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**An integrative approach to assess the behavioral impacts of noise stimuli on the Australian
black field cricket, *Teleogryllus commodus***

By

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DISSERTATION

Submitted to the University of New Hampshire

In Partial Fulfillment of

The Requirements for the Degree of

Doctor of Philosophy

In

Biological Sciences: Integrative and Organismal Biology

May 2023

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Jessica R. Briggs

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ABSTRACT

For acoustically oriented species, elevated levels of ambient sound can interfere with an organism's ability to detect and assess acoustic signals and cues needed for making important decisions. Ambient noise, defined as any unwanted or non-focal acoustic signal, can impact behavior and decision-making by disrupting auditory sensory perception. As a result, noise in the context of this dissertation can be further delineated as excess sound that hinders a receiver's ability to detect and distinguish acoustic signals. Noise consists of either airborne or substrate-borne modalities or both. While many studies focus on the impact of airborne noise, many species have evolved the ability to detect both airborne and substrate-borne sounds. This bias towards airborne stimuli has left researchers with only a partial understanding of the impact of noise on animal behavior. Taking an integrative approach, this dissertation identifies the impacts of multisensory noise on the behavior of the Australian black field cricket (*Teleogryllus commodus*). First, I established the sensitivity of the auditory system to airborne sonic (1-20 kHz), airborne ultrasonic (>20 kHz), and substrate-borne stimuli (50-1600 Hz). I also determined that noise regardless of modality or bandwidth (sonic, ultrasonic, and substrate vibrations) has a significant impact on female phonotaxis. Finally, I tested how each noise type influences female choice regarding male calling phenotype and found that all noise types and bandwidths disrupt the mate choice process. I identified two possible causes for these shifts in behavior: energetic and informational masking. Energetic masking occurs when noise energetically overlaps with the signal and prevents detection of the signal. Informational masking occurs when the noise does not energetically overlap with the signal but still interferes with the

female's ability to extract information. The findings of this dissertation demonstrate the complexities of noise and its impacts on animal behavior, emphasizing the need to consider the sensory sensitivity of animals in studying the effects of noise. By furthering our understanding of how different noise types inform how animals interact with their environment, we can better determine the constraints and adaptations of living in an increasingly noisy world.

INTRODUCTION

Sound is an essential component of ecological and biological systems that plays a crucial role in the functioning of ecosystems. However, the presence of extraneous sound in the form of acoustic noise can disrupt the normal functioning of these systems. Noise can be defined as any excessive sound that interferes with the receiver's ability to detect and discriminate different signals and cues, leading to errors in perception and decision-making (Brumm and Slabbekoorn 2005a; Wiley 2015). Noise interferes with the detection of signals across the landscape, creating barriers to communication and disrupting the ability of animals to detect important non-communicative cues, such as the approach of predators. Sound, by contrast, can be considered a neutral or focal acoustic signal. The sources of sound can be broadly classified into three categories: biotic, abiotic, and anthropogenic (Pijanowski, Farina, et al. 2011). Biotic sound can arise from a diverse range of organisms, with chorusing species such as birds, anurans, and insects being a dominant source. Abiotic sound can come from natural phenomena such as wind, water, and seismic activity. Anthropogenic sounds result from human activities such as transportation, construction, and urbanization. (Pijanowski, Villanueva-Rivera, et al. 2011). Noise, regardless of its source, is a pervasive and complex issue for animals in most environments, creating significant challenges for communication, navigation, and survival; however, some animals have adapted to use noise to their advantage. Some prey species use areas with high noise as a refuge from disturbance-sensitive predator species (Berger 2007; Shannon, Cordes, et al. 2014). Given the complexity and pervasiveness of noise on the landscape, it is essential to understand the ecological and evolutionary implications of noise and its effects on animal behavior.

For many animals, sound is a complex stimulus that can manifest in two different auditory sensory modalities, airborne sounds or substrate-borne vibrations, and detected by different sensory organs (Halfwerk and Slabbekoorn 2015). Furthermore, airborne sound has been categorized into three different auditory channels based on human auditory sensitivities: infrasonic (<1 kHz), sonic (1-20 kHz), and ultrasonic (>20 kHz). The presence of sound in multiple sensory channels poses a challenge for animals, as they need to balance their attention between detecting signals and cues related to mating, foraging, and avoiding predators or other risks (Lima and Bednekoff 1999). This tradeoff can be further complicated by environmental conditions, which can affect how animals integrate and process signals and cues from various sensory inputs.

Multisensory perception plays a critical role in determining how animals respond to sounds in different sensory channels. Multisensory perception refers to the ability of animals to use multiple auditory sensory modalities such as airborne and substrate borne. Some animals rely on multiple sensory inputs to detect and locate prey, navigate, or communicate with conspecifics. Animals that have been documented to use sounds from both airborne and substrate-borne modalities include: katydids (*Tettigonia cantans*) (Keuper and Kuhne 1983), mole crickets (*Gryllotalpa major*) (Howard and Hill 2006), white-lipped tree frogs (*Leptodactylus albilabris*) (Lewis and Narins 1985), and African elephants (*Loxodonta africana*) (O'Connell-Rodwell 2007). The integration of information from different sensory modalities can enhance the detection and discrimination of relevant signals and cues. For example, male katydids produce airborne signals while perched on vegetation, which also generates substrate vibrations in the plant. When environmental conditions make it challenging to localize the source of the airborne signal, both males and females show a higher tendency to move toward the branch where

substrate vibrations are being transmitted (Latimer and Schatral 1983). This suggests that katydids may use substrate vibrations as a secondary cue to locate potential mates or competitors in their environment, highlighting the importance of multisensory perception.

