting trip length were responsible for the site differences we found in our predictor variables (proportion of time spent building, number of collecting trips per hour, miss rate), we re-ran our models with collecting trip length as a random effect.

Next, we assessed the effect of mounds on offspring mortality in mason spider egg sacs between sites. In our model, we assigned dead/live offspring as our response variable with the cbind function in R and site as our predictor variable. We accounted for overdispersion in our data by using a quasibinomial distribution.

## 5.4 RESULTS

### *Substrate-borne noise*

Our study sites differed in amount of traffic and amplitude of substrate-borne sounds. We found that vehicles passed Site A at a rate of 5.6 vehicles per minute with an average RMS amplitude of 21.49 ± 0.92 dB and a maximum RMS amplitude of 25.87 ± 1.09 dB. No vehicles passed Site B during our recordings. Site B had an average RMS amplitude of 3.97 ± 5.18 dB and a maximum RMS amplitude of 5.43 ± 4.51 dB.

### *Behavioral responses to substrate-borne noise*

Mason spiders at Site A made significantly longer collecting trips on average than spiders at Site B (22.13 ± 6.95 cm (N=22) and 16.89 ± 8.02 cm (N=22), respectively) (Figure 5.2A). However, there was no difference in the straightness of collecting trips. We found that substrate-borne noise significantly impacted nest-building behavior in multiple ways with or without controlling for collecting trip length (Table 5.1). Spiders at Site A spent 46% of their time actively building nests and made 74.67 collecting trips per hour (N = 28) while spiders at Site B spent 56% of their time actively building nests and made 122.49 collecting trips per hour (N = 24) (Figure 5.2B, C). Additionally, spiders were more likely to miss their nests in the presence of more substrate-borne noise. Spiders at Site A missed their nest in 13% (N = 28) of collecting trips while spiders at Site B missed their nest in 8% of collecting trips (N = 24) (Figure 5.2D).

We recovered 45 of 52 egg sacs. Of those, three (Site A = 2, Site B = 1) showed signs of predation or parasitism and 16 (Site A = 9, Site B = 7) showed signs of mortality due to desiccation or mold. We did not find any effect of substrate-borne noise on offspring mortality (Figure 5.3).

## 5.5 DISCUSSION

We found that substrate-borne noise levels differed across the landscape. Noise recorded in close proximity to a paved road with traffic (Site A) was about 20 dB higher than noise recorded in close proximity to a dirt road with no traffic (Site B). Despite there being little traffic on the dirt road, we recorded substrate-borne noise levels at 5.4 dB presumably from distant roads with traffic. These results suggest anthropogenic substrate-borne noise can be transmitted relatively long distances. In urban areas, human activity is responsible for up to 50 percent of substrate-borne noise (Lecocq et al., 2020), but little is known about substrate-borne noise in protected areas and the way it impacts animals sensitive to substrate-borne sounds, including invertebrates, rodents, and amphibians, among others (Cocroft & Rodriguez, 2005; Hill, 2008). Anthropogenic airborne noise can disrupt the ability of many animals to communicate and perceive natural sounds important for reproduction and survival (Shannon et al., 2016). Our results suggest that anthropogenic substrate-borne noise is widespread in protected areas and could impact many animals in ways similar to airborne noise (Buxton et al., 2017).

We found that anthropogenic substrate-borne noise significantly alters the parental care behavior of mason spiders. When road noise was relatively loud, mason spiders spent less time constructing nests and made fewer collecting trips per hour than when road noise was relatively quiet, suggesting that road traffic distracted mason spiders from parental care. Intermittent anthropogenic noise, like that from road traffic, is hypothesized to increase antipredator and hiding behavior in some animals (Francis & Barber, 2013). Animals distracted by intermittent noise may experience an involuntary shift in their attention from an important task, like providing parental care, to an unimportant one, like hiding from a non-existent predator (Chan et al., 2010; Simpson et al., 2016). Substrate-borne noise, in particular, can resemble foraging predators and illicit antipredator behaviors (Catania, 2008). Mason spider nests are conspicuously built atop large rocks in fields that are otherwise covered in vegetation (Raboin & Elias, 2021). As with other animals engaged in nest-building behavior, mason spider nest construction likely leaves animals vulnerable to predators and therefore, vigilant (Lima, 2009). During our study, we often observed mason spiders startle, run, and freeze in the vegetation surrounding their nests, which we interpreted as hiding. Our results indicate that although spiders at our loud site conducted longer collecting trips, this alone does not account for our finding that they spent less time actively building nests and fewer collecting trips per hour. These results could be due to mason spiders hiding more often in the presence of noise.

When mason spiders did venture to collect nesting material, spiders conducted longer collecting trips at the loud site and became lost more often in returning to their nest than those at the quiet site. Mason spiders search for, identify, and assess nesting items in a way that resembles foraging. Anthropogenic noise has been shown to impair foraging behaviors of animals by not only masking the sounds of prey (Mason et al., 2016; Siemers & Schaub, 2011), but also by distracting or misleading foragers (Dominoni et al., 2020; Luo et al., 2015). For example, some animals have been found to be less efficient foragers even when anthropogenic noise does not spectrally overlap with the sounds of prey, suggesting that noise can act as a distraction or aversive stimulus (Luo et al., 2015; Purser & Radford, 2011). In the presence of distracting noise, mason spiders may cover more ground in searching for nesting material because they are less efficient in identifying and assessing items for their nest. However, differences in collecting trip length might also be accounted for by subtle differences in habitat at our two sites.

Most spiders use path integration to navigate through environments (Gaffin & Curry, 2020). Navigation, via a mechanism like path integration, requires cognitive processes that are subject to error in the presence of overwhelming or distracting stimuli (Heinze et al., 2018). We hypothesize that substrate-borne noise from road traffic disrupted cognitive processes in mason spiders, resulting in more navigational errors for spiders at our loud site. Some have suggested that anthropogenic noise may impact navigation by some whales and bats by masking echolocation ticks (McGregor et al., 2013). However, we do not know of any examples where noise has been shown to disrupt navigation through distraction. Here, we present one of the first examples of the kind.

Mason spider nests are instrumental in protecting offspring from predation, parasitism, and abiotic factors that contribute to offspring mortality, but only for a short amount of time (Raboin & Elias, 2021). We found a significant effect of substrate-borne noise on nest construction but not offspring mortality. Similarly, Pandit et al. (2021) found that noise altered the parental care behavior of bluebirds (*Sialia sialis*), but that it did not result in altered fledgling body condition. In these cases, parents maybe compensating for inadequate conditions by providing more parental care. Behavioral compensation for noise is common in communication contexts, for example many bird and frog species compensate for the presence of masking noise by adjusting frequency and amplitude of their song, however these studies often fail to include measures of reproductive success (Read et al., 2014; Roca et al., 2016). In parental care contexts, birds have been found to increase their feeding rate of nestlings to compensate for noise with varying success (Injaian, Taff, Pearson, et al., 2018; Pandit et al., 2021). Mason spiders might have compensated for the behavioral impacts of noise (e.g., slower rate of building, getting lost more often) by taking more time overall to complete their nests. Future work should examine differences in the size of nests and the overall time building nests at quiet and loud sites.

In this study, we made behavioral and mortality measurements for a single reproductive event; however, it is likely that mason spiders lay multiple egg sacs over a lifetime as seen in other spiders (Foelix, 2011). We also did not examine other measures of reproduction like the number of eggs or spiderlings in each egg sac or brood mass, which have been shown to be negatively impacted by substrate-borne noise in burying beetles (*Nicrophorus marginatus*) (Phillips et al., 2020). Under one scenario, we predict that spiders might compensate for noise at loud sites by taking longer to build a single nest. In this scenario, they may lay less egg sacs over their lifetime than spiders at quiet sites. Future studies should seek to examine mason spider behavior with more replicates of loud and quiet sites, include substrate-borne noise playbacks, and measure indirect and sublethal effects of noise on mason spider reproductive success.

Our study indicates that anthropogenic substrate-borne noise in protected areas has the potential to impact animals in profound ways and adds to a growing body of evidence that substrate-borne noise can alter animal behaviors (Caorsi et al., 2019; Phillips et al., 2020; Roberts et al., 2016; Velilla et al., 2021; Wu & Elias, 2014), including through distraction. Most terrestrial invertebrates, like mason spiders, are highly sensitive to substrate-borne sounds (Cocroft & Rodriguez, 2005). They contribute immensely to biodiversity and are experiencing declines in abundances and species across ecosystems (Hallmann et al., 2017; Lister & Garcia, 2018). While these historic changes have been attributed to several factors (Goulson, 2019) most models of invertebrate decline fail to account for the magnitude of loss (Goulson, 2019; Hladik et al., 2018; Lister & Garcia, 2018). Future research into substrate-borne noise and its impact on invertebrate species, populations, and communities will inform conservation as anthropogenic noise continues to be a widespread environmental issue.

### *Acknowledgements*

We acknowledge the Shoshone-Bannock, Eastern Shoshone, and Cheyenne nations and tribes on whose unceded, ancestral lands we conducted our field experiments and collections. This work was supported by the Boyd Evison Graduate Research Fellowship sponsored by the Grand Teton Association, the University of Wyoming – National Park Service small grants program, and the Margaret C. Walker Fund for teaching and research in systematic entomology from UC Berkeley. We thank S. J. Karikó for the use of her photograph (Figure 5.1A). S. J. Karikó was generously supported by Canon USA and used a Canon EOS 5D Mark IV camera, EF 100-400mm f/4.5-5.6L IS II USM lens, Canon Extension Tube EF25 II, and Canon Extension Tube EF12 II for the field photograph. In addition, we are grateful to Blakeney Spong, Blair Loughrie, Sarah Knight, Daniel Stelling, Hayes McCord, and Rip Lambert for provided housing and support during the field season in which this work was conducted. Finally, we thank the Elias laboratory members for their many helpful comments on this manuscript.

5.6 FIGURES

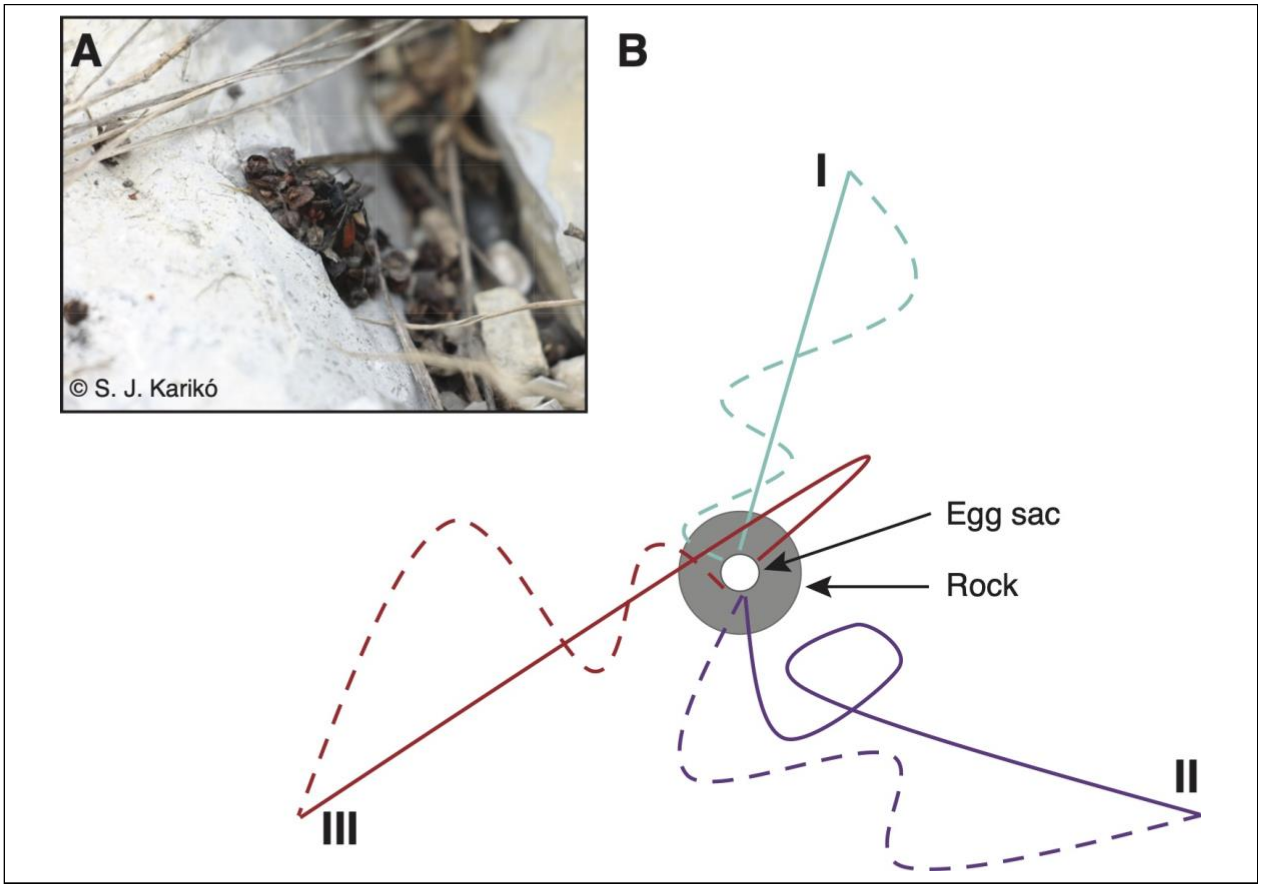

**Figure 5.1.** Mason spider constructing a nest (A) and examples of collecting trips taken to (solid line) and from (dotted line) a nest by a mason spider during nest construction (B). During most collecting trips, mason spiders returned directly to the nest (BI). However, in some instances mason spiders did at least one 360 degree turn (BII) or overshot the nest (BIII). In these cases, the collecting trip was categorized as a "miss".

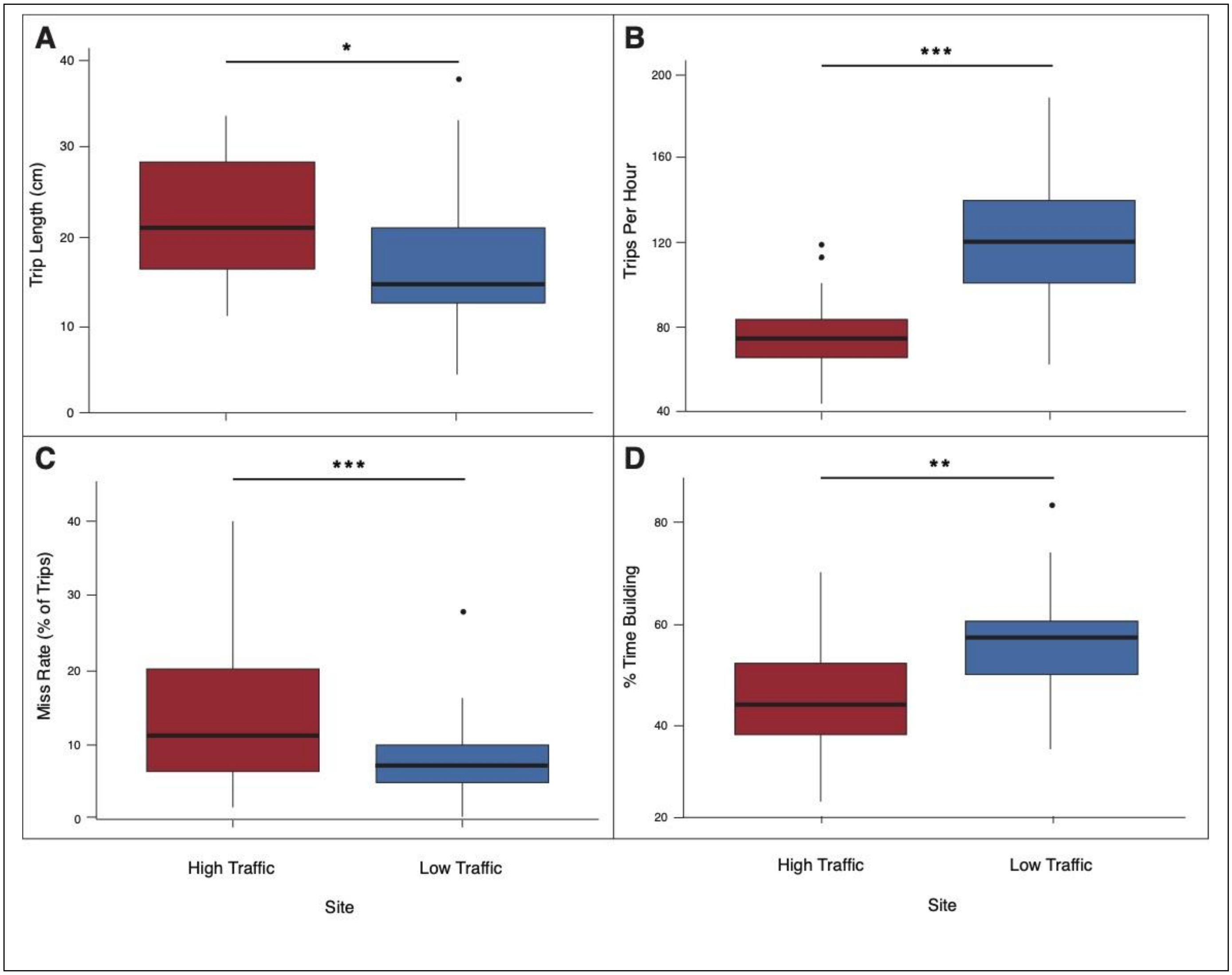

**Figure 5.2.** Box plots representing mason spider nest-building behaviors at high and low traffic sites. Nest-building behaviors include collecting trip length (A), number of collecting trips per hour (B), miss rate (C), and percentage of time spent actively nest-building (D). The line within each box denotes the median value and the lower and upper borders of each box represent the first and third quartiles. Whiskers above and below the boxes mark the range of maximally 1.5 times the interquartile range. Outliers are indicated with circles. * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$.

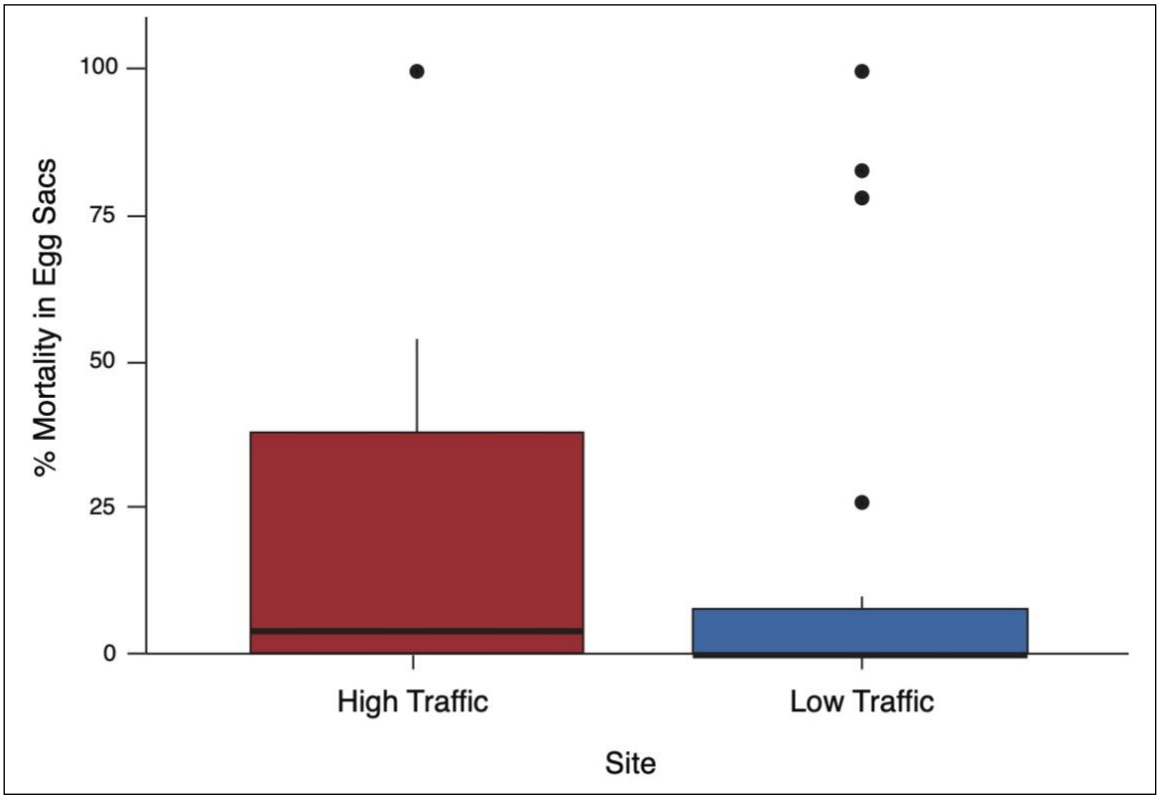

**Figure 5.3.** Box plots representing the percentage of mason spider offspring mortality in egg sacs at high and low traffic sites. The line within each box denotes the median value and the lower and upper borders of each box represent the first and third quartiles. Whiskers above and below the boxes mark the range of maximally 1.5 times the interquartile range. Outliers are indicated with circles.

## 5.7. TABLES

| Variable | Parameter | Quiet | Loud | Test Statistic | P |
|---|---|---|---|---|---|
| Collecting trip length (cm) | Mean ± SD | 16.89 ± 8.02 (N=22) | 22.13 ± 6.95 (N=22) | ANOVA<br>F (1, 1) = 5.37, | 0.025 |
| Time spent building (%) | Mean ± SD | 56% ± 12% (N=24) | 46% ± 11% (N=28) | ANOVA<br>F (1, 1) = 10.69 | 0.002 |
| | | | | ANCOVA<br>F (1, 1) = 10.66 | 0.002 |
| Collecting trips/hour | Mean ± SD | 122.49 ± 31.95 (N=24) | 74.67 ± 18.44 (N=28) | ANOVA<br>F (1, 1) = 45.25 | < 0.001 |
| | | | | ANCOVA<br>F (1, 1) = 36.40 | < 0.001 |
| Miss Rate (%) | Mean ± SD | 8% ± 6% (N=24) | 13% ± 9% (N=28) | ANOVA<br>F (1, 1) = 6.01 | 0.018 |
| | | | | ANCOVA<br>F (1, 1) = 12.15 | 0.001 |
| Collecting trip straightness | Mean ± SD | 0.79 ± 0.09 (N=22) | 0.78 ± 0.07 (N=22) | ANOVA<br>F (1, 1) = 0.01 | 0.940 |
| | | | | ANCOVA<br>F (1, 1) = <0.01 | 0.947 |
| Mortality (%) | Mean ± SD | 16% ± 33% (N=18) | 21% ± 33% (N=27) | GLM<br>(quasibinomial) | 0.654 |

**Table 5.1.** Summary of results for linear regressions, including those that control for collecting trip length, and generalized linear model assessing the effects of low and high road traffic on mason spider nest-building behaviors and mortality in egg sacs.

# CHAPTER 6 CONCLUDING REMARKS

Invertebrates were once so abundant that their swarms darkened skies, fields, and intertidal zones. Perhaps most telling, invertebrates were once so numerous that their services to ecosystems were once incalculable and their disappearance inconceivable. However, in the last decade, the scientists that collect and identify invertebrates began to notice a concerning trend, a precipitate drop-off in the number of invertebrates visiting their traps. In fact, in parts of the world such as Germany, Puerto Rico, and the United States mainland, scientists have reported up to a 90% loss in the abundance of some invertebrate populations (Goulson, 2019).

It just so happens that over the past century, while invertebrate populations have been in free fall, sound from increased human activity has been rising (Buxton et al., 2017; Goulson, 2019). For vertebrates, anthropogenic sound has been found to impact behavior and physiology, leading, in some cases, to reductions in vertebrate species abundances (Shannon et al., 2016). However, much less is known about the impact of anthropogenic sound on invertebrates.

This dissertation attempts to bridge the gap between two fields of study, invertebrate bioacoustics and anthropogenic sound. Chapter 2 emphasizes how our scientific understandings of evolution and ecology are limited when invertebrates and their ways of sensing the world, are ignored. By including these animals in previously accepted models, we suggested a shift in the current broad theoretical framework that attempts to explain the diversity of all acoustic communication and recommended one that is more complex. In reviewing the available literature related to invertebrate bioacoustics and anthropogenic noise, we found that invertebrates might be impacted by anthropogenic noise is vastly different ways than vertebrates. Therefore, they should be studied in their own right. We presented a set of hypotheses and predictions to guide this research in the future and underlined a need to investigate substrate-borne anthropogenic noise. By focusing our efforts on a single species of invertebrate, the mason spider, in Chapters 4 and 5, we were able to test our own predictions. We found that substrate-borne anthropogenic noise can have major implications on invertebrate behavior.

In total, this collection of studies suggests that in searching for the major contributors to invertebrate decline, we might look first to anthropogenic noise. While much more research is needed, I hope this dissertation contributes to a better understanding of how noise may impact invertebrates and their conservation.

## REFERENCES

Abé, H., Nabeshima, M., & Tanaka, Y. (2017). Structural comparisons of isomorphic breeding nests between closely allied spiders *Cheiracanthium japonicum* and *Cheiracanthium lascivum* (Araneae: Eutichuridae). *Journal of Natural History*, *51*(41–42), 2417–2428. https://doi.org/10.1080/00222933.2017.1381773

Aicher, B., & Tautz, J. (1990). Vibrational communication in the fiddler crab, *Uca pugilator*. *Journal of Comparative Physiology A*, *166*(3), 345–353. https://doi.org/10.1007/bf00204807

Albert, J. T., & Kozlov, A. S. (2016). Comparative Aspects of Hearing in Vertebrates and Insects with Antennal Ears. *Current Biology*, *26*(20), R1050–R1061. https://doi.org/10.1016/j.cub.2016.09.017

Aldersley, A., Champneys, A., Homer, M., Bode, N. W. F., & Robert, D. (2017). Emergent acoustic order in arrays of mosquitoes. *Current Biology*, *27*(22), R1208–R1210. https://doi.org/10.1016/j.cub.2017.09.055

Alonso-Alvarez, C., & Velando, A. (2012). Benefits and costs of parental care. In N. J. Royle, P. T. Smiseth, & M. Kölliker (Eds.), *The Evolution of Parental Care* (pp. 40–61). Oxford University Press. https://doi.org/10.1093/acprof:oso/9780199692576.003.0003

Angilletta, M. J., Sears, M. W., & Pringle, R. M. (2009). Spatial dynamics of nesting behavior: Lizards shift microhabitats to construct nests with beneficial thermal properties. *Ecology*, *90*(10), 2933–2939. https://doi.org/10.1890/08-2224.1

Audacity Team. (2021). *Audacity(R): Free Audio Editor and Recorder [Computer application]* (Version 3.0.0). https://audacityteam.org/

Augustine, S., Lika, K., & Kooijman, S. A. L. M. (2019). Altricial-precocial spectra in animal kingdom. *Journal of Sea Research*, *143*(December 2017), 27–34. https://doi.org/10.1016/j.seares.2018.03.006

Bailey, W. J., & Morris, G. K. (1986). Confusion of Phonotaxis by Masking Sounds in the Bushcricket *Conocephalus brevipennis* (Tettigoniidae: Conocephalinae). *Ethology*, *73*(1), 19–28. https://doi.org/10.1111/j.1439-0310.1986.tb00996.x

Barber, J. R., Burdett, C. L., Reed, S. E., Warner, K. A., Formichella, C., Crooks, K. R., Theobald, D. M., & Fristrup, K. M. (2011). Anthropogenic noise exposure in protected natural areas : estimating the scale of ecological consequences. *Landscape Ecology*, *26*, 1281–1295. https://doi.org/10.1007/s10980-011-9646-7

Barber, J. R., Crooks, K. R., & Fristrup, K. M. (2009). The costs of chronic noise exposure for terrestrial organisms. *Trends in Ecology & Evolution*, *25*(3), 180–189. https://doi.org/10.1016/j.tree.2009.08.002

Baroni-Urbani, C., Buser, M. W., & Schilliger, E. (1988). Substrate vibration during recruitment in ant social organization. *Insectes Sociaux*, *35*(3), 241–250. https://doi.org/10.1007/BF02224057

Barth, F. G. (2000). How to catch the wind: Spider hairs specialized for sensing the movement of air. *Naturwissenschaften*, *87*(2), 51–58. https://doi.org/10.1007/s001140050010

Barth, Fiedrich G., & Höller, A. (1999). Dynamics of arthropod filiform hairs. V. The response of spider trichobothria to natural stimuli. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *354*(1380), 183–192. https://doi.org/10.1098/rstb.1999.0370

Barth, Friedrich G., & Geethabali. (1982). Threshold Curves of Individual Slits in the Metatarsal Lyriform Organ. *Journal of Comparative Physiology - A Sensory, Neural, and Behavioral Physiology*, *148*, 175–185.

Barth, Friedrich G, Wastl, U., Humphrey, J. A. C., & Devarakonda, R. (1993). Dynamics of arthropod filiform hairs. II. Mechanical properties of spider trichobothria (*Cupiennius salei* Keys.). *Philosophical Transactions of the Royal Society B: Biological Sciences*, *340*, 445–461.

Bass, A. H., & McKibben, J. R. (2003). Neural mechanisms and behaviors for acoustic communication in teleost fish. *Progress in Neurobiology*, *69*(1), 1–26. https://doi.org/10.1016/S0301-0082(03)00004-2

Bathellier, B., Steinmann, T., Barth, F. G., & Casas, J. (2012). Air motion sensing hairs of arthropods detect high frequencies at near-maximal mechanical efficiency. *Journal of the Royal Society Interface*, *9*(71), 1131–1143. https://doi.org/10.1098/rsif.2011.0690

Benediktov, A., Korsunovskaya, O., Polilov, A., & Zhantiev, R. (2020). Unusual mechanism of emission of vibratory signals in pygmy grasshoppers *Tetrix tenuicornis* (Sahlberg, 1891) (Orthoptera: Tetrigidae). *Science of Nature*, *107*(2), 1–5. https://doi.org/10.1007/s00114-020-1668-z

Bennet-Clark, H. C. (1998). Size and scale effects as constraints in insect sound communication. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *353*(1367), 407–419. https://doi.org/10.1098/rstb.1998.0219

Bennet-Clark, H. C. (1999). Resonators in insect sound production: how insects produce loud pure-tone songs. *The Journal of Experimental Biology*, *202*, 3347–3357.

Bent, A. M., Ings, T. C., & Mowles, S. L. (2018). Anthropogenic noise disrupts mate searching in Gryllus bimaculatus. *Behavioral Ecology*, *29*(6), 1271–1277. https://doi.org/10.1093/beheco/ary126

Blamires, S. J. (2010). Plasticity in extended phenotypes: Orb web architectural responses to variations in prey parameters. *Journal of Experimental Biology*, *213*(18), 3207–3212. https://doi.org/10.1242/jeb.045583

Blaustein, A. R., & Belden, L. K. (2003). Amphibian defenses against ultraviolet-B radiation. *Evolution and Development*, *5*(1), 89–97.

Bomphrey, R. J., Lawson, N. J., Harding, N. J., Taylor, G. K., & Thomas, A. L. R. (2005). The aerodynamics of Manduca sexta: digital particle image velocimetry analysis of the leading-edge vortex. *Journal of Experimental Biology*, *208*(6), 1079–1094. https://doi.org/10.1242/jeb.01471

Bonter, D. N., Maclean, S. A., Shah, S. S., & Moglia, M. C. (2014). Storm-induced shifts in optimal nesting sites : a potential effect of climate change. *Journal of Ornithology*, *155*, 631–638. https://doi.org/10.1007/s10336-014-1045-9

Bothwel, M. L., Sherbot, D. M. J., & Pollock, C. M. (1994). Ecosystem Response to Solar Ultraviolet-B Radiation : Influence of Trophic-Level Interactions. *Science*, *265*(5168), 97–100.

Boughman, J. W. (2002). How sensory drive can promote speciation. *Trends in Ecology and Evolution*, *17*(12), 571–577. https://doi.org/10.1016/S0169-5347(02)02595-8

Bradbury, J. W., & Vehrencamp, S. L. (2011). *The Principles of Animal Communication, 2nd edn Sunderland*. MA: Sinauer Associates.

Brandt, E. E., Roberts, K. T., Williams, C. M., & Elias, D. O. (2020). Low temperatures impact species distributions of jumping spiders across a desert elevational cline. *Journal of Insect Physiology*, *122*(September 2019), 104037. https://doi.org/10.1016/j.jinsphys.2020.104037

Brown, W. D., Smith, A. T., Moskalik, B., & Gabriel, J. (2006). Aggressive contests in house crickets: size, motivation and the information content of aggressive songs. *Animal Behaviour*, *72*(1), 225–233. https://doi.org/10.1016/j.anbehav.2006.01.012

Brownell, P. H. (1977). Compressional and Surface Waves in Sand : Used by Desert Scorpions to Locate Prey. *Science*, *197*(4302), 479–482.

Brumm, H., & Slabbekoorn, H. (2005). Acoustic Communication in Noise. *Advances in the Study of Behavior*, *35*, 151–209. https://doi.org/10.1016/S0065-3454(05)35004-2

Bunkley, J. P., McClure, C. J. W., Kawahara, A. Y., Francis, C. D., & Barber, J. R. (2017). Anthropogenic noise changes arthropod abundances. *Ecology and Evolution*, *7*(9), 2977–2985. https://doi.org/10.1002/ece3.2698

Bunkley, J. P., McClure, C. J. W., Kleist, N. J., Francis, C. D., & Barber, J. R. (2015). Anthropogenic noise alters bat activity levels and echolocation calls. *Global Ecology and Conservation*, *3*, 62–71. https://doi.org/10.1016/j.gecco.2014.11.002

Bushnell, P. J. (1998). Behavioral approaches to the assessment of attention in animals. *Psychopharmacology*, *138*(3–4), 231–259. https://doi.org/10.1007/s002130050668

Buxton, R. T., McKenna, M. F., Mennitt, D., Fristrup, K. M., Crooks, K. R., Angeloni, L. M., & Wittemyer, G. (2017). Noise pollution is pervasive in U.S. protected areas. *Science*, *356*, 531–533. https://doi.org/10.1177/1757913914566549.

Cade, W. (1975). Acoustically Orienting Parasitoids : Fly Phonotaxis to Cricket. *Science*, *190*(4221), 1312–1313.

Caldwell, M. S. (2014). Interactions between airborne sound and substrate vibration in animal communication. In *Studying vibrational communication* (pp. 65–92). Springer Berlin Heidelberg.

Caorsi, V., Guerra, V., Furtado, R., Llusia, D., Miron, L. R., Borges-Martins, M., Both, C., Narins, P. M., Meenderink, S. W. F., & Márquez, R. (2019). Anthropogenic substrate-borne vibrations impact anuran calling. *Scientific Reports*, *9*(1), 1–10. https://doi.org/10.1038/s41598-019-55639-0

Casas, J., Magal, C., & Sueur, J. (2007). Dispersive and non-dispersive waves through plants: Implications for arthropod vibratory communication. *Proceedings of the Royal Society B: Biological Sciences*, *274*(1613), 1087–1092. https://doi.org/10.1098/rspb.2006.0306

Casas, J., Steinmann, T., & Dangles, O. (2008). The aerodynamic signature of running spiders. *PLoS ONE*, *3*(5), 3–8. https://doi.org/10.1371/journal.pone.0002116

Castellanos, I., & Barbosa, P. (2006). Evaluation of predation risk by a caterpillar using substrate-borne vibrations. *Animal Behaviour*, *72*(2), 461–469. https://doi.org/10.1016/j.bios.2011.11.019

Catania, K. C. (2008). Worm grunting, fiddling, and charming - Humans unknowingly mimic a predator to harvest bait. *PLoS ONE*, *3*(10). https://doi.org/10.1371/journal.pone.0003472

Cator, L. J., Arthur, B. J., Harrington, L. C., & Hoy, R. R. (2009). Harmonic convergence in the love songs of the dengue vector mosquito. *Science*, *323*(5917), 1077–1079. https://doi.org/10.1126/science.1166541.Harmonic

Chan, A. A. Y. H., Giraldo-Perez, P., Smith, S., & Blumstein, D. T. (2010). Anthropogenic noise affects risk assessment and attention: The distracted prey hypothesis. *Biology Letters*, *6*(4), 458–461. https://doi.org/10.1098/rsbl.2009.1081

Chapman, R. F. (1998). *The insects: structure and function*. Cambridge University Press.

Chivers, B. D., Jonsson, T., Soulsbury, C. D., & Montealegre-Z, F. (2017). Structural biomechanics determine spectral purity of bush-cricket calls. *Biology Letters*, *13*(11), 0–5.

https://doi.org/10.1098/rsbl.2017.0573

Clutton-Brock, T. H. (2001). *The Evolution of Parental Care*. Princeton University Press.

Cocroft, R. B., Hamel, J., Su, Q., & Gibson, J. (2014). Vibrational playback experiments: challenges and solutions. In *Studying Vibrational Communication* (pp. 249–274). Springer Berlin Heidelberg.

Cocroft, R. B., Shugart, H. J., Konrad, K. T., & Tibbs, K. (2006). Variation in plant substrates and its consequences for insect vibrational communication. *Ethology*, *112*(8), 779–789. https://doi.org/10.1111/j.1439-0310.2006.01226.x

Cocroft, R. B., & Rodriguez, R. L. (2005). The behavioral ecology of insect vibrational communication. *BioScience*, *55*(4), 323–334. https://doi.org/10.1641/0006-3568(2005)055[0323:TBEOIV]2.0.CO;2

Cocroft, Reginald B., RodrÍguez, R. L., & Hunt, R. E. (2010). Host shifts and signal divergence: Mating signals covary with host use in a complex of specialized plant-feeding insects. *Biological Journal of the Linnean Society*, *99*(1), 60–72. https://doi.org/10.1111/j.1095-8312.2009.01345.x

Čokl, A., & Virant-Doberlet, M. (2003). Communication with substrate-borne signals in small plant-dwelling insects. *Annual Review of Entomology*, *48*(1), 29–50. https://doi.org/10.1146/annurev.ento.48.091801.112605

Cokl, A., Zorovic, M., Zunic, A., & Virant-Doberlet, M. (2005). Tuning of host plants with vibratory songs of *Nezara viridula* L (Heteroptera: Pentatomidae). *Journal of Experimental Biology*, *208*(8), 1481–1488. https://doi.org/10.1242/jeb.01557

Costello, R. A., & Symes, L. B. (2014). Effects of anthropogenic noise on male signalling behaviour and female phonotaxis in *Oecanthus* tree crickets. *Animal Behaviour*, *95*, 15–22. https://doi.org/10.1016/j.anbehav.2014.05.009

De Souza, L. R., Kasumovic, M. M., Judge, K. A., & Morris, G. K. (2011). Communicating male size by tremulatory vibration in a Columbian rainforest katydid, *Gnathoclita sodalis* (Orthoptera, Tettigoniidae). *Behaviour*, *148*(3), 341–357. https://doi.org/10.1163/000579511X559418

DeVries, P. J. (1990). Enhancement of Symbioses Between Butterfly Caterpillars and Ants by Vibrational Communication. *Science*, *248*(4959), 1104–1106.

Doherty, J. A. (1985). Trade-off phenomena in calling song recognition and phonotaxis in the cricket, *Gryllus bimaculatus* (Orthoptera, Gryllidae). *Journal of Comparative Physiology A*, *156*(6), 787–801. https://doi.org/10.1007/BF00610831

Dominoni, D. M., Halfwerk, W., Baird, E., Buxton, R. T., Fernández-Juricic, E., Fristrup, K. M., McKenna, M. F., Mennitt, D. J., Perkin, E. K., Seymoure, B. M., Stoner, D. C., Tennessen, J. B., Toth, C. A., Tyrrell, L. P., Wilson, A., Francis, C. D., Carter, N. H., & Barber, J. R. (2020). Why conservation biology can benefit from sensory ecology. *Nature Ecology and Evolution*, *4*(4), 502–511. https://doi.org/10.1038/s41559-020-1135-4

Dowding, C. H. (1996). *Construction Vibrations*. Prentice Hall.

Einhäupl, A., Stange, N., Hennig, R. M., & Ronacher, B. (2011). Attractiveness of grasshopper songs correlates with their robustness against noise. *Behavioral Ecology*, *22*(4), 791–799. https://doi.org/10.1093/beheco/arr064

Elias, D. O., Kasumovic, M. M., Punzalan, D., Andrade, M. C. B., & Mason, A. C. (2008). Assessment during aggressive contests between male jumping spiders. *Animal Behaviour*, *76*(3), 901–910. https://doi.org/10.1016/j.anbehav.2008.01.032.Assessment

Elias, D. O., & Mason, A. C. (2011). Signaling in variable environments: substrate-borne signaling mechanisms and communication behavior in spiders. In *The Use of Vibrations in Communication: properties, mechanisms and function across taxa*. Kerala: Research Signpost.

Elias, D. O., & Mason, A. C. (2014). *The Role of Wave and Substrate Heterogeneity in Vibratory Communication : Practical Issues in Studying the Effect of Vibratory Environments in Communication* (R. B. Cocroft (ed.)). Springer-Verlag Berlin Heidelberg. https://doi.org/10.1007/978-3-662-43607-3

Elias, D. O., Mason, A. C., & Hebets, E. A. (2010). A signal-substrate match in the substrate-borne component of a multimodal courtship display. *Current Zoology*, *56*(3), 370–378. http://www.actazool.org/chinese/paperdetail.asp?id=11497

Elias, D. O., Mason, A. C., & Hoy, R. R. (2004). The effect of substrate on the efficacy of seismic courtship signal transmission in the jumping spider *Habronattus dossenus* (Araneae: Salticidae). *Journal of Experimental Biology*, *207*, 4105–4110. https://doi.org/10.1242/jeb.01261

Elias, D. O., Mason, A. C., Maddison, W. P., & Hoy, R. R. (2003). Seismic signals in a courting male jumping spider (Araneae: Salticidae). *Journal of Experimental Biology*, *206*(22), 4029–4039. https://doi.org/10.1242/jeb.00634

Endler, J. A. (1992). Signals, Signal Conditions, and the Direction of Evolution. *The American Naturalist*, *139*, S125-153.

Endo, J., Takanashi, T., Mukai, H., & Numata, H. (2019). Egg-Cracking Vibration as a Cue for Stink Bug Siblings to Synchronize Hatching. *Current Biology*, *29*(1), 143–148. https://doi.org/10.1016/j.cub.2018.11.024

Erens, H., Boudin, M., Mees, F., Mujinya, B. B., Baert, G., Van Strydonck, M., Boeckx, P., &

Van Ranst, E. (2015). The age of large termite mounds-radiocarbon dating of *Macrotermes falciger* mounds of the Miombo woodland of Katanga, DR Congo. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *435*, 265–271. https://doi.org/10.1016/j.palaeo.2015.06.017

Eriksson, A., Anfora, G., Lucchi, A., Lanzo, F., Virant-Doberlet, M., & Mazzoni, V. (2012). Exploitation of insect vibrational signals reveals a new method of pest management. *PLoS ONE*, *7*(3), 1–5. https://doi.org/10.1371/journal.pone.0032954

Evans, J. E., Cuthill, I. C., & Bennett, A. T. D. (2006). The effect of flicker from fluorescent lights on mate choice in captive birds. *Animal Behaviour*, *72*(2), 393–400. https://doi.org/10.1016/j.anbehav.2005.10.031

Evans, T. A., Lai, J. C. S., Toledano, E., Mcdowall, L., Rakotonarivo, S., & Lenz, M. (2005). Termites assess wood size by using vibration signals. *Proceedings of the National Academy of Sciences*, *102*(10), 1–6. https://doi.org/10.1073/pnas.0408649102

Fertin, A., & Casas, J. (2007). Orientation towards prey in antlions: efficient use of wave propagation in sand. *Journal of Experimental Biology*, *210*(19), 3337–3343. https://doi.org/10.1242/jeb.004473

Fidell, S., Pearsons, K., Silvati, L., & Sneddon, M. (2002). Relationship between low-frequency aircraft noise and annoyance due to rattle and vibration. *The Journal of the Acoustical Society of America*, *111*(4), 1743–1750. https://doi.org/10.1121/1.1448339

Foelix, R. F. (2011). *Biology of spiders*. Oxford University Press.