Despite the importance of multisensory perception in shaping animal behavior, most research on the impacts of noise has focused on airborne noise and its effects on airborne signals. This approach has left a gap in our understanding of how noise from other auditory modalities, such as substrate-borne vibrations, influences animal behavior. Species have been found to be sensitive to substrate-borne vibrations from nearly all taxon examined so far; therefore, given the widespread detection of substrate-borne vibrations in many animal species (Hill 2008), it is crucial to expand our research focus to include the impacts of noise on this auditory modality. To fully understand the effects of noise on animal behavior, a multisensory and interdisciplinary approach needs to be taken, that considers the complex interactions between different auditory modalities and their ecological and evolutionary implications. This approach can help to identify the mechanisms underlying the tradeoffs and compromises animals make in response to noise and develop effective strategies for mitigating the negative impacts of noise on animal populations that rely on sound to assess their environment to make decisions crucial to survival.

The negative impacts of noise on animals have been extensively studied, with documented effects ranging from physiological changes and death to disruptions in communication and reproduction (Kight and Swaddle 2011). One common physiological response to loud noise is an increase in cortisol levels, which has been observed in species such as the lined seahorse (*Hippocampus erectus*) (Anderson et al. 2011), dogs (*Canis lupus familiaris*) (Gue et al. 1987), and goldfish (*Carassius auratus*) (Smith et al. 2004). In addition to physiological changes, noise can also interfere with communication among animals, by

disrupting the receiver's ability to detect and assess relevant signals. Some species have been observed to adapt their signaling behavior to overcome noisy environments, such as the American robin (*Turdus migratorius*), which exhibits temporal shifts in signaling (Fuller et al. 2007). Others, like the song sparrow (*Melospiza melodia*) and great tit (*Parus major*), shift the frequency of their signals to overcome low-frequency noise (Slabbekoorn and Peet 2003; Wood and Yezerinac 2006). Noise can also affect reproductive behavior. An example of this was found in domestic canaries (*Serinus canaria*), in which smaller clutch sizes were observed in areas with high levels of noise (des Aunay et al. 2017). Female Cope's gray treefrog (*Hyla chrysoscelis*), shows a reduction in responsiveness to the advertisement calls of males when broadcast concurrently with biological sounds (Gupta and Bee 2022). Túngara frogs (*Physalaemus pustulosus*), which use acoustic signals to assess male quality, were found to exhibit a decrease in mating preference as noise levels increased (Coss et al. 2021). The effects of noise on animals are varied, while some animals are significantly affected some show little to no effect of noise on their behavior, highlighting the need for expanding noise research to include more taxa to make more informed mitigation and management decisions.

Currently, most terrestrial research on the effects of noise has focused on the effects of airborne noise on vertebrates. Although invertebrates comprise 97% of all identified species, only 4% of peer review publications focus on invertebrates (Shannon, McKenna, et al. 2016). Insects are ideal for studying the impact of many airborne and substrate-borne noise sources due to the diversity of their auditory sensory system, a diverse range of behaviors, small size and ease of observation in the laboratory, and their ecological significance (Wilson Horch et al. 2017). The detection of airborne sounds evolved 24 times in at least seven insect families, leading to a great diversity of auditory sensory systems in insects (Greenfield 2016). Many insects have

evolved the capability to detect sound in a broad frequency range, from low-frequency sonic sounds (1-17 kHz) to the ultrasonic range (>20 kHz) and into the seismic range via substrate vibrations (<1 Hz) (Greenfield 2014). It is thought that approximately 70% of insects communicate through substrate vibrations alone, 20% through both airborne and substrate vibrations, and only 5% communicate via airborne acoustic signals alone (Cocroft and Rodríguez 2005). Although very few insects solely use airborne signals, most research into the impacts of noise focuses only on airborne noise. Mechanoreceptors for the detection of substrate-borne vibrations are broadly documented across insects, and the detection of substrate-borne vibrations is more widespread than the detection of airborne sound (Cocroft and Rodríguez 2005). This underscores the importance of focusing on noise types relevant to the auditory sensory system of the focal animal.

The ability of insects to detect both airborne and substrate-borne sounds has evolved in numerous behavioral contexts. Some insects, for example, rely on both types of signals to locate and assess potential mates. Male gryllid species produce airborne signals to attract females, which use the temporal components of the signal to evaluate the male's quality (Otte 1992; Gray 1997; Bertram 2000). Moreover, individuals also use airborne signals to locate the signaler (Göpfert and Hennig 2016). Ultrasonic hearing has evolved in many aerial species to detect and avoid predators such as bats (Greenfield 2016). For instance, some noctuid moths have evolved hearing specifically for detecting the ultrasonic echolocation clicks from bats, while not producing sound themselves. When a moth detects an ultrasonic echolocation click, it automatically moves away from the sound in an evasive maneuver (Nakano et al. 2015). Additionally, leafhoppers and planthoppers, which live on plants, use vibrations propagated through the leaves and stems to attract and locate potential mates (Michelsen et al. 1982).