Forman, R. T. T. (2000). Estimate of the area affected ecologically by the road system in the United States. *Conservation Biology*, *14*(1), 31–35. https://doi.org/10.1046/j.1523-1739.2000.99299.x

Francis, C. D., & Barber, J. R. (2013). A framework for understanding noise impacts on wildlife: An urgent conservation priority. *Frontiers in Ecology and the Environment*, *11*(6), 305–313. https://doi.org/10.1890/120183

Francis, C. D., Kleist, N. J., Ortega, C. P., & Cruz, A. (2012). Noise pollution alters ecological services: Enhanced pollination and disrupted seed dispersal. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1739), 2727–2735. https://doi.org/10.1098/rspb.2012.0230

Friard, O., & Gamba, M. (2016). BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. *Methods in Ecology and Evolution*, *7*(11), 1325–1330. https://doi.org/10.1111/2041-210X.12584

Gaffin, D. D., & Curry, C. M. (2020). Review: Arachnid navigation-a review of classic and emerging models. *Journal of Arachnology*, *48*(3), 1–25. https://doi.org/10.1636/0161-8202-

48.3.351

García-Hernández, S., & Machado, G. (2017). Effectiveness of maternal egg attendance in an exclusively cave-dwelling harvestman (Arachnida: Opiliones). *Journal of Zoology*, *302*(4), 228–235. https://doi.org/10.1111/jzo.12452

Gerhardt, H. C. (1994). The evolution of vocalization in frogs and toads. *Annual Review of Ecology and Systematics*, *25*, 293–324. https://doi.org/10.1146/annurev.es.25.110194.001453

Gerhardt, H. C., & Huber, F. (2002). *Acoustic communication in insects and anurans: common problems and diverse solutions.* University of Chicago Press.

Ghalambor, C. K., & Martin, T. E. (2002). Comparative manipulation of predation risk in incubating birds reveals variability in the plasticity of responses. *Behavioral Ecology*, *13*(1), 101–108. https://doi.org/10.1093/beheco/13.1.101

Giaretta, A. A., & Menin, M. (2004). Reproduction, phenology and mortality sources of a species of Physalaemus (Anura: Leptodactylidae). *Journal of Natural History*, *38*(13), 1711–1722. https://doi.org/10.1080/00222930310001597286

Gibson, G., & Russell, I. (2006). Flying in Tune: Sexual Recognition in Mosquitoes. *Current Biology*, *16*(13), 1311–1316. https://doi.org/10.1016/j.cub.2006.05.053

Gillooly, J. F., Brown, J. H., West, G. B., Savage, V. M., & Charnov, E. L. (2001). Effects of size and temperature on metabolic rate. *Science*, *293*(5538), 2248–2251. https://doi.org/10.1126/science.1061967

Gillooly, James F., & Ophir, A. G. (2010). The energetic basis of acoustic communication. *Proceedings of the Royal Society B: Biological Sciences*, *277*(1686), 1325–1331. https://doi.org/10.1098/rspb.2009.2134

Gogala, M., & Riede, K. (1995). Time sharing of song activity by cicadas in Temengor forest reserve, Hulu Perak, and in Sabah, Malaysia. *Marayan Nature Journal*, *48*(January), 297–305.

Golet, G. H., Schmutz, J. A., Irons, D. B., & Estes, J. A. (2004). Determinants of reproductive costs in the long-lived black-legged Kittiwake: A multiyear experiment. *Ecological Monographs*, *74*(2), 353–372. https://doi.org/10.1890/02-4029

Gopfert, M. C., Humphris, A. D. L., Albert, J. T., Robert, D., & Hendrich, O. (2005). Power gain exhibited by motile mechanosensory neurons in *Drosophila* ears. *Proceedings of the National Academy of Sciences*, *102*(2), 325–330. papers2://publication/uuid/75FA1133-55C7-42EE-8FEA-F713FAFFF573

Göpfert, M. C., & Robert, D. (2001). Active auditory mechanics in mosquitoes. *Proceedings of* *the Royal Society B: Biological Sciences*, *268*(1465), 333–339. https://doi.org/10.1098/rspb.2000.1376

Göpfert, Martin C, & Robert, D. (2002). The mechanical basis of *Drosophila* audition. *Journal of Experimental Biology*, *205*, 1199–1208.

Gordon, S. D., & Uetz, G. W. (2012). Environmental interference: Impact of acoustic noise on seismic communication and mating success. *Behavioral Ecology*, *23*(4), 707–714. https://doi.org/10.1093/beheco/ars016

Goulson, D. (2019). The insect apocalypse, and why it matters. *Current Biology*, *29*(19), R967–R971. https://doi.org/10.1016/j.cub.2019.06.069

Greenfield, M. D. (2016). Evolution of Acoustic Communication in Insects. In G. S. Pollack, A. C. Mason, A. N. Popper, & R. R. Fay (Eds.), *Insect Hearing* (pp. 17–48). Springer International Publishing. https://doi.org/10:1007/978-3-319-28890-1

Haddad, C. R. (2012). A revision of the Afrotropical spider genus *Cambalida* Simon, 1909 (Araneae, Corinnidae). *ZooKeys*, *234*, 67–119. https://doi.org/10.3897/zookeys.234.3417

Haddad, C. R. (2013). A revision of the continental species of Copa Simon, 1885 (Araneae, Corinnidae) in the afrotropical region. In *ZooKeys* (Vol. 276). https://doi.org/10.3897/zookeys.276.4233

Halfwerk, W., & Slabbekoorn, H. (2015). Pollution going multimodal: The complex impact of the human-altered sensory environment on animal perception and performance. *Biology Letters*, *11*(4). https://doi.org/10.1098/rsbl.2014.1051

Halfwerk, W., & Van Oers, K. (2020). Anthropogenic noise impairs foraging for cryptic prey via cross-sensory interference. *Proceedings of the Royal Society B: Biological Sciences*, *287*(1924). https://doi.org/10.1098/rspb.2019.2951

Hallmann, C. A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., Stenmans, W., Müller, A., Sumser, H., Hörren, T., Goulson, D., & De Kroon, H. (2017). More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PLoS ONE*, *12*(10). https://doi.org/10.1371/journal.pone.0185809

Hanssen, S. A., Hasselquist, D., Folstad, I., & Erikstad, K. E. (2005). Cost of reproduction in a long-lived bird: Incubation effort reduces immune function and future reproduction. *Proceedings of the Royal Society B: Biological Sciences*, *272*(1567), 1039–1046. https://doi.org/10.1098/rspb.2005.3057

Harvey, J. A. (2008). Comparing and contrasting development and reproductive strategies in the pupal hyperparasitoids *Lysibia nana* and *Gelis agilis* (Hymenoptera: Ichneumonidae). *Evolutionary Ecology*, *22*, 153–166. https://doi.org/10.1007/s10682-007-9164-x

Hawkins, A. D., Hazelwood, R. A., Popper, A. N., & Macey, P. C. (2021). Substrate vibrations and their potential effects upon fishes and invertebrates. *The Journal of the Acoustical Society of America*, *149*(4), 2782–2790. https://doi.org/10.1121/10.0004773

Hayek, S. I. (1990). Mathematical Modeling of Absorbent Highway Noise Barriers. *Applied Acoustics*, *31*, 77–100.

Heckl, M., Hauck, G., & Wettschureck, R. (1996). Structure-borne sound and vibration from rail traffic. *Journal of Sound and Vibration*, *193*(1), 175–184. https://doi.org/10.1006/jsvi.1996.0257

Heinze, S., Narendra, A., & Cheung, A. (2018). Principles of Insect Path Integration. *Current Biology*, *28*(17), R1043–R1058. https://doi.org/10.1016/j.cub.2018.04.058

Hieber, C. S. (1992a). Spider cocoons and their suspension systems as barriers to generalist and specialist predators. *Oecologia*. https://doi.org/10.1007/BF00650327

Hieber, C. S. (1992b). The role of spider cocoons in controlling desiccation. *Oecologia*, *89*(3), 442–448. https://doi.org/10.1007/BF00317424

Hill, P. S. M. (2008). *Vibrational communication in animals*. Harvard University Press.

Hill, P. S. M. (2014). Stretching the Paradigm or Building a New? Development of a Cohesive Language for Vibrational Communication. In Reginald B. Cocroft, M. Gogala, P. S. M. Hill, & A. Wessel (Eds.), *Studying Vibrational Communication* (pp. 13–30). Springer-Verlag Berlin Heidelberg.

Hill, P. S. M., & Wessel, A. (2016). Biotremology. *Current Biology*, *26*(5), R187–R191. https://doi.org/10.1016/j.cub.2016.01.054

Hladik, M. L., Main, A. R., & Goulson, D. (2018). Environmental Risks and Challenges Associated with Neonicotinoid Insecticides. *Environmental Science and Technology*, *52*(6), 3329–3335. https://doi.org/10.1021/acs.est.7b06388

Hoch, H., Deckert, J., & Wessel, A. (2006). Vibrational signalling in a Gondwanan relict insect (Hemiptera: Coleorrhyncha: Peloridiidae). *Biology Letters*, *2*(2), 222–224. https://doi.org/10.1098/rsbl.2006.0451

Hofstetter, R. W., Dunn, D. D., Mcguire, R., & Potter, K. A. (2014). Using acoustic technology to reduce bark beetle reproduction. *Pest Management Science*, *70*(1), 24–27. https://doi.org/10.1002/ps.3656

Hoy, R. R., Pollack, G. S., & Moiseff, A. (1982). Species-Recognition in the Field Cricket, *Teleogryllus oceanicus*: Behavioral and Neural Mechanisms. *American Zoologist*, *22*, 597–607.

Humphrey, J. A. C., & Barth, F. G. (2008). Medium Flow-Sensing Hairs: Biomechanics and Models. In *Advances in Insect Physiology* (Vol. 34). https://doi.org/10.1016/S0065-2806(07)34001-0

Hunt, R. E., & Morton, T. L. (2001). Regulation of Chorusing in the Vibrational Communication System of the Leafhopper Graminella nigrifrons. *American Zoology*, *41*, 1222–1228.

Injaian, A. S., Poon, L. Y., & Patricelli, G. L. (2018). Effects of experimental anthropogenic noise on avian settlement patterns and reproductive success. *Behavioral Ecology*, *29*(5), 1181–1189. https://doi.org/10.1093/beheco/ary097

Injaian, A. S., Taff, C. C., & Patricelli, G. L. (2018). Experimental anthropogenic noise impacts avian parental behaviour, nestling growth and nestling oxidative stress. *Animal Behaviour*, *136*, 31–39. https://doi.org/10.1016/j.anbehav.2017.12.003

Injaian, A. S., Taff, C. C., Pearson, K. L., Gin, M. M. Y., Patricelli, G. L., & Vitousek, M. N. (2018). Effects of experimental chronic traffic noise exposure on adult and nestling corticosterone levels, and nestling body condition in a free-living bird. *Hormones and Behavior*, *106*(September), 19–27. https://doi.org/10.1016/j.yhbeh.2018.07.012

Ishimatsu, A., Yoshida, Y., Itoki, N., Takeda, T., Lee, H. J., & Graham, J. B. (2007). Mudskippers brood their eggs in air but submerge them for hatching. *Journal of Experimental Biology*, *210*(22), 3946–3954. https://doi.org/10.1242/jeb.010686

Jacobsen, F. (2007). Sound Intensity. In *Springer Handbook of Acoustics* (pp. 1053–1075). Springer.

Jain, M., Diwakar, S., Bahuleyan, J., Deb, R., & Balakrishnan, R. (2014). A rain forest dusk chorus: Cacophony or sounds of silence? *Evolutionary Ecology*, *28*(1), 1–22. https://doi.org/10.1007/s10682-013-9658-7

Kämper, G., & Kleindienst, H. U. (1990). Oscillation of cricket sensory hairs in a low-frequency sound field. *Journal of Comparative Physiology A*, *167*(2), 193–200. https://doi.org/10.1007/BF00188111

Kinsler, L. E., Frey, A. R., Coppens, A. B., & Sanders, J. V. (1999). *Fundamentals of Acoustics, 4th Edition*. Wiley-VCH.

Kirchner, W. H. (1994). Hearing in honeybees: the mechanical response to the bee’s antenna to near field sound. *Journal Of Comparative Physiology A*, *175*, 261–265. https://doi.org/10.1007/BF00192985

Klärner, D., & Barth, F. G. (1982). Vibratory signals and prey capture in orb-weaving spiders (*Zygiella x-notata*, *Nephila clavipes*; Araneidae). *Journal of Comparative Physiology A*, *148*(4), 445–455. https://doi.org/10.1007/BF00619783

Koch, U. T., Elliott, C. J. H., Schäffner, K. H., & Kleindienst, H. U. (1988). The mechanics of stridulation of the cricket *Gryllus campestris*. *Journal of Comparative Physiology A*, *162*(2), 213–223. https://doi.org/10.1007/BF00606086

Lampe, U., Reinhold, K., & Schmoll, T. (2014). How grasshoppers respond to road noise: Developmental plasticity and population differentiation in acoustic signalling. *Functional Ecology*, *28*(3), 660–668. https://doi.org/10.1111/1365-2435.12215

Lampe, U., Schmoll, T., Franzke, A., & Reinhold, K. (2012). Staying tuned: Grasshoppers from noisy roadside habitats produce courtship signals with elevated frequency components. *Functional Ecology*, *26*(6), 1348–1354. https://doi.org/10.1111/1365-2435.12000

Lapshin, D. N., & Vorontsov, D. D. (2017). Frequency organization of the Johnston organ in male mosquitoes (Diptera, Culicidae). *The Journal of Experimental Biology*, *220*, 3927–3938. https://doi.org/10.1242/jeb.152017

Larkin, R. P., Pater, L. L., & Tazik, D. J. (1996). *Effects of Military Noise on Wildlife: A Literature Review*.

Lecocq, T., Hicks, S. P., Noten, K. Van, Wijk, K. Van, & Koelemeijer, P. (2020). Global quieting of high-frequency seismic noise due to COVID-19 pandemic lockdown measures. *Science*, *369*(September), 1338–1343.

Lee, N., & Mason, A. C. (2017). How spatial release from masking may fail to function in a highly directional auditory system. *ELife*, *6*, 1–24. https://doi.org/10.7554/eLife.20731

Lee, R. E. (2010). A primer on insect cold tolerance. In D. L. Denlinger & R. E. Lee (Eds.), *Low Temperature Biology of Insects* (pp. 3–34). Cambridge University Press.

Li, D., & Jackson, R. R. (1996). How temperature affects development and reproduction in spiders: A review. *Journal of Thermal Biology*, *21*(4), 245–274. https://doi.org/10.1016/0306-4565(96)00009-5

Lima, S. L. (2009). Predators and the breeding bird: Behavioral and reproductive flexibility under the risk of predation. *Biological Reviews*, *84*(3), 485–513. https://doi.org/10.1111/j.1469-185X.2009.00085.x

Lister, B. C., & Garcia, A. (2018). Climate-driven declines in arthropod abundance restructure a rainforest food web. *Proceedings of the National Academy of Sciences of the United States of America*, *115*(44), E10397–E10406. https://doi.org/10.1073/pnas.1722477115

Lohrey, A. K., Clark, D. L., Gordon, S. D., & Uetz, G. W. (2009). Antipredator responses of wolf spiders (Araneae: Lycosidae) to sensory cues representing an avian predator. *Animal Behaviour*, *77*(4), 813–821. https://doi.org/10.1016/j.anbehav.2008.12.025

Long, C. V., Lepper, P. A., & Flint, J. A. (2011). Ultrasonic noise emissions from wind turbines:

potential effects on bat species. *11th International Congress on Noise as a Public Health Problem (ICBEN)*.

Losey, J. E., & Vaughan, M. (2006). The Economic Value of Ecological Services Provided by Insects. *BioScience*, *56*(4), 311. https://doi.org/10.1641/0006-3568(2006)56[311:TEVOES]2.0.CO;2

Luo, J., Siemers, B. M., & Koselj, K. (2015). How anthropogenic noise affects foraging. *Global Change Biology*, *21*(9), 3278–3289. https://doi.org/10.1111/gcb.12997

Luther, D., & Gentry, K. (2013). Sources of background noise and their influence on vertebrate acoustic communication. *Behaviour*, *150*(9–10), 1045–1068. https://doi.org/10.1163/1568539X-00003054

Lynch, H. J., Hodge, S., Albert, C., & Dunham, M. (2008). The greater yellowstone ecosystem: Challenges for regional ecosystem management. *Environmental Management*, *41*(6), 820–833. https://doi.org/10.1007/s00267-007-9065-3

Magal, C., Schöller, M., Tautz, J., & Casas, J. (2000). The role of leaf structure in vibration propagation. *The Journal of the Acoustical Society of America*, *108*(5), 2412–2418. https://doi.org/10.1121/1.1286098

Magnhagen, C. (1992). Parental care and predation risk in fish. *Annales Zoologici Fennici*, *29*, 227–232.

Mainwaring, M. C., & Hartley, I. R. (2013). The energetic costs of nest building in birds. *Avian Biology Research*, *6*(1), 12–17. https://doi.org/10.3184/175815512X13528994072997

Mainwaring, M. C., Hartley, I. R., Lambrechts, M. M., & Deeming, D. C. (2014). The design and function of birds' nests. *Ecology and Evolution*, *4*(20), 3909–3928. https://doi.org/10.1002/ece3.1054

Manley, G. A. (2012). Vertebrate hearing: Origin, evolution and functions. In F. G. Barth, P. Giampieri-Deutsch, & H. D. Klein (Eds.), *Sensory perception: Mind and matter* (pp. 23–40). Springer-Verlag Berlin Heidelberg.

Markl, H. (1983). Vibrational Communication. In H. Huber & H. Markl (Eds.), *Neuroethology and behavioral physiology* (pp. 332–353). Springer-Verlag Berlin Heidelberg.

Martin, T. E., Tobalske, B., Riordan, M. M., Case, S. B., & Dial, K. P. (2018). Age and performance at fledging are a cause and consequence of juvenile mortality between life stages. *Science Advances*, *4*(6), 1–9. https://doi.org/10.1126/sciadv.aar1988

Mason, J. T., McClure, C. J. W., & Barber, J. R. (2016). Anthropogenic noise impairs owl hunting behavior. *Biological Conservation*, *199*, 29–32. https://doi.org/10.1016/j.biocon.2016.04.009

Matsumoto, Y., & Mizunami, M. (2000). Olfactory learning in the cricket *Gryllus bimaculatus*. *Journal of Experimental Biology*, *203*(17), 2581–2588.

Mazzoni, V., Lucchi, A., Čokl, A., Prešern, J., & Virant-Doberlet, M. (2009). Disruption of the reproductive behaviour of *Scaphoideus titanus* by playback of vibrational signals. *Entomologia Experimentalis et Applicata*, *133*(2), 174–185. https://doi.org/10.1111/j.1570-7458.2009.00911.x

McGregor, P. K., Horn, A. G., Leonard, M. L., & Thomsen, F. (2013). Anthropogenic noise and conservation. In *Animal Communication and Noise* (pp. 409–444). Springer.

McLean, M. J., Bishop, P. J., & Nakagawa, S. (2012). Male quality, signal reliability and female choice: Assessing the expectations of inter-sexual selection. *Journal of Evolutionary Biology*, *25*(8), 1513–1520. https://doi.org/10.1111/j.1420-9101.2012.02533.x

McNett, G. D., & Cocroft, R. B. (2008). Host shifts favor vibrational signal divergence in Enchenopa binotata treehoppers. *Behavioral Ecology*, *19*(3), 650–656. https://doi.org/10.1093/beheco/arn017

Mcnett, G. D., Luan, L. H., & Cocroft, R. B. (2010). Wind-induced noise alters signaler and receiver behavior in vibrational communication. *Behavioral Ecology and Sociobiology*, *64*, 2043–2051. https://doi.org/10.1007/s00265-010-1018-9

Menda, G., Nitzany, E. I., Shamble, P. S., Wells, A., Harrington, L. C., Miles, R. N., & Hoy, R. R. (2019). The Long and Short of Hearing in the Mosquito Aedes aegypti. *Current Biology*, *29*(4), 709-714.e4. https://doi.org/10.1016/j.cub.2019.01.026

Mhatre, N., Montealegre-Z, F., Balakrishnan, R., & Robert, D. (2012). Changing resonator geometry to boost sound power decouples size and song frequency in a small insect. *Proceedings of the National Academy of Sciences*, *109*(22), E1444–E1452. https://doi.org/10.1073/pnas.1200192109

Mhatre, Natasha, & Robert, D. (2013). A tympanal insect ear exploits a critical oscillator for active amplification and tuning. *Current Biology*, *23*(19), 1952–1957. https://doi.org/10.1016/j.cub.2013.08.028

Michelsen, A., Fink, F., Gogala, M., & Traue, D. (1982). Plants as transmission channels for insect vibrational songs. *Behavioral Ecology and Sociobiology*, *11*(4), 269–281. https://doi.org/10.1007/BF00299304

Michelsen, A., Kirchner, W. H., Andersen, B. B., & Lindauer, M. (1986). The tooting and quacking vibration signals of honeybee queens: a quantitative analysis. *Journal of Comparative Physiology - A Sensory, Neural, and Behavioral Physiology, 158,* 605–611.

Miklas, N., Stritih, N., Čokl, A., Virant-Doberlet, M., & Renou, M. (2001). The influence of substrate on male responsiveness to the female calling song in *Nezara viridula*. *Journal of Insect Behavior*, *14*(3), 313–332. https://doi.org/10.1023/A:1011115111592

Montealegre-Z, F., & Mason, A. C. (2005). The mechanics of sound production in *Panacanthus pallicornis* (Orthoptera: Tettigoniidae: Conocephalinae): the stridulatory motor patterns. *Journal of Experimental Biology*, *208*(7), 1219–1237. https://doi.org/10.1242/jeb.01526

Montgomery, T. H. (1909). Further Studies on the Activities of Araneads, II. *Proceedings of the National Academy of Sciences of Philadelphia*, *61*(3), 548–569.

Morley, E. L., Jones, G., & Radford, A. N. (2014). The importance of invertebrates when considering the impacts of anthropogenic noise. *Proceedings of the Royal Society B: Biological Sciences*, *281*, 1–8. https://doi.org/10.1098/rspb.2013.2683

Morley, E. L., Jonsson, T., & Robert, D. (2018). Auditory sensitivity, spatial dynamics, and amplitude of courtship song in *Drosophila melanogaster*. *The Journal of the Acoustical Society of America*, *144*(2), 734–739. https://doi.org/10.1121/1.5049791

Morley, E. L., & Mason, A. C. (2015). Active auditory mechanics in female black-horned tree crickets (*Oecanthus nigricornis*). *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, *201*(12), 1147–1155. https://doi.org/10.1007/s00359-015-1045-0

Morris-Drake, A., Kern, J. M., & Radford, A. N. (2016). Cross-modal impacts of anthropogenic noise on information use. *Current Biology*, *26*(20), R911–R912. https://doi.org/10.1016/j.cub.2016.08.064

Morse, D. H. (1971). The Insectivorous Bird as an Adaptive Strategy. *Annual Review of Ecology and Systematics*, *2*(1), 177–200. https://doi.org/10.1146/annurev.es.02.110171.001141

Mortimer, B., Rees, W. L., Koelemeijer, P., & Nissen-Meyer, T. (2018). Classifying elephant behaviour through seismic vibrations. *Current Biology*, *28*(9), R547–R548. https://doi.org/10.1016/j.cub.2018.03.062

Morton, E. S. (1977). On the Occurrence and Significance of Motivation-Structural Rules in Some Bird and Mammal Sounds. *The American Naturalist*, *111*(981), 855–869. https://doi.org/10.1086/283219

Mulder, C. P. H., Koricheva, J., Huss-Danell, K., Högberg, P., & Joshi, J. (1999). Insects affect relationships between plant species richness and ecosystem processes. *Ecology Letters*, *2*(4), 237–246. https://doi.org/10.1046/j.1461-0248.1999.00070.x

Narins, P. M. (1990). Seismic Communication in Anuran Amphibians. *BioScience*, *40*(4), 268–274.

Narins, P. M. (2001). Vibration Communication in Vertebrates. In Friedrich G. Barth & A.

Schmidt (Eds.), *Ecology of Sensing* (pp. 127–148). Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-662-22644-5_7

Nedelec, S. L., Radford, A. N., Pearl, L., Nedelec, B., McCormick, M. I., Meekan, M. G., & Simpson, S. D. (2017). Motorboat noise impacts parental behaviour and offspring survival in a reef fish. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1856). https://doi.org/10.1098/rspb.2017.0143

Nemeth, E., & Brumm, H. (2010). Birds and Anthropogenic Noise: Are Urban Songs Adaptive? *The American Naturalist*, *176*(4), 465–475. https://doi.org/10.1086/656275

Ng, C. S., Des Brisay, P. G., & Koper, N. (2019). Chestnut-collared longspurs reduce parental care in the presence of conventional oil and gas development and roads. *Animal Behaviour*, *148*, 71–80. https://doi.org/10.1016/j.anbehav.2018.12.001

Nieri, R., & Mazzoni, V. (2018). Vibrational mating disruption of *Empoasca vitis* by natural or artificial disturbance noises. *Pest Management Science*. https://doi.org/10.1002/ps.5216

Noriega, J. A., Hortal, J., Azcárate, F. M., Berg, M. P., Bonada, N., Briones, M. J. I., Del Toro, I., Goulson, D., Ibanez, S., Landis, D. A., Moretti, M., Potts, S. G., Slade, E. M., Stout, J. C., Ulyshen, M. D., Wackers, F. L., Woodcock, B. A., & Santos, A. M. C. (2018). Research trends in ecosystem services provided by insects. *Basic and Applied Ecology*, *26*, 8–23. https://doi.org/10.1016/j.baae.2017.09.006

O'Connell-Rodwell, C. E., Arnason, B. T., & Hart, L. A. (2000). Seismic properties of Asian elephant ( Elephas maximus ) vocalizations and locomotion . *The Journal of the Acoustical Society of America*, *108*(6), 3066–3072. https://doi.org/10.1121/1.1323460

Oberweger, K., & Goller, F. (2001). The metabolic cost of birdsong production. *Journal of Experimental Biology*, *204*(19), 3379–3388. https://doi.org/10.1242/jeb.204.19.3379

Orci, K. M., Petroczki, K., & Barta, Z. (2016). Instantaneous song modification in response to fluctuating traffic noise in the tree cricket *Oecanthus pellucens*. *Animal Behaviour*, *112*, 187–194.

Ortega, C. P. (2012). Chapter 2 : Effects of noise pollution on birds : A brief review of our knowledge. *Ornithological Monographs*, *74*(1), 6–22. https://doi.org/10.1525/om.2012.74.1.6.6

Ota, D., & Čokl, A. (1991). Mate location in the southern green stink bug, *Nezara Viridula* (Heteroptera: Pentatomidae), mediated through substrate-borne signals on ivy. *Journal of Insect Behavior*, *4*(4), 441–447. https://doi.org/10.1007/BF01049329

Ota, N. (2020). Tap dancers in the wild: field observations of multimodal courtship displays in socially monogamous songbirds. *Science of Nature*, *107*(4). https://doi.org/10.1007/s00114-020-01686-x

Pandit, M. M., Eapen, J., Pineda-Sabillon, G., Caulfield, M. E., Moreno, A., Wilhelm, J., Ruyle, J. E., Bridge, E. S., & Proppe, D. S. (2021). Anthropogenic noise alters parental behavior and nestling developmental patterns, but not fledging condition. *Behavioral Ecology*, 1–9. https://doi.org/10.1093/beheco/arab015

Patricelli, G. P., & Blickley, J. L. (2006). Avian communication in urban noise: causes and consequences of vocal adjustment. *The Auk*, *123*(3), 639–649. https://doi.org/10.1642/0004-8038(2006)123[639:ACIUNC]2.0.CO;2

Pfannenstiel, R. S., Hunt, R. E., & Yeargan, K. V. (1995). Orientation of a hemipteran predator to vibrations produced by feeding caterpillars. *Journal of Insect Behavior*, *8*(1), 1–9. https://doi.org/10.1007/BF01990965

Phillips, M. E., Chio, G., Hall, C. L., ter Hofstede, H. M., & Howard, D. R. (2020). Seismic noise influences brood size dynamics in a subterranean insect with biparental care. *Animal Behaviour*, *161*, 15–22. https://doi.org/10.1016/j.anbehav.2019.12.010

Picciulin, M., Sebastianutto, L., Codarin, A., Farina, A., & Ferrero, E. A. (2010). In situ behavioural responses to boat noise exposure of *Gobius cruentatus* (Gmelin, 1789; fam. Gobiidae) and *Chromis chromis* (Linnaeus, 1758; fam. Pomacentridae) living in a Marine Protected Area. *Journal of Experimental Marine Biology and Ecology*, *386*(1–2), 125–132. https://doi.org/10.1016/j.jembe.2010.02.012

Pike, D. a., Webb, J. K., & Shine, R. (2012). Hot mothers, cool eggs: nest-site selection by egg-guarding spiders accommodates conflicting thermal optima. *Functional Ecology*, *26*(2), 469–475. https://doi.org/10.1111/j.1365-2435.2011.01946.x

Polajnar, J., & Čokl, A. (2008). The effect of vibratory distrubance on sexual behaviour of the southern green stink bug *Nezara viridula*. *Central European Journal of Biology*, *3*(2), 189–197. https://doi.org/10.2478/s11535-008-0008-7

Polajnar, J., Eriksson, A., Lucchi, A., Anfora, G., Virant-Doberlet, M., & Mazzoni, V. (2015). Manipulating behaviour with substrate-borne vibrations - Potential for insect pest control. *Pest Management Science*, *71*(1), 15–23. https://doi.org/10.1002/ps.3848

Potts, S. G., Biesmeijer, J. C., Kremen, C., Neumann, P., Schweiger, O., & Kunin, W. E. (2010). Global pollinator declines: trends, impacts and drivers. *Trends in Ecology and Evolution*, *25*(6), 345–353. https://doi.org/10.1016/j.tree.2010.01.007

Press, F., & Ewing, M. (1951). Theory of air-coupled flexural waves. *Journal of Applied Physics*, *22*, 892–899. https://doi.org/10.1063/1.1700069

Prestwich, K. N. (1994). The energetics of acoustic signaling in anurans and insects. *American Zoology*, *34*(6), 625–643. https://doi.org/10.1093/icb/34.6.625

Prestwich, K. N., Brugger, K. E., & Topping, M. (1989). Energy and Communication in Three Species of Hylid Frogs: Power Input, Power Output and Efficiency. *Journal of Experimental Biology*, *144*, 53–80.

Purser, J., & Radford, A. N. (2011). Acoustic noise induces attention shifts and reduces foraging performance in three-spined sticklebacks (*Gasterosteus aculeatus*). *PLoS ONE*, *6*(2). https://doi.org/10.1371/journal.pone.0017478

Quiroga, N., Muñoz, M. I., Pérez-Espinoza, S. A., Penna, M., & Botto-Mahan, C. (2020). Stridulation in the wild kissing bug *Mepraia spinolai*: description of the stridulatory organ and vibratory disturbance signal. *Bioacoustics*, *29*(3), 266–279. https://doi.org/10.1080/09524622.2019.1603120

R Core Team. (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Raboin, M., & Elias, D. O. (2019). Anthropogenic noise and the bioacoustics of terrestrial invertebrates. *Journal of Experimental Biology*, *222*(12). https://doi.org/10.1242/jeb.178749

Raboin, M., & Elias, D. O. (2021). Built to last a day: The function and benefits of spider mound nests. *Ethology*, *127*(3), 238–245. https://doi.org/10.1111/eth.13120

Radford, A. N., Kerridge, E., & Simpson, S. D. (2014). Acoustic communication in a noisy world: Can fish compete with anthropogenic noise? *Behavioral Ecology*, *25*(5), 1022–1030. https://doi.org/10.1093/beheco/aru029

Read, J., Jones, G., & Radford, A. N. (2014). Fitness costs as well as benefits are important when considering responses to anthropogenic noise. *Behavioral Ecology*, *25*(1), 4–7. https://doi.org/10.1093/beheco/art102

Reguera, P., & Gomendio, M. (1999). Predation costs associated with parental care in the golden egg bug *Phyllomorpha laciniata* (Heteroptera: Coreidae). *Behavioral Ecology*, *10*(5), 541–544. https://doi.org/10.1093/beheco/10.5.541

Reichert, M. S. (2015). Effects of noise on sound localization in male grasshoppers, *Chorthippus biguttulus*. *Animal Behaviour*, *103*, 125–135. https://doi.org/10.1016/j.anbehav.2015.02.020

Reichert, M. S., & Ronacher, B. (2015). Noise affects the shape of female preference functions for acoustic signals. *Evolution*, *69*(2), 381–394. https://doi.org/10.1111/evo.12592

Reichman, O. J., & Smith, S. C. (1990). Burrows and Burrowing Behavior by Mammals. In H. H. Genoways (Ed.), *Current Mammalogy* (pp. 197–244). Plenum Press.

Reiskind, J. (1969). Spider Subfamily Castianeirinae of North and Central America (Araneae, Clubionidae). *Harvard Univ Mus Compar Zool Bull*, *138*, 163–326.

Riahi, N., & Gerstoft, P. (2015). The seismic traffic footprint: Tracking trains, aircraft, and cars seismically. *Geophysical Research Letters*, *42*(8), 2674–2681. https://doi.org/10.1002/2015GL063558

Riechert, S. E., & Hedrick, A. V. (1990). Levels of predation and genetically based anti-predator behaviour in the spider, *Agelenopsis aperta*. *Animal Behaviour*, *40*(4), 679–687. https://doi.org/10.1016/S0003-3472(05)80697-9

Riffell, J. A., Shlizerman, E., Sanders, E., Abrell, L., Medina, B., Hinterwirth, A. J., & Kutz, J. N. (2014). Flower discrimination by pollinators in a dynamic chemical environment. *Science*, *344*(6191), 1515–1518. https://doi.org/10.1126/science.1251041

Roberts, L., Cheesman, S., Elliott, M., & Breithaupt, T. (2016). Sensitivity of *Pagurus bernhardus* (L.) to substrate-borne vibration and anthropogenic noise. *Journal of Experimental Marine Biology and Ecology*, *474*, 185–194. https://doi.org/10.1016/j.jembe.2015.09.014

Roca, I. T., Desrochers, L., Giacomazzo, M., Bertolo, A., Bolduc, P., Deschesnes, R., Martin, C. A., Rainville, V., Rheault, G., & Proulx, R. (2016). Shifting song frequencies in response to anthropogenic noise: A meta-analysis on birds and anurans. *Behavioral Ecology*, *27*(5), 1269–1274. https://doi.org/10.1093/beheco/arw060

Rodríguez, R. L., Araya-Salas, M., Gray, D. A., Reichert, M. S., Symes, L. B., Wilkins, M. R., Safran, R. J., & Höbel, G. (2015). How acoustic signals scale with individual body size: Common trends across diverse taxa. *Behavioral Ecology*, *26*(1), 168–177. https://doi.org/10.1093/beheco/aru174

Rohrig, A., Kirchner, W. H., & Leuthold, R. H. (1999). Vibrational alarm communication in the African fungus-growing termite genus Macrotermes (Isoptera, Termitidae). *Insectes Sociaux*, *46*, 71–77.

Rojas, A., Solano-brenes, D., Muniz, D. G., & Machado, G. (2019). Gone with the rain : negative effects of rainfall on male reproductive success in a nest-building arachnid. *Behavioral Ecology*, *30*(4), 1145–1156. https://doi.org/10.1093/beheco/arz063

Romer, H. (2013). Masking by Noise in Acoustic Insects: Problems and Solutions. In H. Brumm (Ed.), *Animal Communication and Noise* (pp. 33–63). Springer-Verlag Berlin Heidelberg.

Rosenthal, M. F., Gertler, M., Hamilton, A. D., Prasad, S., & Andrade, M. C. B. (2017). Taxonomic bias in animal behaviour publications. *Animal Behaviour*, *127*, 83–89. https://doi.org/10.1016/j.anbehav.2017.02.017

Rosenthal, M. F., & Hebets, E. A. (2012). Resource heterogeneity interacts with courtship rate to influence mating success in the wolf spider *Schizocosa floridana*. *Animal Behaviour*, *84*(6), 1341–1346. https://doi.org/10.1016/j.anbehav.2012.08.028

Ryan, M. J. ., & Brenowitz, E. A. (2010). The Role of Body Size, Phylogeny, and Ambient Noise in the Evolution of Bird Song. *The American Naturalist*, *126*(1), 87–100.

Sabat, A. M. (1994). Costs and benefits of parental effort in a brood-guarding fish (Ambloplites rupestris, Centrarchidae). *Behavioral Ecology*, *5*(2), 195–201. https://doi.org/10.1093/beheco/5.2.195

Sage, R. (1982). Wet and Dry-weight Estimates of Insects and Spiders Based on Length Author ( s ): Richard D . Sage Source : The American Midland Naturalist , Vol . 108 , No . 2 ( Oct ., 1982 ), pp . 407-411 Published by : The University of No. *The American Midland Naturalist*, *108*(2), 407–411.

Samarra, F. I. R., Klappert, K., Brumm, H., & Miller, P. J. O. (2009). Background noise constrains communication : acoustic masking of courtship song in the fruit fly *Drosophila montana*. *Behaviour*, *146*(12), 1635–1648.

Sanborn, A. F. (1997). Body temperature and the acoustic behavior of the cicada *Tibicen winnemanna* (Homoptera: Cicadidae). *Journal of Insect Behavior*, *10*(2), 257–264. https://doi.org/10.1007/BF02765558

Sane, S. P., & Jacobson, N. P. (2006). Induced airflow in flying insects II. Measurement of induced flow. *Journal of Experimental Biology*, *209*(1), 43–56. https://doi.org/10.1242/jeb.01958

Santer, R. D., & Hebets, E. A. (2008). Agonistic signals received by an arthropod filiform hair allude to the prevalence of near-field sound communication. *Proceedings of the Royal Society B: Biological Sciences*, *275*(1633), 363–368. https://doi.org/10.1098/rspb.2007.1466

Schaedelin, F. C., & Taborsky, M. (2009). Extended phenotypes as signals. *Biological Reviews*, *84*(2), 293–313. https://doi.org/10.1111/j.1469-185X.2008.00075.x

Schaub, A., Ostwald, J., & Siemers, B. M. (2008). Foraging bats avoid noise. *Journal of Experimental Biology*, *211*, 3174–3180. https://doi.org/10.1242/jeb.022863

Schmidt, A. K. D., Riede, K., & Romer, H. (2011). High background noise shapes selective auditory filters in a tropical cricket. *Journal of Experimental Biology*, *214*(10), 1754–1762. https://doi.org/10.1242/jeb.053819

Schmidt, Arne K.D., & Balakrishnan, R. (2015). Ecology of acoustic signalling and the problem of masking interference in insects. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, *201*(1), 133–142. https://doi.org/10.1007/s00359-014-0955-6

Schmidt, Arne K.D., & Römer, H. (2011). Solutions to the cocktail party problem in insects: Selective filters, spatial release from masking and gain control in tropical crickets. *PLoS*

*ONE*, *6*(12). https://doi.org/10.1371/journal.pone.0028593

Schmidt, R., Morrison, A., & Kunc, H. P. (2014). Sexy voices - no choices: Male song in noise fails to attract females. *Animal Behaviour*, *94*, 55–59. https://doi.org/10.1016/j.anbehav.2014.05.018

Schneider, C. A., Rasband, W. S., & Eliceiri, K. W. (2012). NIH Image to ImageJ: 25 years of image analysis. *Nature Methods*, *9*(7), 671–675. https://doi.org/10.1038/nmeth.2089

Schneirla, T. C., Brown, R. Z., & Brown, F. C. (1954). The Bivouac or Temporary Nest as an Adaptive Factor in Certain Terrestrial Species of Army Ants. *Ecological Monographs*, *24*(3), 269–296.

Service, N. P. (2021). Yellowstone Visitation Statistics for June 2021. https://www.nps.gov/yell/learn/news/21020.htm

Shamble, P. S., Menda, G., Golden, J. R., Nitzany, E. I., Walden, K., Beatus, T., Elias, D. O., Cohen, I., Miles, R. N., & Hoy, R. R. (2016). Airborne Acoustic Perception by a Jumping Spider. *Current Biology*, *26*(21), 2913–2920. https://doi.org/10.1016/j.cub.2016.08.041

Shannon, G., Mckenna, M. F., Angeloni, L. M., Crooks, K. R., Fristrup, K. M., Brown, E., Warner, K. A., Nelson, M. D., White, C., Briggs, J., Mcfarland, S., & Wittemyer, G. (2016). A synthesis of two decades of research documenting the effects of noise on wildlife. *Biological Reviews*, *91*, 982–1005. https://doi.org/10.1111/brv.12207

Shaw, S. R. (1994). Re-evaluation of the absolute threshold and response mode of the most sensitive know “vibration” detector, the cockroach’s subgenual organ: A cochlea-like displacement threshold and a direct response to sound. *Journal of Neurobiology*, *25*(9), 1167–1185. https://doi.org/10.1002/neu.480250911

Shieh, Bao-sen, Liang, S., & Chiu, Y. (2015). Acoustic and Temporal Partitioning of Cicada Assemblages in City and Mountain Environments. *PLoS ONE*, 1–13. https://doi.org/10.1371/journal.pone.0116794

Shieh, Bao Sen, Liang, S. H., Chen, C. C., Loa, H. H., & Liao, C. Y. (2012). Acoustic adaptations to anthropogenic noise in the cicada *Cryptotympana takasagona* Kato (Hemiptera: Cicadidae). *Acta Ethologica*, *15*(1), 33–38. https://doi.org/10.1007/s10211-011-0105-x

Shier, D. M., Lea, A. J., & Owen, M. A. (2012). Beyond masking: Endangered Stephen’s kangaroo rats respond to traffic noise with footdrumming. *Biological Conservation*, *150*(1), 53–58. https://doi.org/10.1016/j.biocon.2012.03.007

Shimozawa, T., & Kanou, M. (1984). Varieties of filiform hairs: range fractionation by sensory afferents and cercal interneurons of a cricket. *Journal of Comparative Physiology A*, *155*, 485–493. https://doi.org/10.1097/00063110-199912000-00020

Siemers, B. M., & Schaub, A. (2011). Hunting at the highway: Traffic noise reduces foraging efficiency in acoustic predators. *Proceedings of the Royal Society B: Biological Sciences*, *278*(1712), 1646–1652. https://doi.org/10.1098/rspb.2010.2262

Simmons, L. W. (1995). Correlates of male quality in the field cricket, *Gryllus campestris* L.: Age, size, and symmetry determine pairing success in field populations. *Behavioral Ecology*, *6*(4), 376–381. https://doi.org/10.1093/beheco/6.4.376

Simpson, S. D., Radford, A. N., Nedelec, S. L., Ferrari, M. C. O., Chivers, D. P., McCormick, M. I., & Meekan, M. G. (2016). Anthropogenic noise increases fish mortality by predation. *Nature Communications*, *7*. https://doi.org/10.1038/ncomms10544

Slabbekoorn, H., & Ripmeester, E. A. P. (2008). Birdsong and anthropogenic noise: Implications and applications for conservation. *Molecular Ecology*, *17*(1), 72–83. https://doi.org/10.1111/j.1365-294X.2007.03487.x

Starck, M. J., & Ricklefs, R. E. (1998). Patterns of Development: The Altricial-Precocial Spectrum. In M. J. Starck & R. E. Ricklefs (Eds.), *Avian Growth and Development. Evolution within the altricial precocial spectrum* (pp. 3–30). Oxford University Press.