Substrate-borne vibrations are also crucial in the detection of approaching predators, often triggering a startle response and cessation of calling activity (Hoy et al. 1989).

Orthopteran insects, an order including grasshoppers, crickets, and locusts, are known for producing a wide range of signal types, and their large size allows for detailed neurological and anatomical research on the nervous system. As a result, they have become the most extensively studied and modeled insect sensory system (Robinson and Hall 2002). Within the order Orthoptera, crickets have a mating system in which females rely on detecting and responding to male airborne signals, while simultaneously monitoring for predators using both auditory (airborne sound, such as that produced by bats) and subgenual (substrate-borne vibration, such as produced by terrestrial predators) organs (Browning 1954). *Teleogryllus commodus*, an endemic species of Australasia, is a black field cricket whose mating success depends on the female's ability to detect and locate the singing male (Evans 1988). Male *T. commodus* produce conspicuous advertisement calls consisting of a single chirp series followed by a trill sequence with a higher pulse rate (Bentley and Hoy 1972; Hill et al. 1972; Loher and Rence 1978). Since the mating system of *T. commodus* is well understood, easy to rear in the lab, and has a well-documented auditory system, these crickets are a good system to test the impacts of noise on well-characterized behaviors such as phonotaxis and mate choice.

This dissertation aimed to investigate the effects of noise on *T. commodus* localization and to examine how female discrimination of conspecific call quality is impaired by noise. Additionally, the study sought to establish the auditory thresholds of the auditory sensory system. A systematic approach was employed to test the behavioral response of crickets under different noise conditions, including airborne sonic and ultrasonic, and substrate-borne vibrations. The research addresses four main questions: (1) what is the range of sensitivity of the auditory

sensory system to sonic, ultrasound, and substrate-borne vibrations in *T. commodus*, (2) how does interference from airborne and substrate-borne vibrational noise affect a female's ability to locate signaling males, and (3) how does interference in airborne (sonic and ultrasonic) and substrate-borne vibrational noise affect female discrimination of male calling phenotypes.

**CHAPTER 1: AUDITORY RESPONSE THRESHOLDS FOR AIRBORNE
FREQUENCIES AND SUBSTRATE VIBRATIONS IN AUSTRALIAN BLACK FIELD
CRICKETS (*TELEOGRYLLUS COMMODUS*)**

Abstract

For many species, the ability to detect acoustic signals from conspecifics is essential for reproduction, and the ability to detect signals from heterospecifics is essential for predator avoidance. To improve the detection of relevant signals, neural filters have evolved to increase the signal-to-noise ratio of responding to a signal over noise. Identifying auditory sensitivities can help identify neural filters and biologically relevant frequencies. This study aims to measure the auditory system sensitivities of the Australian black field cricket, *Teleogryllus commodus*. Extracellular recordings were taken from the neck connectives of individuals. Auditory neural responses were recorded by presenting tones at combinations of frequencies and sound pressure levels for both airborne frequencies (1-64 kHz) and substrate-borne frequencies (50-1600 Hz). The neural responses were inspected to identify the auditory threshold for each frequency. *Teleogryllus commodus* is sensitive to both sonic and ultrasonic frequencies with sensitivity peaks at 4 kHz and 32 kHz. The most sensitive substrate-borne frequencies were 635-1600 Hz and in the lower frequency range the most sensitive frequencies were 159, 200, and 400 Hz. The sensitivities of the airborne frequencies overlap with the frequency of conspecific signals and the echolocation clicks of bat predators. The use of substrate-borne vibrations in *T. commodus* communication has yet to be identified but these results can help identify relevant frequencies to target future research. By identifying the auditory sensitivities of a species, a better understanding of

biologically relevant frequencies can be established which has broad applications.

Introduction

The auditory system evolved for animals to detect and process relevant acoustic information from their environment. Challenges arise when excess sounds such as interspecific chorusing interfere with the detection and processing of relevant sounds, this excess sound is defined as noise. One way to prioritize biologically relevant signals is for an organism to be unable to detect auditory information outside the relevant frequency range. Natural and sexual selection has led organisms to evolve such adaptations known as matched neural filters (Warrant 2016). These neural filters are specifically tuned to frequencies carrying biologically relevant information, allowing for the detection of useful signals and the exclusion of irrelevant information. Sounds that are relevant to biological processes can be classified into two modalities: airborne and substrate borne. Airborne sounds can be further divided into three channels: infrasonic (<1 kHz), ultrasonic (>20 kHz), and sonic (1-20 kHz). These signals can be unimodal, consisting of components from one modality (such as airborne), or multimodal, components from both airborne and substrate-borne sources.

Animals that rely on acoustic signals for crucial activities such as mate-finding and group cohesion often possess a neural filter that matches the frequency of their conspecific's acoustic signal (Romer 2013a). This filter enables the auditory system to maximize the signal-to-noise ratio by filtering out extraneous acoustic noise. Evidence of matched filters for conspecific signals has been observed in various taxa, including frogs (Gerhardt and Schwarz 2001) and crickets (Kostarakos et al. 2009). Many frogs and crickets signal in mixed species choruses to advertise to potential mates creating high levels of background noise. Neural filters enhance the

detection of conspecific signals and enable females to filter out background noise, increasing their chances of locating and responding to appropriate mates. Another example of matched filters can be found in moths. Some species of moths do not produce auditory signals but detect specific sounds made by predators, including bat echolocation clicks, using matched neural filters (Nakano et al. 2015). This allows the moths to acoustically detect threats and respond accordingly to potential predators.