Stritih-Peljhan, N., & Virant-Doberlet, M. (2021). Vibrational signalling, an underappreciated mode in cricket communication. *Science of Nature*, *108*(5). https://doi.org/10.1007/s00114-021-01749-7

Takegaki, T., & Nakazono, A. (2000). The role of mounds in promoting water-exchange in the egg-tending burrows of monogamous goby, *Valenciennea longipinnis* (Lay et Bennett). *Journal of Experimental Marine Biology and Ecology*, *253*(2), 149–163. https://doi.org/10.1016/S0022-0981(00)00251-3

Talotte, C., Gautier, P. E., Thompson, D. J., & Hanson, C. (2003). Identification, modelling and reduction potential of railway noise sources: A critical survey. *Journal of Sound and Vibration*, *267*(3), 447–468. https://doi.org/10.1016/S0022-460X(03)00707-7

Tauber, E., & Eberl, D. F. (2003). Acoustic communication in Drosophila. *Behavioural Processes*, *64*(2), 197–210. https://doi.org/10.1016/S0376-6357(03)00135-9

Tautz, J., & Markl, H. (1978). Caterpillars detect flying wasps by hairs sensitive to airborne vibration. *Behavioral Ecology and Sociobiology*, *4*, 101–110. https://doi.org/10.1111/jace.13793

ter Hofstede, H. M., & Ratcliffe, J. M. (2016). Evolutionary escalation: the bat–moth arms race. *The Journal of Experimental Biology*, *219*(11), 1589–1602. https://doi.org/10.1242/jeb.086686

Thompson, K. R., & Furness, R. W. (1991). The influence of rainfall and nest-site quality on the population dynamics of the Manx shearwater *Puffinus puffinus* on Rhum. *Journal of Zoology London*, *225*, 427–437.

Tonini, J. F. R., Provete, D. B., Maciel, N. M., Morais, A. R., Goutte, S., Toledo, L. F., & Pyron, R. A. (2020). Allometric escape from acoustic constraints is rare for frog calls. *Ecology and Evolution*, *10*(8), 3686–3695. https://doi.org/10.1002/ece3.6155

Toyama, M. (1999). Adaptive Advantages of Maternal Care and Matriphagy in a Foliage Spider. *Journal of Ethology*, *17*, 33–39.

Tsujiuchi, S., Sivan-Loukianova, E., Eberl, D. F., Kitagawa, Y., & Kadowaki, T. (2007). Dynamic range compression in the honey bee auditory system toward waggle dance sounds. *PLoS ONE*, *2*. https://doi.org/10.1371/journal.pone.0000234

Tuckerman, J. F., Gwynne, D. T., & Morris, G. K. (1993). Reliable acoustic cues for female mate preference in a katydid (*Scudderia curvicauda*, Orthoptera: Tettigoniidae). *Behavioral Ecology*, *4*(2), 106–113.

Van Baarlen, P., Topping, C. J., & Sunderland, K. D. (1996). Host location by *Gelis festinans*, an eggsac parasitoid of the linyphiid spider *Erigone atra*. *Entomologia Experimenmhs EtApplicata*, *81*(155), 155–163. https://doi.org/10.1111/j.1570-7458.1996.tb02027.x

Van Staaden, M. J., & Römer, H. (1997). Sexual Signalling in Bladder Grasshoppers: Tactical Design for Mazimizing Calling Range. *Journal of Experimental Biology*, *200*, 2597–2608.

Velilla, E., Bellato, L., Collinson, E., & Halfwerk, W. (2021). Effect of anthropogenic vibratory noise on plant development and herbivory. *BioRxiv*. https://doi.org/10.1101/2021.04.28.441746

Velilla, E., Collinson, E., Bellato, L., Berg, M. P., & Halfwerk, W. (2021). Vibrational noise from wind energy-turbines negatively impacts earthworm abundance. *Oikos*, *130*(6), 844–849. https://doi.org/10.1111/oik.08166

Wagner, W. E., & Reiser, M. G. (2000). The importance of calling song and courtship song in female mate choice in the variable field cricket. *Animal Behaviour*, *59*(6), 1219–1226. https://doi.org/10.1006/anbe.1999.1428

Wang, J., Hannon, G. J., & Beach, D. H. (2000). Do cockroaches “know” about fluid dynamics? *Nature*, *405*, 756.

Warkentin, K. M. (1995). Adaptive plasticity in hatching age: A response to predation risk trade-offs. *Proceedings of the National Academy of Sciences*, *92*(April), 3507–3510.

Weimerskirch, H. (1995). Regulation of foraging trips and incubation routine in male and female wandering albatrosses. *Oecologia*, *102*(1), 37–43. https://doi.org/10.1007/BF00333308

Wignall, A. E., Jackson, R. R., Wilcox, R. S., & Taylor, P. W. (2011). Exploitation of environmental noise by an araneophagic assassin bug. *Animal Behaviour*, *82*(5), 1037–1042. https://doi.org/10.1016/j.anbehav.2011.07.038

Wignall, A. E., & Taylor, P. W. (2011). Assassin bug uses aggressive mimicry to lure spider prey. *Proceedings of the Royal Society B: Biological Sciences*, *278*(1710), 1427–1433. https://doi.org/10.1098/rspb.2010.2060

Wilcox, R. S., Jackson, R. R., & Gentile, K. (1996). Spiderweb smokescreens: Spider trickster uses background noise to mask stalking movements. *Animal Behaviour*, *51*(2), 313–326. https://doi.org/10.1006/anbe.1996.0031

Wood, W. E., & Yezerinac, S. M. (2006). Song Sparrow (*Melospiza melodia*) Song Varies with Urban Noise. *The Auk*, *123*(3), 650–659.

Wu, C., & Elias, D. O. (2014). Vibratory noise in anthropogenic habitats and its effect on prey detection in a web-building spider. *Animal Behaviour*, *90*, 47–56. https://doi.org/10.1016/j.anbehav.2014.01.006

Wyatt, T. D. (1986). How a subsocial intertidal beetle, *Bledius spectabilis*, prevents flooding and anoxia in its burrow. *Behavioral Ecology and Sociobiology*, *19*(5), 323–331. https://doi.org/10.1007/BF00295705

Yack, J. E., Smith, M. L., & Weatherhead, P. J. (2001). Caterpillar talk: Acoustically mediated territoriality in larval Lepidoptera. *Proceedings of the National Academy of Sciences*, *98*(20), 11371–11375. https://doi.org/10.1073/pnas.191378898

Yang, L. H., & Gratton, C. (2014). Insects as drivers of ecosystem processes. *Current Opinion in Insect Science*, *2*, 26–32. https://doi.org/10.1016/j.cois.2014.06.004

Zhou, J., & Miles, R. N. (2017). Sensing fluctuating airflow with spider silk. *Proceedings of the National Academy of Sciences*, *114*, 12120–12125. https://doi.org/10.1073/pnas.1710559114

Appendix 1. Data shown in Figures 2.1-2.4. Body mass (grams wet), temperature (°C), frequency (*f*) in kHz, and (*r*) in calls per second.

| Class | Order | Family | Genus species | body mass | temp | f | r | habitat | mech. | context | Ref. |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Amphibia | | | | | | | | | | | |
| | Anura | | | | | | | | | | |
| | | Aromobatidae | | | | | | | | | |
| | | | Anomaloglossus beebei | | 25.2 | 5.200 | | plants | tremulation | mating | 1 |
| | | Leptodactylidae | | | | | | | | | |
| | | | Leptodactylus albilabris | | | 0.045 | 4 | plants | percussion | mating | 2 |
| | | Phyllomedusidae | | | | | | | | | |
| | | | Agalychnis callidryas | | | | 13.28 | plants | tremulation | agonistic interactions | 3 |
| | | | Agalychnis moreletii | | | 0.007 | | plants | tremulation | agonistic interactions | 4 |
| Arachnida | | | | | | | | | | | |
| | Araneae | | | | | | | | | | |
| | | Lycosidae | | | | | | | | | |
| | | | Gladicosa gulosa | 0.200 | 24 | | 3.00 | litter | percussion | mating | 5 |
| | | | Gladicosa gulosa | 0.200 | 24 | | 1.49 | litter | stridulation | mating | 5 |
| | | | Hygrolycosa rubrofasciata | 0.015 | 22 | | 29.00 | plants | percussion | mating | 6 |
| | | | Lycosa tarentula | 1.422 | 24.5 | 1.260 | | litter | unknown | mating | 7 |
| | | | Schizocosa stridulans | 0.021 | 21 | 1.045 | 80.00 | plants | stridulation | mating | 8 |
| | | | Schizocosa stridulans | 0.021 | 21 | 0.106 | 33.00 | plants | tremulation | mating | 8 |
| | | Salticidae | | | | | | | | | |
| | | | Cosmophasis umbratica | 0.014 | 25 | | 7.30 | plants | percussion | mating | 9 |
| | | | Cosmophasis umbratica | 0.014 | 25 | 0.133 | 0.70 | plants | tremulation | mating | 9 |
| | | | Habronattus dossenus | | 21 | 0.230 | 5.70 | litter | stridulation | mating | 10 |
| | | | Habronattus dossenus | | 21 | 0.065 | | litter | tremulation | mating | 10 |
| | | | Habronattus pugillis | | 21 | 1.082 | | litter | unknown | mating | 11 |
| | | | Maratus volans | 0.010 | 21 | 0.084 | 12.10 | litter | unknown | mating | 12 |

|  |  |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|---|
| Phidippus clarus | 0.044 | 21 | 0.068 | 2.14 | soil | tremulation | mating | 13 |
| Sicariidae |  |  |  |  |  |  |  |  |
| Loxosceles intermedia | 0.038 | 25 | 0.049 | 3.68 | unknown | stridulation | mating | 14 |
| Sparassidae |  |  |  |  |  |  |  |  |
| Heteropoda venatoria | 0.102 | 19.5 | 0.108 |  | plants | unknown | mating | 15 |
| Trechaleidae |  |  |  |  |  |  |  |  |
| Cupiennius salei | 1.984 | 21 | 0.075 | 2.68 | plants | tremulation | mating | 16 |
| Uloboridae |  |  |  |  |  |  |  |  |
| Uloborus plumipes | 0.009 | 21 | 0.023 |  | webs | web-shaking | agonistic interactions | 17 |
| Opiliones |  |  |  |  |  |  |  |  |
| Stygnopsidae |  |  |  |  |  |  |  |  |
| Hoplobunus mexicanus |  | 21 | 3.000 | 4.35 | plants | stridulation | distress | 18 |
| Scorpiones |  |  |  |  |  |  |  |  |
| Buthidae |  |  |  |  |  |  |  |  |
| Centruroides margaritatus | 0.037 | 25 | 0.487 | 35.71 | litter | tremulation | mating | 19 |
| Insecta |  |  |  |  |  |  |  |  |
| Blattodea |  |  |  |  |  |  |  |  |
| Rhinotermitidae |  |  |  |  |  |  |  |  |
| Reticulitermes flavipes | 0.005 | 26 |  | 31.00 | soil | percussion | alarm calling | 20 |
| Termitidae |  |  |  |  |  |  |  |  |
| Constrictotermes cyphergaster | 0.003 | 27 |  | 23.64 | soil | percussion | alarm calling | 21 |
| Macrotermes bellicosus |  |  | 0.977 | 26.00 | soil | percussion | alarm calling | 22 |
| Macrotermes natalensis |  | 21 | 2.600 | 11.00 | soil | percussion | alarm calling | 23 |
| Macrotermes subhyalinus |  |  | 0.852 | 13.00 | soil | percussion | alarm calling | 22 |
| Mastotermes darwiniensis | 0.036 | 26 |  | 18.18 | plants | percussion | alarm calling | 24 |
| Coleoptera |  |  |  |  |  |  |  |  |
| Cerambycidae |  |  |  |  |  |  |  |  |
| Hylotrupes bajulus | 0.119 | 20 | 0.550 | 11.11 | plants | stridulation | mating | 25 |
| Curculionidae |  |  |  |  |  |  |  |  |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Dendroctonus ponderosae | 0.011 | 22 | 4.900 | 2.10 | plants | stridulation | mating | 26 |
| Ips pini | 0.006 | 21 | | 7.28 | plants | stridulation | distress | 27 |
| Platypus quercivorus | 0.008 | 27.5 | | 6.31 | plants | stridulation | mating | 28 |
| Polygraphus nigrielytris | 0.004 | 21 | 8.018 | 4.34 | plants | stridulation | mating | 29 |
| Polygraphus proximus | 0.004 | 21 | 7.961 | 1.03 | plants | stridulation | mating | 29 |
| Polygraphus subopacus | 0.003 | 21 | 8.715 | 3.13 | plants | stridulation | mating | 29 |
| Geotrupidae | | | | | | | | |
| Trypocorpris alpinus | 0.088 | 21 | 1.280 | | soil | stridulation | distress | 30 |
| Trypocorpris pyrenaeus | 0.214 | 21 | 1.160 | | soil | stridulation | distress | 30 |
| Trypocorpris vernalis | 0.209 | 21 | 1.910 | | soil | stridulation | distress | 30 |
| Ptinidae | | | | | | | | |
| Xestobium rufovillosum | 0.009 | 19 | | 11.60 | plants | percussion | mating | 31 |
| Scarabaeidae | | | | | | | | |
| Trypoxylus dichotoma | 25.000 | 25.5 | 0.100 | 0.77 | soil | percussion | agonistic interactions | 32 |
| Tenebrionidae | | | | | | | | |
| Eupsophulus castaneus | | 25 | | 5.35 | plants | percussion | mating | 33 |
| Eusattus convexus | 0.054 | 21 | | 25.60 | litter | percussion | mating | 34 |
| Eusattus muricatus | 0.081 | 25 | | 23.40 | litter | percussion | mating | 35 |
| Eusattus reticulatus | 0.114 | 25 | | 30.00 | litter | percussion | mating | 35 |
| Eusattus robustus | 0.189 | 25 | | 12.00 | litter | percussion | mating | 35 |
| Diptera | | | | | | | | |
| Agromyzidae | | | | | | | | |
| Liriomyza huidobrensis | 0.001 | 25 | 0.231 | 14.44 | plants | unknown | mating | 36 |
| Chloropidae | | | | | | | | |
| Lipara lucens | | 25 | 0.202 | | plants | tremulation | mating | 37 |
| Drosophilidae | | | | | | | | |
| Drosophila biarmipes | | 25 | | 14.49 | plants | tremulation | mating | 38 |
| Drosophila biarmipes | | 24.5 | 0.304 | | plants | wing fanning | mating | 38 |
| Drosophila melanogaster | 0.001 | 24 | | 6.90 | plants | tremulation | mating | 38 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Drosophila persimilis | 0.001 | 23 | | 5.78 | plants | tremulation | mating | 39 |
| Drosophila sechellia | | 25 | | 7.13 | plants | tremulation | mating | 40 |
| Drosophila suzukii | | 25.5 | | 12.99 | plants | tremulation | mating | 38 |
| Drosophila suzukii | | 25 | 0.450 | | plants | wing fanning | mating | 38 |
| Drosophila yakuba | | 25 | | 6.80 | plants | tremulation | mating | 40 |
| Embioptera | | | | | | | | |
| Clothodidae | | | | | | | | |
| Antipaluria urichi | 0.100 | 21 | 0.473 | | plants | tremulation | mating | 41 |
| Hemiptera | | | | | | | | |
| Aleyrodidae | | | | | | | | |
| Aleurothrixus floccosus | 0.001 | 25 | 0.293 | 1.10 | plants | tremulation | mating | 42 |
| Siphoninus phillyreae | 0.001 | 25 | 0.300 | 8.16 | plants | tremulation | mating | 42 |
| Trialeurodes vaporariorum | 0.001 | 25 | 0.323 | 15.37 | plants | stridulation | mating | 43 |
| Aphalaridae | | | | | | | | |
| Anoeconeossa bundoorensis | 0.001 | 21 | 0.660 | 1.11 | plants | stridulation | mating | 44 |
| Cicadellidae | | | | | | | | |
| Amrasca devastans | | 28 | | 5.78 | plants | tymbalation | mating | 45 |
| Aphrodes makarovi | 0.008 | 22.5 | 0.398 | 21.98 | plants | tymbalation | mating | 46 |
| Empoasca vitis | 0.001 | 22 | 0.253 | 25.64 | plants | tymbalation | mating | 47 |
| Graphocephala atropunctata | 0.008 | 25 | 0.235 | 11.62 | plants | tremulation | mating | 48 |
| Homalodisca liturata | 0.041 | 25 | 0.095 | 7.90 | plants | tymbalation | mating | 48 |
| Homalodisca vitripennis | 0.054 | 25 | 0.059 | 10.55 | plants | tymbalation | mating | 48 |
| Psammotettix alienus | 0.002 | 22.5 | 0.492 | 166.67 | plants | tymbalation | mating | 49 |
| Psammotettix alienus | 0.002 | 22.5 | 0.140 | 3.33 | plants | wing fanning | mating | 49 |
| Scaphoideus titanus | 0.004 | 23.5 | 0.560 | | plants | tremulation | mating | 50 |
| Cixiidae | | | | | | | | |
| Apartus michalki | 0.005 | 20 | 0.375 | | plants | tymbalation | mating | 51 |
| Hyalesthes obsoletus | 0.003 | 23.5 | 0.576 | 14.29 | plants | tymbalation | mating | 52 |
| Typhlobrixia namorokensis | | 20.15 | 0.155 | 8.33 | plants | tymbalation | mating | 53 |