Identifying neural filters and biologically relevant frequencies have broad applications including conservation, pest control applications, and understanding the impact of elevated ambient noise on behavior. Critical to identifying neural filters, auditory thresholds need to be established for species of interest. Auditory thresholds are defined as the lowest intensity an individual can detect at a particular frequency, representing the minimum sound intensity required to elicit a response from the auditory system. For animals capable of detecting auditory signals in multiple acoustic modalities, including many invertebrates, it is also necessary to consider the complete range of the auditory system inclusive of both airborne and substrate-borne vibrations. Failure to do so omits critical sound sources that play important roles in a species' biology and ecology.

Insects provide an excellent model for studying the auditory sensory system. While substrate-borne vibration detection is widespread among invertebrates, the ability to detect airborne signals has mainly evolved in insects (Stumpner and Von Helversen 2001). The ability of insects to detect both airborne and substrate-borne sounds has been well studied at different levels of behavior, ecology, and neurophysiology. Insect auditory systems are morphologically and functionally diverse, which has driven substantial variation in the auditory sensory system (Göpfert and Hennig 2016). Organs to detect acoustic signals have been found on all parts of the

insect body and the mechanisms to produce acoustic signals vary widely from stridulation to drumming (Hoy and Robert 1996; Virant-Doberlet and Cockl 2004).

The insect auditory system has evolved to function in a variety of behavioral contexts, particularly in mate recognition and finding. Many species rely on airborne signals or substrate-borne signals or a combination of both to assess and locate potential mates in the landscape. In addition to mate recognition and localization, the auditory system of insects also has evolved as an adaptation for predator detection. For aerial species such as moths and crickets, the ultrasonic echolocation clicks of bats trigger evasive behaviors (Miller and Surlykke 2001), while substrate-borne vibrations elicit a startle response (Cocroft and Rodríguez 2005). Studying the neural responses to various types of sounds can help us gain insights into relevant frequencies, even if they don't elicit an observable behavioral response. This understanding can be leveraged to create more effective approaches to pest management and develop conservation strategies for endangered species. By analyzing the neural mechanisms underlying sound perception, we can identify the most significant auditory cues for different species and use this information to devise targeted interventions that minimize harm to non-target organisms while maximizing benefits for the target species.

The auditory sensory system in Orthopterans is one of the most extensively studied insect sensory systems. Both airborne and substrate-borne signals are detected by the peripheral sensory system on the foreleg and relayed to the complex tibial organ (CTO) located proximally to the femoral-tibial joint (Ball et al. 1989). Airborne signals are processed by the tympanal organ (TO), and substrate-borne vibrations by the subgenual organ (SGO) (Figure 1). Campaniform sensilla (CS) located in the legs, also responds to substrate-borne vibrations mainly below 200 Hz and are less sensitive than the SGO (Kuhne et al. 1984). The CTO plays a

central role in airborne and substrate vibration detection and reflects the coevolution of signal production and signal detection in taxa that have elaborate acoustic communication signals, extracting information from both acoustic modalities (Ball et al. 1989). The broad range of detection, above 200 Hz, in the CTO overlaps with the frequency of the stridulatory signals produced by male field crickets. Sensory input arrives at the peripheral sensory system on the leg where airborne and substrate vibrational information is relayed from the leg to the prothoracic ganglion via auditory receptors (Young and Ball 1974). The signals from different auditory sensory organs are integrated into the prothoracic ganglion and relayed to the brain via ascending neurons inducing motor activity (Römer et al. 1988).

Crickets are capable of categorical perception of sounds in which different frequencies trigger different behavioral responses, as evidenced by their tendency to turn towards airborne sonic stimuli and away from stimuli in the ultrasonic range during tethered flight studies (Nolen and Hoy 1986). These opposing motor responses are due to two ascending neurons in the prothoracic ganglion that detect sonic or ultrasonic frequencies received from the tympanal organ. The AN1 ascending neuron specifically responds to the frequency of the male song and triggers positive phonotaxis (Schildberger and Hörner 1988). The AN2 ascending neuron is sensitive to frequencies up to 100 kHz and triggers negative phonotaxis (Marsat and Pollack 2012). This suggests that detecting conspecifics and predators, such as bats, are crucial roles of the cricket auditory system (Moiseff et al. 1978; Fullard and Yack 1993; Hoy and Robert 1996). Although there is evidence that the detection of both sonic and ultrasonic frequencies is important to crickets, there is limited knowledge of the sensitivity of the auditory system to ultrasonic frequencies (>20 kHz) with only a few species having been studied (Moiseff et al. 1978; Farris and Hoy 2002; Howard et al. 2008). More orthopteran species have had their

auditory thresholds established to estimate their sensitivity to detecting airborne sounds in the sonic range (1-20 kHz) (Kostarakos et al. 2009).

Like airborne sounds, crickets use substrate-borne vibrations for mate localization (Latimer and Schatral 1983; Weidemann and Keuper 1987), the establishment of territories (Keuper and Kuhne 1983), and courtship displays (Broder et al. 2021). Substrate-borne vibrations are also used for predator detection, with low frequencies (<200 Hz) eliciting a startle and freeze response (Ter Hofstede et al. 2015). However, for many Orthopteran species, the use of substrate-borne vibrations and the auditory threshold for substrate-borne vibrations is poorly characterized, having only been established in *Gryllus bimaculatus* and *G. campestris* (Dambach 1972). Vibratory interneurons extending from the thorax to the head have been found to be sensitive to frequencies from 50-2000 Hz (Dambach 1972; Kuhne et al. 1984). Since very little is known about how they use vibrations, by establishing auditory sensitivities, we can develop a better understanding of biologically relevant frequencies crickets rely on to assess and respond to their environment.

Using the Australian black field cricket (*Teleogryllus commodus*) as a model, the aim of this research was to establish the auditory thresholds for sounds in the airborne sonic range (1-20 kHz), airborne ultrasonic range (20-64 kHz), and in substrate-borne vibrations (50-1600 Hz). Currently, only the auditory sensitivities of *T. commodus* within the sonic range have been established. Like other cricket species, *T. commodus* is sensitive to the male call within the frequency range of 3.9-4.1 kHz (Kostarakos et al. 2009). However, the thresholds for their auditory sensory system in response to ultrasonic and substrate-borne vibrations remain unknown. Using extracellular recordings, the neural response to different frequencies broadcast at multiple intensities was recorded to determine the lowest intensity in which each frequency

can be detected. As crickets are increasingly used in research aimed at understanding the effects of noise on communication, mate selection, and predator detection and avoidance, it is critical to gain insight into their complete auditory sensory systems.

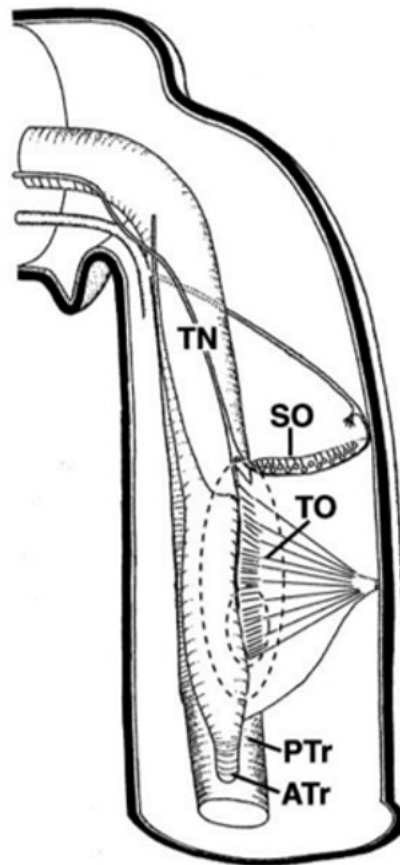


Figure 1: The complex tibial organ (CTO) in the tibia of the foreleg of *Gryllus bimaculatus*. The CTO is comprised of the tympanal organ (TO) and the subgenual organ (SO) (Yack 2004).

Methods

Animals

Teleogryllus commodus were obtained from colonies maintained at the University of New Hampshire derived from a wild population for New South Wales, Australia. Crickets were kept in containers at a constant 26°C on a 14/10 light/dark schedule. Food and water were provided *ad libitum*.

Electrophysiology

Action potentials for the auditory neurons were recorded from exposed cervical connectives using extracellular electrodes. Crickets were cold anesthetized and after removing the wings, secured ventral side up to a plastic block using low melting point wax. The mid and hind legs were removed and the contralateral leg was secured to the block. The ipsilateral leg was attached via low melting point wax by the tarsus to ensure the tympanum was not covered. Cervical connectives were exposed by cutting a square over the neck from just under the jaw to just above the prothoracic sternum. The contralateral connective was severed at the connection to the prothoracic ganglion to prevent inhibition from the contralateral receptors. The intact ipsilateral connective was draped over a 78.2 μm tungsten hook using a micromanipulator (Figure 2). A reference electrode was placed in the abdomen. Vaseline was used to fill the cavity under the connectives to prevent desiccation but did not contact the tungsten hook electrode.

Acoustic Stimuli

To record the neural response to free-field airborne acoustic pulses, a speaker (vifa ultrasound dynamic speaker, Avisoft Bioacoustics) was set up 30 cm perpendicular to the tympanum on the cricket's foreleg. Responses were recorded by presenting tones at combinations of frequency (19 values between 1,000-64000 Hz, 1/3 octave steps) and sound pressure levels (29 levels between 20 and 90 dB re 20 μPa in 2.5 dB steps). Pulses were 30 ms which included a 5 ms rise and fall. To elicit a neural response to substrate-borne vibrations, the cricket's foreleg was attached to a metal rod extending from an electromagnetic shaker that produced substrate vibrations (The Modal Shop, TMS 2004E). Substrate vibrations were presented at a combination of frequency (16 values between 50-1600 Hz, 1/3 octave steps) and

velocity (16 values between 0.125-10 mm/s). Substrate vibrations were 10 ms with a 1 ms rise and fall. The order of the frequency and sound pressure level were presented randomly for both the airborne tones and substrate-borne vibrations. Each airborne tone was calibrated to 75 dB SPL re 20 μ Pa at the position of the cricket's tympanum with a sound level meter (Brüel & Kjær Type 2250). Substrate-borne vibration pulses were each calibrated at 5 mm/s at the point of contact with the leg and shaker bar using a laser doppler vibrometer (Polytec PDV 100).