|  |  |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|---|
| Coreidae |  |  |  |  |  |  |  |  |
| Leptoglossus occidentalis | 0.151 | 24.5 | 0.145 |  | plants | percussion | mating | 54 |
| Flatidae |  |  |  |  |  |  |  |  |
| Metcalfa pruinosa | 0.005 | 23.5 | 0.442 | 40.00 | plants | unknown | mating | 55 |
| Homotomidae |  |  |  |  |  |  |  |  |
| Macrohomotoma gladiata | 0.001 | 25 | 0.906 |  | plants | stridulation | mating | 56 |
| Macrohomotoma robusta |  | 25 | 0.672 |  | plants | stridulation | mating | 56 |
| Membracidae |  |  |  |  |  |  |  |  |
| Ennya chrysura |  | 24.5 | 0.107 |  | plants | tremulation | mating | 57 |
| Umbonia crassicornis | 0.030 | 21 | 0.150 |  | plants | tremulation | mating | 58 |
| Umbonia crassicornis | 0.030 | 21 |  | 15.50 | plants | tymbalation | mating | 58 |
| Miridae |  |  |  |  |  |  |  |  |
| Macrolophus costalis | 0.002 | 25 | 0.300 |  | plants | unknown | mating | 59 |
| Macrolophus pygmaeus | 0.002 | 25 | 0.295 |  | plants | unknown | mating | 59 |
| Peloridiidae |  |  |  |  |  |  |  |  |
| Hackeriella veitchi | 0.002 | 21 | 0.082 |  | plants | unknown | unknown | 60 |
| Pentatomidae |  |  |  |  |  |  |  |  |
| Acrosternum hilare | 0.124 | 26 | 0.082 | 0.58 | plants | tremulation | mating | 61 |
| Aelia acuminata | 0.010 | 23 | 0.166 | 6.13 | plants | tremulation | mating | 62 |
| Arma custos | 0.054 | 24 | 0.125 |  | plants | tremulation | unknown | 63 |
| Carpocoris fuscispinus | 0.061 | 23 | 0.151 | 12.32 | plants | tremulation | mating | 62 |
| Carpocoris pudicus | 0.041 | 23 | 0.140 | 3.09 | plants | tremulation | mating | 62 |
| Carpocoris purpuriepennis | 0.054 | 23 | 0.149 | 4.39 | plants | tremulation | mating | 62 |
| Chinavia impicticornis |  | 26 | 0.093 | 3.99 | plants | tremulation | mating | 64 |
| Chinavia ubica |  | 26 | 0.123 | 5.98 | plants | tremulation | mating | 64 |
| Chlorochroa juniperina |  | 23 | 0.157 | 0.32 | plants | tremulation | mating | 62 |
| Chlorochroa ligata | 0.124 | 25 | 0.089 | 0.05 | plants | tremulation | mating | 65 |
| Chlorochroa pinicola |  | 23 | 0.172 | 0.20 | plants | tremulation | mating | 62 |
| Chlorochroa sayi |  | 25 | 0.108 | 0.09 | plants | tremulation | mating | 65 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Chlorochroa uhleri | 0.086 | 25 | 0.093 | 0.05 | plants | tremulation | mating | 65 |
| Codophila varia | 0.056 | 23 | 0.173 | 2.73 | plants | tremulation | mating | 62 |
| Dichelops melacanthus | 0.040 | 26 | 0.110 | 0.94 | plants | tremulation | mating | 66 |
| Dolycoris baccarum | 0.047 | 23 | 0.151 | | plants | tremulation | mating | 62 |
| Edessa meditabunda | | 26 | 0.080 | 3.27 | plants | tremulation | mating | 67 |
| Eurydema oleracea | 0.007 | 23 | 0.183 | | plants | tremulation | mating | 62 |
| Eurydema ornata | 0.015 | 23 | 0.107 | | plants | tremulation | mating | 62 |
| Euschistus heros | 0.054 | 26 | | 2.33 | plants | percussion | mating | 68 |
| Euschistus heros | 0.054 | 26 | 0.200 | | plants | tremulation | mating | 68 |
| Euschistus servus | 0.049 | 21 | 0.136 | 1.83 | plants | tremulation | mating | 69 |
| Graphosoma lineatum | | 23 | 0.151 | 0.43 | plants | tremulation | mating | 62 |
| Graphosoma semipunctatum | | 23 | 0.193 | 0.49 | plants | tremulation | mating | 62 |
| Halyomorpha halys | 0.095 | 21 | 0.067 | | plants | tremulation | mating | 70 |
| Holcostethus strictus | | 23 | 0.155 | 0.03 | plants | tremulation | mating | 71 |
| Holcostethus vernalis | | 23 | 0.167 | 3.12 | plants | tremulation | mating | 62 |
| Murgantia histrionica | 0.025 | 26 | 0.087 | 8.55 | plants | tremulation | mating | 72 |
| Nezara viridula | 0.072 | 26 | 0.094 | 0.29 | plants | tremulation | mating | 61 |
| Palomena prasina | | 21 | 0.095 | 3.22 | plants | tremulation | mating | 73 |
| Pentatoma rufipes | 0.078 | 23 | 0.086 | 0.33 | plants | tremulation | mating | 62 |
| Picromerus bidens | 0.061 | 23 | 0.107 | 4.37 | plants | tremulation | mating | 74 |
| Podisus maculiventris | 0.054 | 23 | 0.097 | 2.05 | plants | percussion | mating | 75 |
| Podisus maculiventris | 0.054 | 23 | 0.009 | 3.34 | plants | tremulation | mating | 75 |
| Podisus nigrispinus | 0.044 | 26 | 0.127 | 3.48 | plants | tremulation | mating | 76 |
| Staria lunata | 0.010 | 23 | 0.125 | | plants | tremulation | mating | 62 |
| Thyanta custator accerra | | 26 | 0.097 | 0.93 | plants | tremulation | mating | 77 |
| Thyanta pallidovirens | 0.062 | 26 | 0.101 | 1.40 | plants | tremulation | mating | 77 |
| Troilus luridus | 0.041 | 22 | 0.113 | 4.04 | plants | tremulation | mating | 63 |
| Zicrona caerulea | 0.015 | 23 | 0.110 | | plants | tremulation | unknown | 63 |
| Psyllidae | | | | | | | | |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Cacopsylla multijuga | | 25 | 0.794 | 6.69 | plants | stridulation | mating | 78 |
| Cacopsylla oluanpiensis | | 25 | 1.015 | 4.15 | plants | stridulation | mating | 78 |
| Cacopsylla picta | | 18 | 0.257 | 1.05 | plants | stridulation | mating | 79 |
| Cacopsylla pyri | 0.002 | 22.5 | 0.689 | 19.61 | plants | stridulation | mating | 80 |
| Cacopsylla tobirae | 0.001 | 25 | 0.993 | 6.89 | plants | stridulation | mating | 78 |
| Diaphorina citri | 0.001 | 25.5 | 0.205 | | plants | wing fanning | mating | 81 |
| Reduviidae | | | | | | | | |
| Dipetalogaster maxima | 0.013 | 25 | 2.200 | 5.78 | plants | stridulation | distress | 82 |
| Mepraia spinolai | 0.179 | 24.9 | 1.524 | 30.54 | plants | stridulation | distress | 83 |
| Rhodnius prolixus | 0.055 | 25 | 1.500 | 35.60 | plants | stridulation | mating | 84 |
| Triatoma guasayana | 0.181 | 25 | 1.900 | 5.22 | plants | stridulation | distress | 82 |
| Triatoma infestans | 0.173 | 25 | 0.750 | 23.80 | plants | stridulation | mating | 85 |
| Triatoma sordida | 0.135 | 25 | 2.100 | 9.64 | plants | stridulation | distress | 82 |
| Rhopalidae | | | | | | | | |
| Jadera haematoloma | 0.047 | 26 | 3.250 | 20.50 | plants | stridulation | facilitating social relationships | 86 |
| Triozidae | | | | | | | | |
| Aacanthocnema dobsoni | 0.000 | 20 | 0.240 | | plants | stridulation | mating | 87 |
| Schedotrioza apicobystra | | 24 | 0.615 | 74.13 | plants | stridulation | mating | 88 |
| Schedotrioza distorta | | 24 | 0.576 | 12.22 | plants | stridulation | mating | 88 |
| Schedotrioza marginata | | 24 | 0.683 | 61.24 | plants | stridulation | mating | 88 |
| Schedotrioza multitudinea | | 24 | 0.869 | 22.89 | plants | stridulation | mating | 88 |
| Trioza acuminatissima | 0.004 | 25 | 0.717 | | plants | stridulation | mating | 89 |
| Trioza neolitseacola | | 25 | 0.728 | | plants | stridulation | mating | 89 |
| Hymenoptera | | | | | | | | |
| Apidae | | | | | | | | |
| Apis cerana | 0.025 | | 0.290 | | hives | tremulation | facilitating social relationships | 90 |
| Apis mellifera | 0.075 | | 0.400 | | hives | tremulation | facilitating social relationships | 91 |
| Bombus impatiens | 0.070 | 30 | 0.595 | 0.04 | plants | wing fanning | facilitating social relationships | 92 |
| Bombus terrestris audax | 0.105 | 21.5 | 0.313 | | plants | wing fanning | foraging | 93 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Dactylurina schmidti | 0.007 | | | 3.90 | hives | tremulation | facilitating social relationships | 94 |
| Hypotrigona gribodoi | 0.001 | | | 8.40 | rock | tremulation | facilitating social relationships | 94 |
| Melipona seminigra | | 21 | 0.500 | 4 | hives | tremulation | foraging | 95 |
| Meliponula bocandei | 0.012 | | | 1.20 | plants | tremulation | facilitating social relationships | 94 |
| Meliponula ferruginea | 0.008 | | 1.100 | 6.30 | plants | tremulation | facilitating social relationships | 94 |
| Plebeina hildebrandti | 0.003 | | 0.290 | 4.40 | hives | tremulation | facilitating social relationships | 94 |
| Braconidae | | | | | | | | |
| Cotesia flavipes | 0.001 | 25 | 0.562 | | plants | wing fanning | mating | 96 |
| Cotesia marginiventris | 0.001 | 25 | 0.310 | | plants | wing fanning | mating | 97 |
| Diachasmimorpha longicaudata | 0.002 | 27 | 0.165 | 6.36 | plants | wing fanning | mating | 98 |
| Doryctobracon crawfordi | 0.005 | 27 | 0.165 | 5.53 | plants | wing fanning | mating | 98 |
| Opius hirtus | | 27 | 0.144 | 7.14 | plants | wing fanning | mating | 98 |
| Utetes anastrephae | 0.003 | 27 | 0.152 | 7.12 | plants | wing fanning | mating | 98 |
| Formicidae | | | | | | | | |
| Atta cephalotes | 0.064 | 21 | | 6.00 | plants | stridulation | facilitating social relationships | 99 |
| Atta laevigata | 0.034 | 21 | 0.698 | | plants | stridulation | facilitating social relationships | 100 |
| Atta vollenweideri | 0.006 | 25 | 1.000 | 4.00 | plants | stridulation | facilitating social relationships | 101 |
| Camponotus herculeanus | 0.015 | 21 | | 20.00 | plants | percussion | facilitating social relationships | 102 |
| Crematogaster rogenhoferi | 0.002 | 25 | 1.904 | | plants | stridulation | facilitating social relationships | 103 |
| Novomessor albisetosus | 0.014 | 21 | | 4.30 | plants | stridulation | facilitating social relationships | 104 |
| Novomessor cockerelli | 0.015 | 21 | | 4.60 | plants | stridulation | facilitating social relationships | 104 |
| Pogonomyrmex barbatus | | 21 | | 665.00 | plants | stridulation | facilitating social relationships | 105 |
| Pogonomyrmex desertorum | | | | 770.00 | plants | stridulation | facilitating social relationships | 105 |
| Pogonomyrmex maricopa | | | | 835.00 | plants | stridulation | facilitating social relationships | 105 |
| Pogonomyrmex rugosus | | | | 770.00 | plants | stridulation | facilitating social relationships | 105 |
| Ichneumonidae | | | | | | | | |
| Pimpla turionellae | 0.043 | 25 | 4.510 | | plants | percussion | foraging | 106 |
| Mutillidae | | | | | | | | |
| Dasymutilla foxi | | | 0.600 | 10.00 | soil | stridulation | mating | 107 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Vespidae | | | | | | | | |
| Polistes dominulus | | 26 | 0.904 | 17.40 | hives | percussion | facilitating social relationships | 108 |
| Polistes fuscatus | 0.177 | 27.5 | | 28.96 | hives | percussion | facilitating social relationships | 109 |
| Isoptera | | | | | | | | |
| Archotermopsidae | | | | | | | | |
| Zootermopsis nevadensis | 0.282 | 21 | 2.000 | 20.00 | plants | percussion | distress | 110 |
| Rhinotermitidae | | | | | | | | |
| Coptotermes gestroi | 0.005 | 27 | | 15.70 | soil | percussion | alarm calling | 111 |
| Lepidoptera | | | | | | | | |
| Drepanidae | | | | | | | | |
| Drepana arcuata | 0.001 | 21 | | 1.16 | plants | percussion | agonistic interactions | 112 |
| Drepana bilineata | | 23.5 | 0.097 | 1.28 | plants | percussion | agonistic interactions | 113 |
| Tethea or | | 23 | 0.007 | 3.45 | plants | mandible scraping | territoriality | 114 |
| Lycaenidae | | | | | | | | |
| Cacyreus marshalli | 0.027 | 24 | 0.520 | 14.26 | plants | unknown | facilitating social relationships | 115 |
| Cupido argiades | 0.010 | 24 | 0.477 | 29.57 | plants | unknown | facilitating social relationships | 115 |
| Feniseca tarquinius | 0.069 | 24 | 0.302 | | plants | unknown | foraging | 116 |
| Jalmenus evagoras | 0.159 | 22 | 0.849 | 1.76 | plants | stridulation | facilitating social relationships | 117 |
| Lycaeides argyrognomon | | 24 | 0.532 | 15.75 | plants | unknown | facilitating social relationships | 115 |
| Lycaena dispar | 0.061 | 24 | 0.689 | 24.30 | plants | unknown | facilitating social relationships | 115 |
| Lycaena helle | 0.090 | 24 | 0.730 | 16.41 | plants | unknown | facilitating social relationships | 115 |
| Lycaena phlaeas | 0.051 | 24 | 0.609 | 25.93 | plants | unknown | facilitating social relationships | 115 |
| Maculinea alcon | 0.026 | 24 | 0.161 | 10.73 | plants | unknown | facilitating social relationships | 115 |
| Plebejus argus | 0.051 | 24 | 0.318 | 10.52 | plants | unknown | facilitating social relationships | 115 |
| Polyommatus bellargus | 0.075 | 24 | 0.528 | 16.51 | plants | unknown | facilitating social relationships | 115 |
| Polyommatus coridon | 0.076 | 24 | 0.374 | 9.25 | plants | unknown | facilitating social relationships | 115 |
| Polyommatus icarus | 0.051 | 24 | 0.653 | 20.00 | plants | unknown | facilitating social relationships | 115 |
| Scolitantides orion | 0.001 | 24 | 0.508 | 9.85 | plants | unknown | facilitating social relationships | 115 |
| Riodinidae | | | | | | | | |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Eurybia elvina | 0.061 | 21 | | 13.50 | plants | stridulation | facilitating social relationships | 118 |
| Neuroptera | | | | | | | | |
| Chrysopidae | | | | | | | | |
| Chrysoperla calocedrii | | 25 | 0.071 | | plants | tremulation | mating | 119 |
| Chrysoperla downesi | | 25 | 0.071 | | plants | tremulation | mating | 120 |
| Chrysoperla heidarii | | 25 | 0.091 | 0.89 | plants | tremulation | mating | 121 |
| Chrysoperla nipponensis | | 25 | 0.049 | | plants | tremulation | mating | 122 |
| Chrysoperla plorabunda | | 25 | 0.064 | | plants | tremulation | mating | 120 |
| Mantophasmatodea | | | | | | | | |
| Austrophasmatidae | | | | | | | | |
| Austrophasma caledonense | 0.054 | 20 | | 8.15 | plants | percussion | mating | 123 |
| Austrophasma gansbaaiense | 0.145 | 20 | | 1.98 | plants | percussion | mating | 123 |
| Austrophasma rawsonvillense | 0.086 | 20 | | 7.07 | plants | percussion | mating | 123 |
| Hemilobophasma montaguense | 0.064 | 20 | | 1.75 | plants | percussion | mating | 123 |
| Karoophasma biedouwensis | 0.069 | 20 | | 10.11 | plants | percussion | mating | 123 |
| Karoophasma botterkloofense | 0.049 | 20 | | 10.74 | plants | percussion | mating | 123 |
| Lobatophasma redelinghuysense | 0.082 | 20 | | 15.00 | plants | percussion | mating | 123 |
| Namaquaphasma ookiepense | 0.088 | 20 | | 10.73 | plants | percussion | mating | 123 |
| Viridiphasma clanwilliamense | 0.036 | 20 | | 5.59 | plants | percussion | mating | 123 |
| Mantophasmatidae | | | | | | | | |
| Praedatophasma maraisi | 0.350 | 20 | | 19.12 | plants | percussion | mating | 123 |
| Sclerophasma paresisense | 0.135 | 20 | | 11.19 | plants | percussion | mating | 123 |
| Orthoptera | | | | | | | | |
| Anostostomatidae | | | | | | | | |
| Deinacrida rugosa | 9.780 | 20 | 0.037 | 0.35 | soil | tremulation | agonistic interactions | 124 |
| Hernideina fernovata | | 22 | 1.375 | | plants | stridulation | distress | 125 |
| Gryllidae | | | | | | | | |
| Agnotecous obscurus | | 21 | 0.048 | | plants | tremulation | mating | 126 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Cardiodactylus muria | | 21 | 0.038 | | plants | tremulation | mating | 126 |
| Lebinthus luae | | 21 | 0.084 | | plants | tremulation | mating | 126 |
| Ponca hebardi | | 23.5 | 0.097 | | plants | tremulation | mating | 127 |
| Gryllotalpidae | | | | | | | | |
| Gryllotalpa major | 2.598 | 20 | 1.971 | 3.14 | plants | stridulation | mating | 128 |
| Rhaphidophoridae | | | | | | | | |
| Troglophilus neglectus | 0.136 | 21 | 0.031 | 0.45 | rock | tremulation | mating | 129 |
| Tetrigidae | | | | | | | | |
| Bolivarittetix chinensis | | 30 | | 17.54 | plants | unknown | mating | 130 |
| Criottetix bispinosus | | 24 | | 15.50 | plants | unknown | mating | 130 |
| Parattetix hirsutus | | 24 | | 28.57 | plants | unknown | mating | 130 |
| Tetrix ceperoi | | 25 | 0.336 | | plants | tremulation | mating | 131 |
| Tetrix ceperoi | | 25 | 0.585 | | plants | wing fanning | mating | 131 |
| Tettigoniidae | | | | | | | | |
| Conocephalus nigropleurum | 0.135 | 27.5 | 0.288 | 0.43 | plants | tremulation | mating | 132 |
| Copiphora rhinoceros | | 20 | | 1.30 | plants | tremulation | mating | 133 |
| Copiphora vigorosa | 0.790 | 30 | 0.012 | 24.00 | plants | tremulation | mating | 134 |
| Gnathoclita sodalis | | 27.5 | | 36.00 | plants | tremulation | agonistic interactions | 135 |
| Meconema thalassinum | 0.066 | 26.1 | | 45.50 | plants | percussion | mating | 136 |
| Onomarchus uninotatus | 2.027 | 21 | 0.048 | 1.25 | plants | tremulation | mating | 137 |
| Tettigonia cantans | 1.200 | 21 | 8.000 | 30 | plants | stridulation | mating | 138 |
| Plecoptera | | | | | | | | |
| Capniidae | | | | | | | | |
| Isocapnia grandis | 0.056 | 22 | | 3.48 | rock | percussion | mating | 139 |
| Chloroperlidae | | | | | | | | |
| Kathroperla perdita | 0.045 | 23 | | 27.78 | rock | percussion | mating | 139 |
| Paraperla frontalis | 0.056 | 22 | | 19.61 | rock | percussion | mating | 139 |
| Leuctridae | | | | | | | | |
| Zealeuctra arnoldi | 0.006 | 24 | | 15.84 | rock | percussion | mating | 140 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Zealeuctra claasseni | | 24 | | 11.53 | rock | percussion | mating | 140 |
| Zealeuctra hitei | 0.010 | 24 | | 16.25 | rock | percussion | mating | 140 |
| Zealeuctra warreni | 0.006 | 24.5 | | 14.60 | rock | percussion | mating | 141 |
| Nemouridae | | | | | | | | |
| Soyedina carolinensis | | 22.5 | | 40.32 | rock | percussion | mating | 141 |
| Peltoperlidae | | | | | | | | |
| Peltoperla arcuata | 0.025 | 23 | 0.550 | 7.19 | rock | percussion | mating | 142 |
| Peltoperla tarteri | | 23.5 | 0.400 | 0.27 | rock | percussion | mating | 142 |
| Sierraperla cora | | 23.5 | | 6.85 | rock | percussion | mating | 143 |
| Soliperla fenderi | | 22 | | 3.27 | rock | percussion | mating | 139 |
| Soliperla quadrispinula | | 22 | | 27.03 | rock | percussion | mating | 139 |
| Soliperla sierra | 0.043 | 23 | | 30.30 | rock | percussion | mating | 139 |
| Soliperla thyra | | 22 | | 52.63 | rock | percussion | mating | 139 |
| Tallaperla anna | 0.016 | 24.5 | 0.350 | | rock | percussion | mating | 142 |
| Tallaperla elisa | 0.012 | 23 | 0.600 | 0.86 | rock | percussion | mating | 142 |
| Tallaperla lobata | 0.014 | 24.5 | 0.550 | | rock | percussion | mating | 142 |
| Tallaperla maria | 0.014 | 23.5 | 0.700 | 2.22 | rock | percussion | mating | 142 |
| Viehoperla ada | | 24 | | 16.39 | rock | percussion | mating | 142 |
| Yoraperla brevis | | 23 | 1.000 | 6.37 | rock | percussion | mating | 142 |
| Perlidae | | | | | | | | |
| Acroneuria mela | 0.206 | 23.5 | | 42.02 | rock | percussion | mating | 142 |
| Attaneuria ruralis | 0.378 | 24 | | 28.90 | rock | percussion | mating | 142 |
| Beloneuria georgiana | | 24.5 | | 23.20 | rock | percussion | mating | 142 |
| Eccoptera xanthenes | | 23.5 | | 27.62 | rock | percussion | mating | 142 |
| Hansonoperla appalachia | 0.057 | 23.5 | | 12.42 | rock | percussion | mating | 142 |
| Neoperla clymene | 0.033 | 24 | | 17.89 | rock | percussion | mating | 142 |
| Paragnetina media | 0.030 | 25.5 | | 21.32 | rock | percussion | mating | 142 |
| Perlodidae | | | | | | | | |
| Acroneuria abnormis | 0.229 | 22.5 | | 30.30 | rock | percussion | mating | 144 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| Acroneuria carolinensis | 0.254 | 25 | 32.26 | rock | percussion | mating | 144 |
| Acroneuria evoluta | 0.104 | 24 | 20.70 | rock | percussion | mating | 145 |
| Acroneuria lycorias | 0.185 | 23 | 23.26 | rock | percussion | mating | 144 |
| Calineuria califomica | 0.454 | | 10.00 | rock | percussion | mating | 144 |
| Calliperla luctuosa | 0.064 | 21 | 40.00 | rock | percussion | mating | 139 |
| Chernokrilus misnomus | 0.064 | 22.75 | 2.49 | rock | percussion | mating | 146 |
| Claassenia sabulosa | 0.454 | 24 | 13.16 | rock | percussion | mating | 144 |
| Clioperla clio | 0.056 | 24 | 3.20 | rock | percussion | mating | 147 |
| Doroneuria baumanni | 0.542 | 23.5 | 5.43 | rock | percussion | mating | 145 |
| Helopicus nalatus | 0.118 | 24 | 12.20 | rock | percussion | mating | 139 |
| Hesperoperla paciflca | | 25 | 8.33 | rock | percussion | mating | 144 |
| Hydroperla crosbyi | 0.043 | 23.5 | 25.00 | rock | percussion | mating | 143 |
| Isogenoides elongatus | 0.148 | 22 | 4.83 | rock | percussion | mating | 139 |
| Isogenoides zionensis | 0.185 | 23 | 2.84 | rock | percussion | mating | 141 |
| Isoperla burksi | | 23.5 | 5.59 | rock | percussion | mating | 148 |
| Isoperla coushatta | 0.009 | 24.25 | 6.82 | rock | percussion | mating | 148 |
| Isoperla decepta | | 24 | 1.97 | rock | percussion | mating | 148 |
| Isoperla fulva | | 22 | 38.61 | rock | percussion | mating | 149 |
| Isoperla holochlora | 0.037 | 24 | 2.10 | rock | percussion | mating | 148 |
| Isoperla mohri | | 24.25 | 2.83 | rock | percussion | mating | 148 |
| Isoperla montana | 0.033 | 23.5 | 5.93 | rock | percussion | mating | 148 |
| Isoperla mormona | | 23 | 21.79 | rock | percussion | mating | 149 |
| Isoperla namata | | 23.5 | 1.75 | rock | percussion | mating | 146 |
| Isoperla ouachita | 0.010 | 24 | 3.77 | rock | percussion | mating | 148 |
| Isoperla phalerata | | 23 | 40.65 | rock | percussion | mating | 149 |
| Isoperla punctata | | 22 | 23.09 | rock | percussion | mating | 149 |
| Isoperla sagittata | 0.010 | 22 | 5.51 | rock | percussion | mating | 148 |
| Isoperla signata | | 23 | 4.43 | rock | percussion | mating | 146 |
| Isoperla similis | 0.064 | 24 | 0.43 | rock | percussion | mating | 148 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Oconoperla innubila | 0.033 | 24 | | 28.17 | rock | percussion | mating | 147 |
| Osobenus yakamae | | 24 | | 2.56 | rock | percussion | mating | 147 |
| Paragnetina fumosa | 0.056 | 25 | | 27.03 | rock | percussion | mating | 144 |
| Paragnetina kansensis | 0.082 | 25 | | 10.99 | rock | percussion | mating | 144 |
| Perlinella drymo | 0.082 | 26.5 | | 26.32 | rock | percussion | mating | 144 |
| Perlinodes aurea | 0.093 | 23.5 | | 1.89 | rock | percussion | mating | 147 |
| Phasganophora capitata | | 23.5 | | 2.43 | rock | percussion | mating | 145 |
| Pictetiella expansa | 0.082 | 22 | | 31.06 | rock | percussion | mating | 146 |
| Yugus arinus | 0.148 | 24.75 | | 14.60 | rock | percussion | mating | 147 |
| Pteronarcyidae | | | | | | | | |
| Allonarcys biloba | 0.753 | 23.5 | | 1.90 | rock | percussion | mating | 150 |
| Allonarcys proteus | 0.753 | 23 | | 3.25 | rock | percussion | mating | 150 |
| Pteronarcella badia Alaska | 0.405 | 25 | | 14.93 | rock | percussion | mating | 150 |
| Pteronarcella badia Colorado | 0.405 | 22 | | 14.08 | rock | percussion | mating | 150 |
| Pteronarcella californica | | 25 | | 4.55 | rock | percussion | mating | 140 |
| Pteronarcella regularis | 0.118 | 23 | | 10.42 | rock | percussion | mating | 143 |
| Pteronarcys californica | 1.012 | 22 | | 3.80 | rock | percussion | mating | 150 |
| Pteronarcys dorsata | 1.652 | 23.5 | | 3.70 | rock | percussion | mating | 150 |
| Pteronarcys princeps | | 23.5 | | 2.58 | rock | percussion | mating | 143 |
| Taeniopterygidae | | | | | | | | |
| Taeniopteryx burksi | | 21.5 | | 8.31 | rock | percussion | mating | 141 |
| Taeniopteryx lonicera | | 23 | | 7.04 | rock | percussion | mating | 148 |
| Taeniopteryx maura | | 24 | | 12.36 | rock | percussion | mating | 148 |
| Taeniopteryx nivalis | | 20.5 | | 10.00 | rock | percussion | mating | 139 |
| Taeniopteryx ugola | | 22.5 | | 5.13 | rock | percussion | mating | 141 |
| Malacostraca | | | | | | | | |
| Decapoda | | | | | | | | |
| Ocypodidae | | | | | | | | |
| Uca mjoebergi | | | 0.544 | | soil | stridulation | mating | 151 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Uca rapax | | 30 | 0.185 | | soil | stridulation | mating | 152 |
| Sesarmidae | | | | | | | | |
| Perisesarma eumolpe | | 21.5 | | 5.00 | soil | stridulation | agonistic interactions | 153 |
| Perisesarma indiarum | | 21.5 | | 7.00 | soil | stridulation | agonistic interactions | 153 |
| Mammalia | | | | | | | | |
| Carnivora | | | | | | | | |
| Phocidae | | | | | | | | |
| Halichoerus grypus | 250000.000 | 37 | | 30 | soil | percussion | agonistic interactions | 154 |
| Diprotodontia | | | | | | | | |
| Macropodidae | | | | | | | | |
| Macropus giganteus | | | 0.652 | 8.20 | plants | percussion | predator avoidance | 155 |
| Proboscidae | | | | | | | | |
| Elephantidae | | | | | | | | |
| Elephas maximus | | 37 | | 20 | soil | percussion | distress | 156 |
| Loxodonta africana | 5150000.000 | 37 | 0.027 | | soil | vocal cords | facilitating social relationships | 157 |
| Rodentia | | | | | | | | |
| Bathyergidae | | | | | | | | |
| Georychus capensis | 270.500 | 24.5 | | 26.00 | soil | percussion | mating | 158 |
| Heteromyidae | | | | | | | | |
| Dipodomys spectabilis | | 37 | | 19.15 | soil | percussion | predator avoidance | 159 |
| Spalacidae | | | | | | | | |
| Spalax ehrenbergi | 141.000 | 37 | 0.200 | 13.23 | soil | percussion | agonistic interactions | 160 |
| Tachyoryctes daemon | 210.000 | 25 | | 11.76 | soil | percussion | facilitating social relationships | 161 |
| Squamata | | | | | | | | |
| Iguania | | | | | | | | |
| Chamaeleonidae | | | | | | | | |
| Chamaeleo calyptratus | | 24 | 0.112 | | plants | tremulation | mating | 162 |