Stimulus presentation and data acquisition were controlled by custom-written software (StimProg v6, NL) running in Matlab. Signals were output via a digital-to-analog acquisition (DAQ) device (NI USB 6259, National Instruments, Austin, Texas, USA), amplified (Crown XLS1000), and broadcast through a speaker for airborne signals and an electromagnetic shaker for vibrational signals. The biological signal was amplified with an A-M Systems Model 1800 extracellular amplifier (Sequim, WA, USA) and digitized at a sampling rate of 250 kHz using the same DAQ device used to output acoustic stimuli.

Data Analysis

Using custom script in Matlab, the neurological response was visually inspected to determine the upper threshold bound (UB) as the lowest signal level at which a neural response was recorded. The next lowest level in which no neurological signal was detected was used as an estimate of a lower bound (LB). To compute the recognition threshold for airborne stimuli, the average of the UB and LB were calculated using the following equation: *threshold* =

$10 \log_{10} \left(\frac{10^{(UB/10)} + 10^{(LB/10)}}{2} \right)$ (Bee and Schwartz 2009). For vibrational stimuli, the average

between the UB and LB was calculated. Generalized linear models were built to test the effects of frequency on the auditory threshold. Models were built with and without individual as a random effect, AIC values were used to determine model fit. All assumptions of normality were

tested. All statistical analyses were performed using R Statistical Software (v4.2.2; R Core Team 2022).

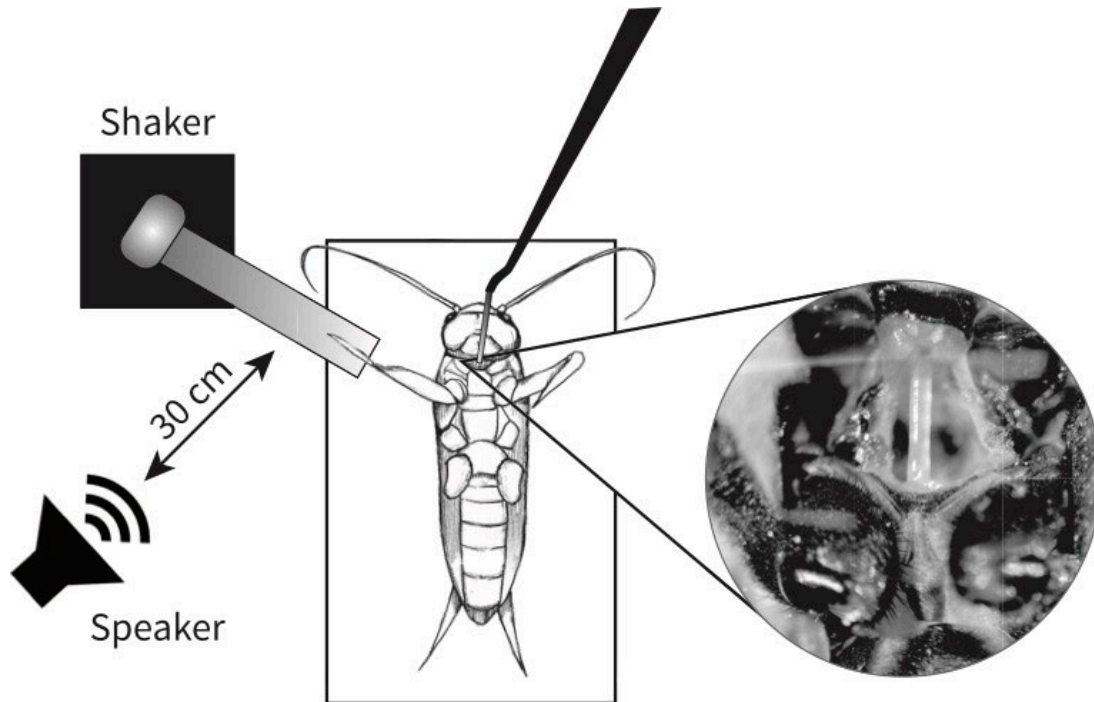


Figure 2: The experimental setup to record the neural response of crickets to airborne tones and substrate-borne vibrations. The female cricket was affixed using low melting point wax to a plastic block with one arm attached via wax to an electromagnetic shaker. A speaker was placed perpendicular to the tympanum 30 cm away in the far field. The inset shows the neck connective that was placed on a tungsten hook to record the neural response to sound.

Results

Auditory thresholds for airborne sonic and ultrasonic frequencies were measured in 19 individuals, and substrate-borne vibrations were measured in 16 individuals. The stimulus sequence was repeated 5-20 times depending on the deterioration of the neural signal. To ensure order did not affect signal strength, each time the sequence was broadcast, the order of the frequency/intensity was randomized. AIC values indicated that the best model for airborne frequencies included individual as a random effect but the best model for substrate vibrations omitted individual as a random effect. Statistical analysis showed that frequency is a function of auditory sensitivity for both airborne ($F_{18, 1615}=66.11$, $p<2.2e-16$) and substrate-borne stimuli ($F_{15, 951}=73.76$, $p<2.2e-16$).