## References

1. Narins PM, Meenderink SWF, Tumulty JP, Cobo-Cuan A, Márquez R. Plant-borne vibrations modulate calling behaviour in a tropical amphibian. *Curr Biol*. 2018;28(23):R1333-R1334. doi:10.1016/j.cub.2018.10.056

2. Lewis ER, Narins PM. Do frogs communicate with seismic signals? *Science (80- )*. 1985;227(4683):187-189. doi:10.1126/science.227.4683.187

3. Caldwell MS, Johnston GR, McDaniel JG, Warkentin KM. Vibrational signaling in the agonistic interactions of red-eyed treefrogs. *Curr Biol*. 2010;20(11):1012-1017. doi:10.1016/j.cub.2010.03.069

4. Serrano M, Cruz JJ, Villatoro-Castañeda M, Ariano-Sánchez D. Tremulation display in male agonistic behavior of the black-eyed leaf frog (*Agalychnis moreletii*: Hylidae). *Anim Behav Cogn*. 2018;5(2):222-228. doi:10.26451/abc.05.02.04.2018

5. Sweger AL, Uetz GW. Characterizing the vibratory and acoustic signals of the "purring" wolf spider, *Gladicosa gulosa* (Araneae: Lycosidae). *Bioacoustics*. 2016;25(3):293-303. doi:10.1080/09524622.2016.1160328

6. Rivero A, Alatalo R V., Kotiaho JS, Mappes J, Parri S. Acoustic signalling in a wolf spider: Can signal characteristics predict male quality? *Anim Behav*. 2000;60(2):187-194. doi:10.1006/anbe.2000.1452

7. Fernandez-Montraveta C, Schmitt A. Substrate-borne Vibrations Produced by Male *Lycosa tarentula fasciiventris* (Araneae, Lycosidae) during Courtship and Agonistic Interactions. *Ethology*. 1994;97(1-2):81-93. doi:10.1111/j.1439-0310.1994.tb01031.x

8. Elias DO, Lee N, Hebets EA, Mason AC. Seismic signal production in a wolf spider: Parallel versus serial multi-component signals. *J Exp Biol*. 2006;209(6):1074-1084. doi:10.1242/jeb.02104

9. Zeng H, Wee SSE, Painting CJ, Zhang S, Li D. Equivalent effect of UV coloration and vibratory signal on mating success in a jumping spider. *Behav Ecol*. 2019;30(2):313-321. doi:10.1093/beheco/ary167

10. Elias DO, Mason AC, Maddison WP, Hoy RR. Seismic signals in a courting male jumping spider (Araneae: Salticidae). *J Exp Biol*. 2003;206(22):4029-4039. doi:10.1242/jeb.00634

11. Elias DO, Hebets EA, Hoy RR, Maddison WP, Mason AC. Regional seismic song differences in sky island populations of the jumping spider *Habronattus pugillis* Griswold (Araneae, Salticidae). *J Arachnol*. 2006;34(3):545-556. doi:10.1636/S05-77.1

12. Girard MB, Kasumovic MM, Elias DO. Multi-modal courtship in the peacock spider, *Maratus volans* (O.P.-Cambridge, 1874). *PLoS One*. 2011;6(9). doi:10.1371/journal.pone.0025390

13. Elias DO, Sivalinghem S, Mason AC, Andrade MCB, Kasumovic MM. Vibratory communication in the jumping spider *Phidippus clarus*: Substrate-borne courtship signals are important for male mating success. *Ethology*. 2010;116(10):990-998. doi:10.1111/j.1439-0310.2010.01815.x

14. Fischer ML, Čokl A, Ramires EN, et al. Sound is involved in multimodal communication of *Loxosceles intermedia* Mello-Leitão, 1934 (Araneae; Sicariidae). *Behav Processes*. 2009;82(3):236-243. doi:10.1016/j.beproc.2009.06.013

15. Rovner JS. Vibration in *Heteropoda venatoria* (Sparassidae): a third method of sound production in spiders. *J Arachnol*. 1980;8(2):193-200. http://agris.fao.org/agris-search/search.do?recordID=US201301358166.

16. Schüch W, Barth FG. Temporal patterns in the vibratory courtship signals of the wandering spider *Cupiennius salei* Keys. *Behav Ecol Sociobiol*. 1985;16(3):263-271. doi:10.1007/BF00310990

17. Joel AC, Habedank A, Mey J. Vibratory movements in contests between females of the feather-legged spider (*Uloborus plumipes*). *Zoology*. 2017;125(September):87-93. doi:10.1016/j.zool.2017.08.009

18. Pomini AM, Machado G, Pinto-da-Rocha R, Macías-Ordóñez R, Marsaioli AJ. Lines of defense in the harvestman *Hoplobunus mexicanus* (Arachnida: Opiliones): Aposematism, stridulation, thanatosis, and irritant chemicals. *Biochem Syst Ecol*. 2010;38(3):300-308. doi:10.1016/j.bse.2010.03.003

19. Briceño RD, Bonilla F. Substrate vibrations in the scorpion *Centruroides margaritatus* (Scorpiones: Buthidae) during courtship. *Rev Biol Trop*. 2009;57:267-274. doi:10.15517/rbt.v57i0.21350

20. Delattre O, Šobotník J, Jandák V, et al. Chemical and vibratory signals used in alarm communication in the termite *Reticulitermes flavipes* (Rhinotermitidae). *Insectes Soc*. 2019;66(2):265-272. doi:10.1007/s00040-018-00682-9

21. Cristaldo PF, Jandák V, Kutalová K, et al. The nature of alarm communication in *Constrictotermes cyphergaster* (Blattodea: Termitoidea: Termitidae): The integration of chemical and vibroacoustic signals. *Biol Open*. 2016;4(12):1649-1659. doi:10.1242/bio.014084

22. Rohrig A, Kirchner WH, Leuthold RH. Vibrational alarm communication in the African fungus-growing termite genus *Macrotermes* (Isoptera, Termitidae). *Insectes Soc*. 1999;46:71-77.

23. Hager FA, Kirchner WH. Vibrational long-distance communication in the termites *Macrotermes natalensis* and *Odontotermes* sp. *J Exp Biol*. 2013;216(17):3249-3256. doi:10.1242/jeb.086991

24. Delattre O, Sillam-Dussès D, Jandák V, et al. Complex alarm strategy in the most basal termite species. *Behav Ecol Sociobiol*. 2015;69(12):1945-1955. doi:10.1007/s00265-015-2007-9

25. Breidbach O. Studies on the stridulation of *Hylotrupes bajulus* (Cerambycidae, Coleoptera): communication through support vibration morphology and mechanics of the signal. *Behaviour*. 1986;12:169-186.

26. Fleming AJ, Lindeman AA, Carroll AL, Yack JE. Acoustics of the mountain pine beetle (*Dendroctonus ponderosae*) (Curculionidae, Scolytinae): Sonic, ultrasonic, and vibration characteristics. *Can J Zool*. 2013;91(4):235-244. doi:10.1139/cjz-2012-0239

27. Dobai A. “Can you hear me?” Investigating the acoustic communication signals and receptor organs of bark beetles. 2017.

28. Ohya E, Kinuura H. Close range sound communications of the oak platypodid beetle *Platypus quercivorus* (Murayama) (Coleoptera: Platypodidae). *Appl Entomol Zool*. 2001;36(3):317-321. doi:10.1303/aez.2001.317

29. Kerchev IA. Interspecific differences of stridulatory signals in three species of bark beetles from the genus *Polygraphus* Er. (Coleoptera: Curculionidae, Scolytinae) inhabiting the island of Sakhalin. *PeerJ*. 2020;2020(1). doi:10.7717/peerj.8281

30. Carisio L, Palestrini C, Rolando A. Stridulation variability and morphology: An examination in dung beetles of the genus *Trypocopris* (Coleoptera, Geotrupidae). *Popul Ecol*. 2004;46(1):27-37. doi:10.1007/s10144-004-0170-3

31. White PR, Birch MC, Church S, Jay C, Rowe E, Keenlyside JJ. Intraspecific variability in the tapping behavior of the deathwatch beetle, *Xestobium rufovillosum* (Coleoptera: Anobiidae). *J Insect Behav*. 1993;6(5):549-562. doi:10.1007/BF01048122

32. Kojima W, Takanashi T, Ishikawa Y. Vibratory communication in the soil: Pupal signals deter larval intrusion in a group-living beetle *Trypoxylus dichotoma*. *Behav Ecol Sociobiol*. 2012;66(2):171-179. doi:10.1007/s00265-011-1264-5

33. Slobodchikoff CN, Splangler HG. Two Types of Sound Production in *Eupsophulus castaneus* (Coleoptera: Tenebrionidae). *Coleopt Bull*. 1979;33(2):239-243.

34. Pearson GA, Allen DM. Vibrational Communication in *Eusattus convexus* LeConte (Coleoptera: Tenebrionidae). *Coleopt Bull*. 1996;50(4):391-394.

35. Tschinkel WR, Doyen JT. Sound Production by Substratal Tapping in Beetles of the Genus *Eusattus* (Tentyriidae: Coniontini). *Coleopt Bull*. 1976;30(4):331-335.

36. Ge J, Wei JN, Zhang DJ, Hu C, Zheng DZ, Kang L. Pea leafminer *Liriomyza huidobrensis* (Diptera: Agromyzidae) uses vibrational duets for efficient sexual communication. *Insect Sci*. 2019;26(3):510-522. doi:10.1111/1744-7917.12598

37. Kanmiya K. Acoustic properties and geographic variation in the vibratory courtship signals of the european chloropid fly, *Lipara lucens meigen* (Diptera, Chloropidae). *J Ethol*. 1990;8(2):105-120. doi:10.1007/BF02350281

38. Mazzoni V, Anfora G, Virant-Doberlet M. Substrate vibrations during courtship in three *Drosophila* species. *PLoS One*. 2013;8(11):1-8. doi:10.1371/journal.pone.0080708

39. Hernández MV, Fabre CCG. The elaborate postural display of courting *Drosophila persimilis* flies produces substrate-borne vibratory signals. *J Insect Behav*. 2016;29(5):578-590. doi:10.1007/s10905-016-9579-8

40. Fabre CCG, Hedwig B, Conduit G, Lawrence PA, Goodwin SF, Casal J. Substrate-borne vibratory communication during courtship in *Drosophila melanogaster*. *Curr Biol*. 2012;22(22):2180-2185. doi:10.1016/j.cub.2012.09.042

41. Dejan KA, Fresquez JM, Meyer AM, Edgerly JS. Maternal territoriality achieved through shaking and lunging: An investigation of patterns in associated behaviors and substrate vibrations in a Colonial Embiopteran, *Antipaluria urichi*. *J Insect Sci*. 2013;13:1-28. doi:10.1673/031.013.8201

42. Kanmiya K, Sonobe R. Records of two citrus pest whiteflies in Japan with special reference to their mating sounds (Homoptera: Aleyrodidae). *Appl Entomol Zool*. 2002;37(3):487-495. doi:10.1303/aez.2002.487

43. Kanmiya K. Discovery of male acoustic signals in the greenhouse whitefly, *Trialeurodes vaporariorum* (Westwood) (Homoptera: Aleyrodidae). *Appl Entomol Zool*. 1996;31(2):255-262.

44. Wood RM, Peters RA, Taylor GS, Steinbauer MJ. Characteristics of the signals of male *Anoeconeossa bundoorensis* Taylor and Burckhardt (Hemiptera: Aphalaridae) associated with female responsiveness. *J Insect Behav*. 2016;29(1):1-14. doi:10.1007/s10905-015-9539-8

45. Saxena KN, Kumar H. Acoustic communication in the sexual behaviour of the leafhopper, *Amrasca devastans*. *Physiol Entomol*. 1984;9:77-86.

46. de Groot M, Derlink M, Pavlovčič P, Prešern J, Čokl A, Virant-Doberlet M. Duetting behaviour in the leafhopper *Aphrodes makarovi* (Hemiptera: Cicadellidae). *J Insect Behav*. 2012;25(5):419-440. doi:10.1007/s10905-011-9304-6

47. Nieri R, Mazzoni V. The reproductive strategy and the vibrational duet of the leafhopper *Empoasca vitis*. *Insect Sci*. 2018;25(5):869-882. doi:10.1111/1744-7917.12454

48. Percy DM, Boyd EA, Hoddle MS. Observations of acoustic signaling in three sharpshooters: *Homalodisca vitripennis*, *Homalodisca liturata*, and *Graphocephala atropunctata* (Hemiptera: Cicadellidae). *Ann Entomol Soc Am*. 2008;101(1):253-259. doi:10.1603/0013-8746(2008)101[253:OOASIT]2.0.CO;2

49. Derlink M, Abt I, Mabon R, Julian C, Virant-Doberlet M, Jacquot E. Mating behavior of *Psammotettix alienus* (Hemiptera: Cicadellidae). *Insect Sci*. 2018;25(1):148-160. doi:10.1111/1744-7917.12379

50. Mazzoni V, Lucchi A, Prešern J, Virant-Doberlet M. Vibrational communication and other behavioural traits in *Scaphoideus titanus*. *Bull Insectology*. 2008;61(1):187-188.

51. Kunz G, Bullerdiek D, Hoch H, Holzinger W, Mühlethaler R, Wessel A. Courtship behaviour and vibrational communication of the planthopper *Apartus michalki* (Wagner, 1948). *Cicadina*. 2014;14(December):55-63.

52. Mazzoni V, Lucchi A, Ioriatti C, Virant-Doberlet M, Anfora G. Mating behavior of *Hyalesthes obsoletus* (Hemiptera: Cixiidae). *Ann Entomol Soc Am*. 2010;103(5):813-822. doi:10.1603/AN09145

53. Soulier-Perkins A, Ouvrard D, Hoch H, Bourgoin T. Singing in the Namoroka caves, first record in situ for a cave dwelling insect: *Typhlobrixia namorokensis* (Hemiptera, Fulgoromorpha, Cixiidae). *J Insect Behav*. 2015;28(6):704-721. doi:10.1007/s10905-015-9531-3

54. Takács S, Hardin K, Gries G, Strong W, Bennett R. Vibratory communication signal produced by male western conifer seed bugs (Hemiptera: Coreidae). *Can Entomol*. 2008;140(2):174-183. doi:10.4039/N07-029

55. Virant-Doberlet M, Žežlina I. Vibrational communication of *Metcalfa pruinosa* (Hemiptera: Fulgoroidea: Flatidae). *Ann Entomol Soc Am*. 2007;100(1):73-82. doi:10.1603/0013-8746(2007)100[73:VCOMPH]2.0.CO;2

56. Liao YC, Yang MM. First evidence of vibrational communication in Homotomidae (Psylloidea) and comparison of substrate-borne signals of two allied species of the genus *Macrohomotoma kuwayama*. *J Insect Behav*. 2017;30(5):567-581. doi:10.1007/s10905-017-9640-2

57. Miranda X. Substrate-borne signal repertoire and courtship jamming by adults of *Ennya chrysura* (Hemiptera: Membracidae). *Ann Entomol Soc Am*. 2006;99(2):374-386. doi:10.1603/0013-8746(2006)099[0374:SSRACJ]2.0.CO;2

58. Miles CI, Allison BE, Losinger MJ, Su QT, Miles RN. Motor and mechanical bases of the courtship call of the male treehopper *Umbonia crassicornis*. *J Exp Biol*. 2017;220(10):1915-1924. doi:10.1242/jeb.147819

59. Gemeno C, Baldo G, Nieri R, Valls J, Alomar O, Mazzoni V. Substrate-borne vibrational signals in mating communication of *Macrolophus* bugs. *J Insect Behav*. 2015;28(4):482-498. doi:10.1007/s10905-015-9518-0

60. Hoch H, Deckert J, Wessel A. Vibrational signalling in a Gondwanan relict insect (Hemiptera: Coleorrhyncha: *Peloridiidae*). *Biol Lett*. 2006;2(2):222-224. doi:10.1098/rsbl.2006.0451

61. Čokl A, McBrien HL, Millar JG. Comparison of substrate-borne vibrational signals of two stink bug species, *Acrosternum hilare* and *Nezara viridula* (Heteroptera: Pentatomidae). *Ann Entomol Soc Am*. 2001;94(3):471-479. doi:10.1603/0013-8746(2001)094[0471:COSBVS]2.0.CO;2

62. Shestakov LS. A comparative analysis of vibrational signals in 16 sympatric bug species (Pentatomidae, Heteroptera). *Entomol Rev*. 2015;95(3):310-325. doi:10.1134/S0013873815030045

63. Shestakov LS. Studies of vibratory signals in pentatomid bugs (Heteroptera, Asopinae) from European Russia. *Entomol Rev*. 2008;88(1):20-25. doi:10.1134/s001387380801003x

64. Laumann RA, Čokl A, Blassioli-Moraes MC, Borges M. Vibratory Communication and its Relevance to Reproductive Isolation in two Sympatric Stink Bug Species (Hemiptera: Pentatomidae: Pentatominae). *J Insect Behav*. 2016;29(6):643-665. doi:10.1007/s10905-016-9585-x

65. Bagwell GJ, Čokl A, Millar JG. Characterization and comparison of substrate-borne vibrational signals of *Chlorochroa uhleri*, *Chlorochroa ligata*, and *Chlorochroa sayi* (Heteroptera: Pentatomidae). *Ann Entomol Soc Am*. 2008;101(1):235-246. doi:10.1603/0013-8746(2008)101[235:CACOSV]2.0.CO;2

66. Blassioli-Moraes MC, Magalhães DM, Čokl A, et al. Vibrational communication and mating behaviour of *Dichelops melacanthus* (Hemiptera: Pentatomidae) recorded from loudspeaker membranes and plants. *Physiol Entomol*. 2014;39(1):1-11. doi:10.1111/phen.12041

67. Silva CCA, Laumann RA, Ferreira JBC, Moraes MCB, Borges M, Čokl A. Reproductive biology, mating behavior, and vibratory communication of the brown-winged stink bug, *Edessa meditabunda* (Fabr.) (Heteroptera: Pentatomidae). *Psyche (Stuttg)*. 2012. doi:10.1155/2012/598086

68. Kavčič A, Čokl A, Laumann RA, Blassioli-Moraes MC, Borges M. Tremulatory and abdomen vibration signals enable communication through air in the stink bug *Euschistus heros*. *PLoS One*. 2013;8(2). doi:10.1371/journal.pone.0056503

69. Lampson B, Han Y, Khalilian A, Greene J, Mankin RW, Foreman E. Characterization of substrate-borne vibrational signals of *Euschistus servus* (Heteroptera : Pentatomidae). *Am J Agric Biol Sci*. 2010;5(1):32-36.

70. Polajnar J, Maistrello L, Bertarella A, Mazzoni V. Vibrational communication of the brown marmorated stink bug (*Halyomorpha halys*). *Physiol Entomol*. 2016;41(3):249-259. doi:10.1111/phen.12150

71. Pavlovčič P, Čokl A. Songs of *Holcostethus strictus* (Fabricius): A different repertoire among landbugs (Heteroptera: Pentatomidae). *Behav Processes*. 2001;53(1-2):65-73. doi:10.1016/S0376-6357(00)00144-3

72. Čokl A, Prešern J, Virant-Doberlet M, Bagwell GJ, Millar JG. Vibratory signals of the harlequin bug and their transmission through plants. *Physiol Entomol*. 2004;29(4):372-380. doi:10.1111/j.0307-6962.2004.00395.x

73. Polajnar J, Kavčič A, Kosi AŽ, Čokl A. *Palomena prasina* (Hemiptera: Pentatomidae) vibratory signals and their tuning with plant substrates. *Cent Eur J Biol*. 2013;8(7):670-680. doi:10.2478/s11535-013-0188-z

74. Čokl A, Žunič A, Virant-Doberlet M. Predatory bug *Picromerus bidens* communicates at different frequency levels. *Cent Eur J Biol*. 2011;6(3):431-439. doi:10.2478/s11535-011-0015-y

75. Žunič A, Cokl A, Doberlet MV, Millar JG. Communication with signals produced by abdominal vibration, tremulation, and percussion in *Podisus maculiventris* (Heteroptera: Pentatomidae). *Ann Entomol Soc Am*. 2008;101(6):1169-1178. doi:10.1603/0013-8746-101.6.1169

76. Laumann RA, Kavčič A, Moraes MCB, Borges M, Čokl A. Reproductive behaviour and vibratory communication of the neotropical predatory stink bug *Podisus nigrispinus*. *Physiol Entomol*. 2013;38(1):71-80. doi:10.1111/phen.12005

77. McBrien HL, Çokl A, Millar JG. Comparison of substrate-borne vibrational signals of two congeneric stink bug species, *Thyanta pallidovirens* and *T. custator accerra* (Heteroptera: Pentatomidae). *J Insect Behav*. 2002;15(6):715-738. doi:10.1023/A:1021164021489

78. Liao YC, Yang MM. Acoustic communication of three closely related psyllid species: A case study in clarifying allied species using substrate-borne signals (Hemiptera: Psyllidae: *Cacopsylla*). *Ann Entomol Soc Am*. 2015;108(5):902-911. doi:10.1093/aesa/sav071

79. Oppedisano T, Polajnar J, Kostanjšek R, et al. Substrate-borne vibrational communication in the vector of apple proliferation disease *Cacopsylla picta* (Hemiptera: Psyllidae). *J Econ Entomol*. 2020;113(2):596-603. doi:10.1093/jee/toz328

80. Eben A, Mühlethaler R, Gross J, Hoch H. First evidence of acoustic communication in the pear psyllid *Cacopsylla pyri* L. (Hemiptera: Psyllidae). *J Pest Sci (2004)*. 2015;88(1):87-95. doi:10.1007/s10340-014-0588-0

81. Wenninger EJ, Hall DG, Mankin RW. Vibrational communication between the sexes in *Diaphorina citri* (Hemiptera: Psyllidae). *Ann Entomol Soc Am*. 2009;102(3):547-555. doi:10.1603/008.102.0327

82. Schilman PE, Lazzari CR, Manrique G. Comparison of disturbance stridulations in five species of Triatominae bugs. *Acta Trop*. 2001;79(2):171-178. doi:10.1016/S0001-706X(01)00095-X

83. Quiroga N, Muñoz MI, Pérez-Espinoza SA, Penna M, Botto-Mahan C. Stridulation in the wild kissing bug *Mepraia spinolai*: description of the stridulatory organ and vibratory disturbance signal. *Bioacoustics*. 2020;29(3):266-279. doi:10.1080/09524622.2019.1603120

84. Manrique G, Schilman PE. Two different vibratory signals in *Rhodnius prolixus* (Hemiptera: Reduviidae). *Acta Trop*. 2000;77(3):271-278. doi:10.1016/S0001-706X(00)00146-7

85. Roces F, Manrique G. Different stridulatory vibrations during sexual behaviour and disturbance in the blood-sucking bug *Triatoma infestans* (Hemiptera: Reduviidae). *J Insect Physiol*. 1996;42(3):231-238. doi:10.1016/0022-1910(95)00099-2

86. Zych AF, Mankin RW, Gillooly JF, Foreman E. Stridulation by *Jadera haematoloma* (Hemiptera: Rhopalidae): Production mechanism and associated behaviors. *Ann Entomol Soc Am*. 2012;105(1):118-127. doi:10.1603/AN11048

87. Lubanga UK, Peters RA, Steinbauer MJ. Substrate-borne vibrations of male psyllids vary with body size and age but females are indifferent. *Anim Behav*. 2016;120:173-182. doi:10.1016/j.anbehav.2016.07.033

88. Percy DM, Taylor GS, Kennedy M. Psyllid communication: Acoustic diversity, mate recognition and phylogenetic signal. *Invertebr Syst*. 2006;20(4):431-445. doi:10.1071/IS05057

89. Liao YC, Huang SS, Yang MM. Substrate-borne signals, specific recognition, and plant effects on the acoustics of two allied species of *Trioza*, with the description of a new species (Psylloidea: Triozidae). *Ann Entomol Soc Am*. 2016;109(6):906-917. doi:10.1093/aesa/saw060

90. Towne WF. Acoustic and visual cues in the dances of four honey-bee species. *Behav Ecol Sociobiol*. 1985;16(2):185-187. doi:10.1007/BF00295154

91. Kirchner WH. Vibrational signals in the tremble dance of the honeybee, *Apis mellifera*. *Behav Ecol Sociobiol*. 1993;33(3):169-172. doi:10.1007/BF00216597

92. Su DK-N. Bumblebee vibration activated foraging. Thesis. 2009.

93. Pritchard DJ, Vallejo-Marín M. Floral vibrations by buzz-pollinating bees achieve higher frequency, velocity and acceleration than flight and defense vibrations. *J Exp Biol*. 2020;223(11). doi:10.1242/jeb.220541

94. Krausa K, Hager FA, Kiatoko N, Kirchner WH. Vibrational signals of African stingless bees. *Insectes Soc*. 2017;64(3):415-424. doi:10.1007/s00040-017-0564-9

95. Hrncir M, Schmidt VM, Schorkopf DLP, Jarau S, Zucchi R, Barth FG. Vibrating the food receivers: A direct way of signal transmission in stingless bees (*Melipona seminigra*). *J Comp Physiol A Neuroethol Sensory, Neural, Behav Physiol*. 2006;192(8):879-887. doi:10.1007/s00359-006-0123-8

96. Joyce AL, White WH, Medina RF. Host plants impact courtship vibration transmission and mating success of a parasitoid wasp, *Cotesia flavipes* (Hymenoptera: Braconidae). *Evol Ecol*. 2014;28(2):361-372. doi:10.1007/s10682-013-9682-7

97. Joyce AL, Hunt RE, Bernal JS, Bradleigh Vinson S. Substrate influences mating success and transmission of courtship vibrations for the parasitoid *Cotesia marginiventris*. *Entomol Exp Appl*. 2008;127(1):39-47. doi:10.1111/j.1570-7458.2008.00670.x

98. Joyce AL, Aluja M, Sivinski J, et al. Effect of continuous rearing on courtship acoustics of five braconid parasitoids, candidates for augmentative biological control of *Anastrepha* species. *BioControl*. 2010;55(5):573-582. doi:10.1007/s10526-010-9278-x

99. Roces F, Hölldobler B. Use of stridulation in foraging leaf-cutting ants: Mechanical support during cutting or short-range recruitment signal? *Behav Ecol Sociobiol*. 1996;39(5):293-299. doi:10.1007/s002650050292

100. Carlos AA, Diniz EA, Da Silva SV, Bueno OC. Vibration of the plant substrate generated by workers' stridulation during fungus garden cultivation in *Atta laevigata* (Smith) (Hymenoptera: Formicidae). *EntomoBrasilis*. 2018;11(2):107-112. doi:10.12741/ebrasilis.v11i2.732

101. Pielström S, Roces F. Vibrational communication in the spatial organization of collective digging in the leaf-cutting ant *Atta vollenweideri*. *Anim Behav*. 2012;84(4):743-752. doi:10.1016/j.anbehav.2012.07.008

102. Fuchs S. The response to vibrations of the substrate and reactions to the specific drumming in colonies of carpenter ants (Camponotus, Formicidae, Hymenoptera). *Behav Ecol Sociobiol*. 1976;1(2):155-184. doi:10.1007/BF00299196

103. Lin YH, Liao YC, Yang CCS, Billen J, Yang MM, Hsu YF. Vibrational communication between a myrmecophilous butterfly *Spindasis lohita* (Lepidoptera: Lycaenidae) and its host ant *Crematogaster rogenhoferi* (Hymenoptera: Formicidae). *Sci Rep*. 2019;9(1):1-10. doi:10.1038/s41598-019-54966-6

104. Markl H, Holldobler B. Recruitment And Food-Retrieving Behavior In *Novomessor* (Formicidae, Hymenoptera) II. Vibration Signals. *Behav Ecol Sociobiol*. 1978;4:183-216.

105. Markl H, Hölldobler B, Hölldobler T. Mating behavior and sound production in harvester ants (Pogonomyrmex, Formicidae). *Insectes Soc*. 1977;24(2):191-212. doi:10.1007/BF02227171

106. Otten H, Waäckers F, Battini M, Dorn S. Efficiency of vibrational sounding in the parasitoid *Pimpla turionellae* is affected by female size. *Anim Behav*. 2001;61(3):671-677. doi:10.1006/anbe.2000.1639

107. Spangler HG, Manley DG. Sounds associated with the mating behavior of a mutillid wasp. *Ann Entomol Soc Am*. 1978;71(3):389-392. doi:10.1093/aesa/71.3.389

108. Brennan BJ. Abdominal wagging in the social paper wasp *Polistes dominulus*: Behavior and substrate vibrations. *Ethology*. 2007;113(7):692-702. doi:10.1111/j.1439-0310.2007.01373.x

109. Pratte M, Jeanne RL. Antennal drumming behavior in *Polistes* Wasps (Hymenoptera: Vespidae). *Z Tierpsychol*. 1984;66:177-188.

110. Kirchner WH, Broecker I, Tautz J. Vibrational alarm communication in the damp-wood termite *Zootermopsis nevadensis. Physiol Entomol*. 1994;19(3):187-190. doi:10.1111/j.1365-3032.1994.tb01041.x

111. Hertel H, Hanspach A, Plarre R. Differences in Alarm Responses in Drywood and Subterranean Termites (Isoptera: Kalotermitidae and Rhinotermitidae) to Physical Stimuli. *J Insect Behav*. 2011;24(2):106-115. doi:10.1007/s10905-010-9240-x

112. Yack JE, Smith ML, Weatherhead PJ. Caterpillar talk: Acoustically mediated territoriality in larval Lepidoptera. *Proc Natl Acad Sci U S A*. 2001;98(20):11371-11375. doi:10.1073/pnas.191378898

113. Bowen JL, Mahony SJ, Mason AC, Yack JE. Vibration-mediated territoriality in the warty birch caterpillar *Drepana bilineata*. *Physiol Entomol*. 2008;33(3):238-250. doi:10.1111/j.1365-3032.2008.00627.x

114. Scott JL, Yack JE. Vibratory territorial signals in caterpillars of the poplar lutestring, *Tethea or* (Lepidoptera: Drepanidae). *Eur J Entomol*. 2012;109(3):411-417. doi:10.14411/eje.2012.053

115. Riva F, Barbero F, Bonelli S, Balletto E, Casacci LP. The acoustic repertoire of lycaenid butterfly larvae. *Bioacoustics*. 2017;26(1):77-90. doi:10.1080/09524622.2016.1197151

116. Yack JE, Smith ML, Weatherhead PJ. Caterpillar talk: Acoustically mediated territoriality in larval Lepidoptera. *Proc Natl Acad Sci*. 2001;98(20):11371-11375. doi:10.1073/pnas.191378898

117. Travassos MA, Pierce NE. Acoustics, context and function of vibrational signalling in a butterfly-ant mutualism. *Anim Behav*. 2000;60(1):13-26. doi:10.1006/anbe.1999.1364

118. Travassos MA, Devries PJ, Pierce NE. A novel organ and mechanism for larval sound production in butterfly caterpillars : *Eurybia elvina*. *Trop Lepid*. 2008;18(1):20-23.

119. Henry CS, Brooks SJ, Duelli P, Johnson JB, Wells MM, Mochizuki A. Parallel evolution in courtship songs of North American and European green lacewings (Neuroptera: Chrysopidae). *Biol J Linn Soc*. 2012;105(4):776-796. doi:10.1111/j.1095-8312.2011.01845.x

120. Henry CS, Wells MLM. Adaptation or random change? the evolutionary response of songs to substrate properties in lacewings (Neuroptera: Chrysopidae: *Chrysoperla*). *Anim Behav*. 2004;68(4):879-895. doi:10.1016/j.anbehav.2003.10.032

121. Henry CS, Brooks SJ, Johnson JB, Mochizuki A, Duelli P. A new cryptic species of the Chrysoperla carnea group (Neuroptera: Chrysopidae) from western Asia: Parallel speciation without ecological adaptation. *Syst Entomol*. 2014;39(2):380-393. doi:10.1111/syen.12061

122. Henry CS, Mochizuki A, Nakahira K, Haruyama N, Nomura M. Courtship songs of *Chrysoperla nipponensis* (Neuroptera: Chrysopidae) delineate two distinct biological species in eastern Asia. *Ann Entomol Soc Am*. 2009;102(5):747-758. doi:10.1603/008.102.0502

123. Eberhard MJB, Eberhard SH. Evolution and Diversity of Vibrational Signals in Mantophasmatodea (Insecta). *J Insect Behav*. 2013;26(3):352-370. doi:10.1007/s10905-012-9352-6

124. Howard DR, Schmidt AP, Hall CL, Mason AC. Substrate-borne vibration mediates intrasexual agonism in the New Zealand Cook Strait giant weta (*Deinacrida rugosa*). *J Insect Behav*. 2018;31(6):599-615. doi:10.1007/s10905-018-9700-2

125. Mcvean A, Field LH. Communication by substratum vibration in the New Zealand tree weta, *Hemideina femorata* (Stenopelmatidae: Orthoptera). *J Zool*. 1996;239(1):101-122. doi:10.1111/j.1469-7998.1996.tb05440.x

126. Ter Hofstede HM, Schöneich S, Robillard T, Hedwig B. Evolution of a communication system by sensory exploitation of startle behavior. *Curr Biol*. 2015;25(24):3245-3252. doi:10.1016/j.cub.2015.10.064

127. Benavides-Lopez JL, ter Hofstede H, Robillard T. Novel system of communication in crickets originated at the same time as bat echolocation and includes male-male multimodal communication. *Sci Nat*. 2020;107(1). doi:10.1007/s00114-020-1666-1

128. Howard DR, Hill PSM. Morphology and calling song characteristics in *Gryllotalpa major* Saussure (Orthoptera: Gryllotalpidae). *J Orthoptera Res*. 2006;15(1):53-57. doi:10.1665/1082-6467(2006)15[53:macsci]2.0.co;2

129. Stritih N, Čokl A. Mating behaviour and vibratory signalling in non-hearing cave crickets reflect primitive communication of *Ensifera*. *PLoS One*. 2012;7(10). doi:10.1371/journal.pone.0047646

130. Benediktov AA. Vibrational signals of the pygmy grasshoppers males (Orthoptera : Tetrigoidea) from Laos and Southern Vietnam. *Russ Entomol J*. 2013;22(4):255-257.

131. Kočárek P. Substrate-borne vibrations as a component of intraspecific communication in the groundhopper *Tetrix ceperoi*. *J Insect Behav*. 2010;23(5):348-363. doi:10.1007/s10905-010-9218-8

132. De Luca PA, Morris GK. Courtship communication in meadow katydids: Female preference for large male vibrations. *Behaviour*. 1988;135(6):777-794.

133. Morris GK. Calling display and mating behaviour of *Copiphora rhinoceros* Pictet (Orthoptera: Tettigoniidae). *Anim Behav*. 1980;28(1):42-51. doi:10.1016/S0003-3472(80)80006-6

134. Sarria-S FA, Buxton K, Jonsson T, Montealegre-Z F. Wing mechanics, vibrational and acoustic communication in a new bush-cricket species of the genus *Copiphora* (Orthoptera: Tettigoniidae) from Colombia. *Zool Anz*. 2016;263:55-65. doi:10.1016/j.jcz.2016.04.008

135. De Souza LR, Kasumovic MM, Judge KA, Morris GK. Communicating male size by tremulatory vibration in a Columbian rainforest katydid, *Gnathoclita sodalis* (Orthoptera, Tettigoniidae). *Behaviour*. 2011;148(3):341-357. doi:10.1163/000579511X559418

136. Sismondo E. Physical characteristics of the drumming of *Meconema thalassinum*. *J Insect Physiol*. 1980;26:209-212.

137. Rajaraman K, Godthi V, Pratap R, Balakrishnan R. A novel acoustic-vibratory multimodal duet. *J Exp Biol*. 2015;218(19):3042-3050. doi:10.1242/jeb.122911

138. Keuper A, Kuhne R. The acoustic behaviour of the bushcricket *Tettigonia catans* II. Transmission of airborne-sound and vibration signals in the biotope. *Behav Processes*. 1983;8:125-145.

139. Stewart KW, Zeigler DD. Drumming behavior of twelve north American stonefly (Plecoptera) species: First descriptions in Peltoperlidae, Taeniopterygidae and Chloroperlidae. *Aquat Insects*. 1984;6(1):49-61. doi:10.1080/01650428409361162

140. Zeigler DD, Stewart KW. Drumming behavior of eleven nearctic stonefly (Plecoptera) species. *Ann Entomol Soc Am*. 1977;70(4):495-505. doi:10.1093/aesa/70.4.495

141. Maketon M, Stewart KW, Kondratieff BC, et al. New descriptions of drumming and evolution of the behavior in North American Perlodidae (Plecoptera). *J Kansas Entomol Soc*. 1988;61(2):161-168.

142. Maketon M, Stewart KW. Patterns and evolution of drumming behavior in the stonefly families Perlidae and Peltoperlidae. *Aquat Insects*. 1988;10(2):77-98. doi:10.1080/01650428809361316

143. Zeigler DD, Stewart KW. Drumming behavior of five stonefly (Plecoptera) species from Central and Western North America. *Ann Entomol Soc Am*. 1985;78(6):717-722. doi:10.1093/aesa/78.6.717

144. Stewart KW, Szczytko SW, Stark BP, Zeigler DD. Drumming behavior of six North American Perlidae (Plecoptera) species. *Ann Entomol Soc Am*. 1982;75(5):549-554.

145. Maketon M, Stewart KW. Further studies of the drumming behavior of North American Perlidae (Plecoptera). *Ann Entomol Soc Am*. 1984b ;77(6):770-778. doi:10.1093/aesa/77.6.770

146. Maketon M, Stewart KW. Drumming behavior in four North American Perlodidae (Plecoptera) species. *Ann Entomol Soc Am*. 1984a ;77(5):621-626. doi:10.1093/aesa/77.5.621

147. Maketon M, Stewart KW, Kondratieff BC, et al. New descriptions of drumming and evolution of the behavior in North American Perlodidae (Plecoptera). *J Kansas Entomol Soc*. 1988;61(2):161-168.

148. Stewart KW, Szczytko SW, Maketon M. Drumming as a behavioral line of evidence for delineating species in the genera *Isoperla*, *Pteronarcys*, and *Taeniopteryx* (Plecoptera). *Ann Entomol Soc Am*. 1988;81(4):689-699. doi:10.1093/aesa/81.4.689

149. Szczytko SW, Stewart KW. Drumming behavior of four western Nearctic *Isoperla* species (Plecoptera: Perlodidae). *Ann Entomol Soc Am*. 1979;72:781-786. doi:10.1093/aesa/83.5.991

150. Stewart KW, Szczytko SW, Stark BP. Drumming behavior of four species of North American Pteronarcyidae (Plectoptera): Dialects in Colorado and Alaska *Pteronarcella badia*. *Ann Entomol Soc Am*. 1982;75:530-533.

151. Mowles SL, Jennions M, Backwell PRY. Multimodal communication in courting fiddler crabs reveals male performance capacities. *R Soc Open Sci*. 2017;4(3). doi:10.1098/rsos.161093

152. Salmon M. Coastal distribution, display and sound production by Florida fiddler crabs (Genus *Uca*). *Anim Behav*. 1967;15(4). doi:10.1016/0003-3472(67)90043-7

153. Boon PY, Yeo DCJ, Todd PA. Sound production and reception in mangrove crabs *Perisesarma* spp. (Brachyura: Sesarmidae). *Aquat Biol*. 2009;5(2):107-116. doi:10.3354/ab00136

154. Bishop AM, Denton P, Pomeroy P, Twiss S. Good vibrations by the beach boys: Magnitude of substrate vibrations is a reliable indicator of male grey seal size. *Anim Behav*. 2015;100:74-82. doi:10.1016/j.anbehav.2014.11.008

155. Bender H. Structure and function of the eastern grey kangaroo (*Macropus giganteus*) foot thump. *J Zool*. 2006;268(4):415-422. doi:10.1111/j.1469-7998.2005.00038.x

156. O'Connell-Rodwell CE, Arnason BT, Hart LA. Seismic properties of Asian elephant (*Elephas maximus*) vocalizations and locomotion. *J Acoust Soc Am*. 2000;108(6):3066-3072. doi:10.1121/1.1323460

157. Günther RH, O'Connell-Rodwell CE, Klemperer SL. Seismic waves from elephant vocalizations: A possible communication mode? *Geophys Res Lett*. 2004;31(11):1-4. doi:10.1029/2004GL019671

158. Narins PM, Reichman OJ, Jarvis JUM, Lewis ER. Seismic signal transmission between burrows of the Cape mole-rat, *Georychus capensis*. *J Comp Physiol A*. 1992;170(1):13-21. doi:10.1007/BF00190397

159. Randall JA, Matocq MD. Why do kangaroo rats (*Dipodomys spectabilis*) footdrum at snakes? *Behav Ecol*. 1997;8(4):404-413. doi:10.1093/beheco/8.4.404

160. Rado R, Levi N, Hauser H, et al. Seismic signaling as a means of communication in a subterranean mammal. *Anim Behav*. 1987;35(4):1249-1251. doi:10.1016/S0003-3472(87)80183-5

161. Hrouzková E, Dvořáková V, Jedlička P, Šumbera R. Seismic communication in demon African mole rat *Tachyoryctes daemon* from Tanzania. *J Ethol*. 2013;31(3):255-259. doi:10.1007/s10164-013-0374-0

162. Kappel L. Substrate-Borne Vibrational Communication in Veiled Chameleons (*Chamaeleo calyptratus*) During Courtship, Breeding, and Territoriality. 2020.