For airborne sonic frequencies, the most sensitive frequency was 4 kHz, with a threshold of 56.23 ± 8.53 dB SPL, while the least sensitive frequency was 1 kHz, with a threshold of 74.80 ± 3.71 dB SPL. The threshold for airborne ultrasonic frequencies was most sensitive at 32 kHz, with a threshold of 56.31 ± 5.17 dB SPL, while the least sensitive frequency was 50.79 kHz, with a threshold of 72.85 ± 7.83 dB SPL (Figure 3).

For substrate-borne vibrations, the sensitive frequencies were 159 Hz (0.74 ± 0.67 mm/s threshold), 200 Hz (0.65 ± 0.44 mm/s threshold), and 400 Hz (0.52 ± 0.72 mm/s threshold). The most sensitive frequencies were from 635-1600 Hz and remained relatively constant, with thresholds less than 0.45 mm/s. The least sensitive frequency was 50 Hz, with a threshold of 4.37 ± 2.68 mm/s. There was a reduction in sensitivity between 200 and 400 Hz, with a threshold of 1.26 ± 1.11 mm/s at 252 Hz (Figure 4).

Overall, these results demonstrate that auditory sensitivity is a function of both the frequency and the mode of stimulus delivery.

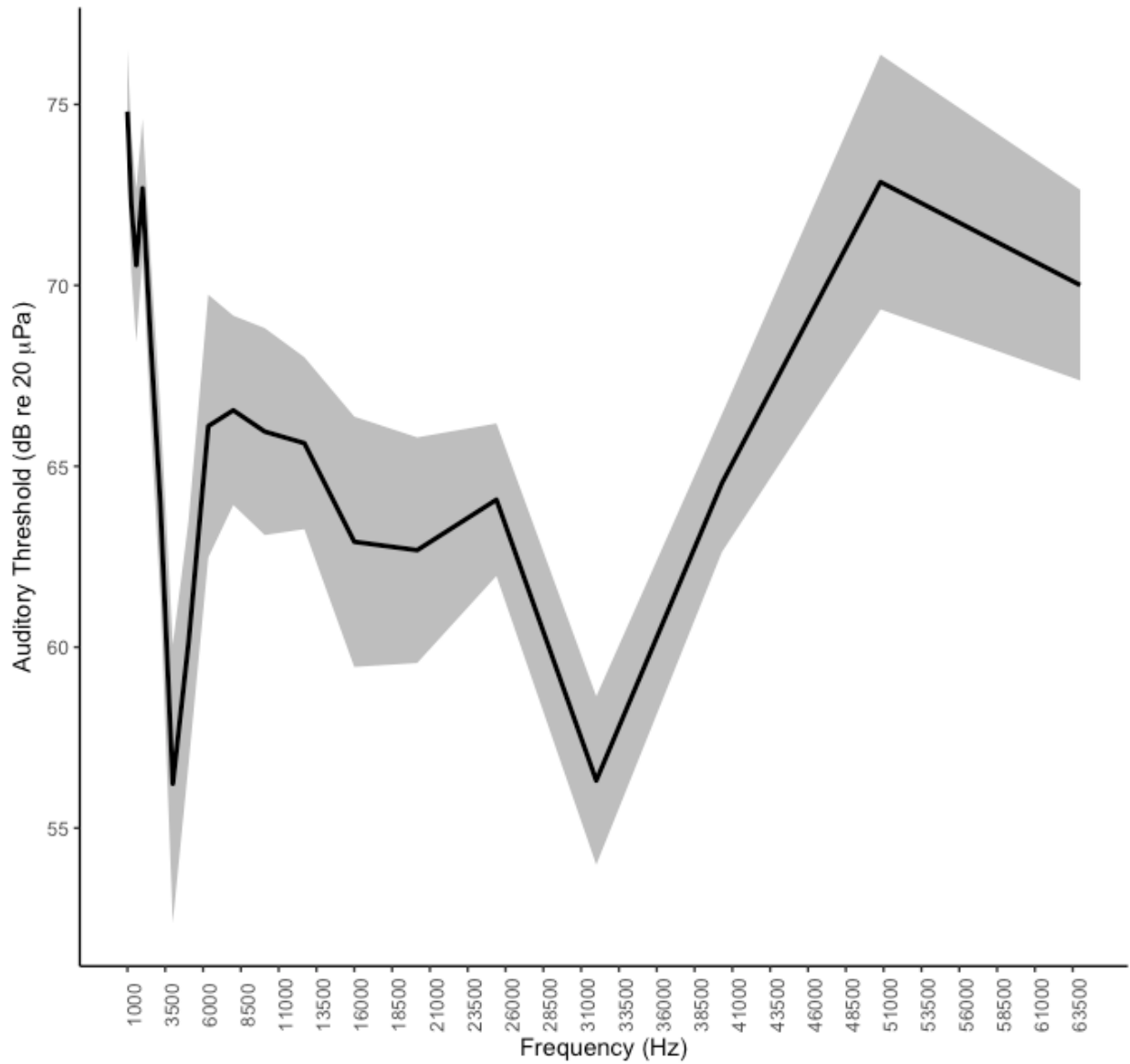


Figure 3: Mean Auditory threshold curves with a 95% confidence interval (gray) from the cervical neck connectives in *T. commodus* for airborne sounds presented in the sonic (1-20 kHz) and ultrasonic (20-64 kHz) frequency range.

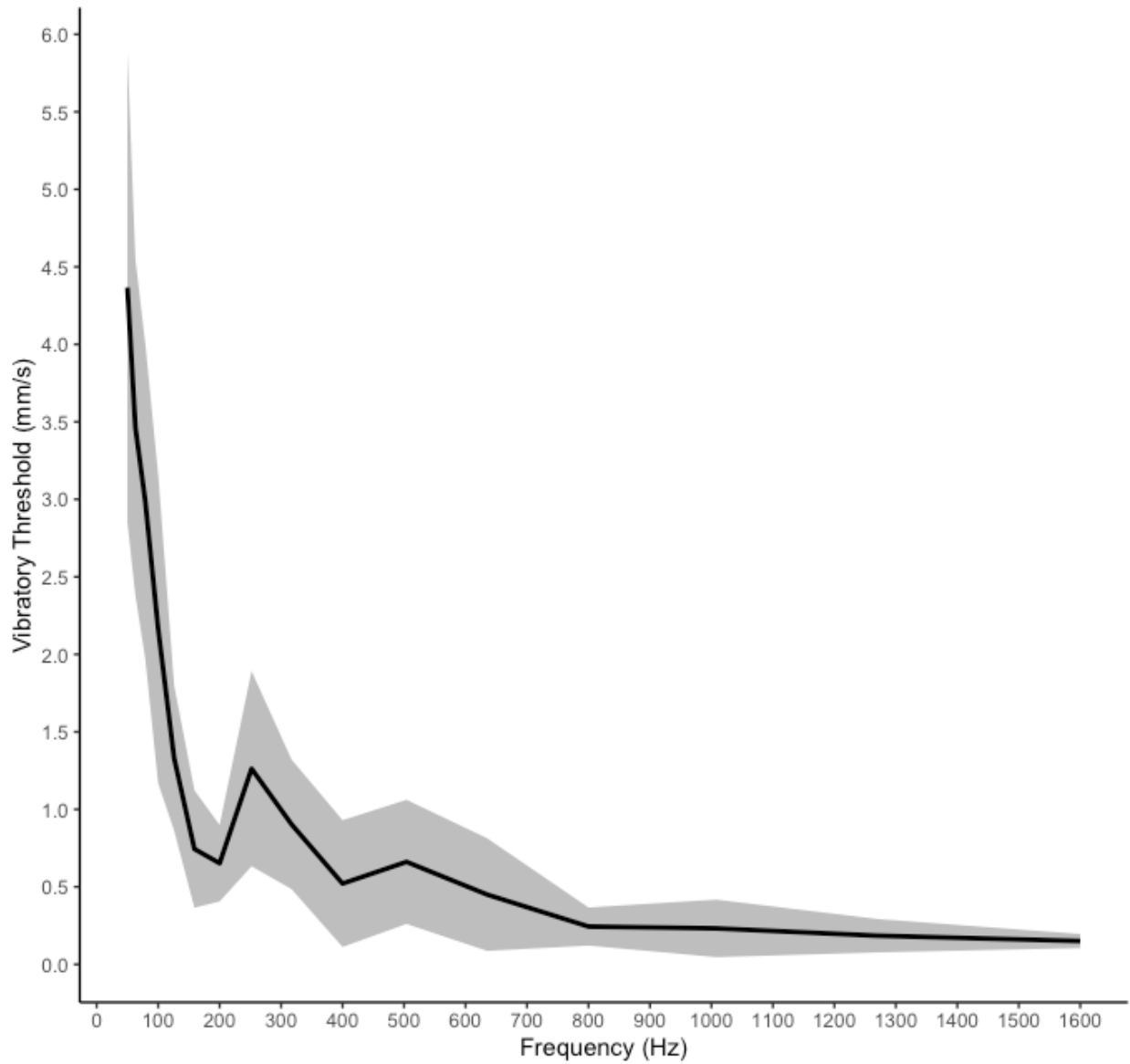


Figure 4: Mean Auditory threshold curves with a 95% confidence interval (gray) from the cervical neck connectives in *T. commodus* for substrate-borne vibrations in the seismic frequency range (50-1600 Hz).

Discussion

This study established the auditory thresholds for airborne and substrate-borne auditory channels in *Teleogryllus commodus*. Extracellular recordings from the neck connectives showed that there was a significant difference in auditory thresholds at different frequencies, for both airborne and substrate-borne pulses. Frequencies eliciting the lowest hearing thresholds were identified for each modality tested.

In the airborne sonic range (1-20 kHz), the most sensitive frequency was at 4 kHz (56.23 dB SPL threshold). This is consistent with previous studies on *T. commodus*, which also found a peak sensitivity to be 4 kHz (Hill and Boyan 1977; Kostarakos et al. 2009). This sensitivity peak coincides with the frequency of the conspecific male's call, which is at 3.9-4.1 kHz. Insects that frequently signal in an environment with multiple acoustically signaling animals often have neural filters, which allow the insect to specifically be more sensitive to conspecific signals, maximizing the signal-to-noise ratio (Warrant 2016). Thus, these results could indicate a neural filter that matches male *T. commodus* calls.

In the airborne ultrasonic range (20-64 kHz), the most sensitive frequency was found to be 32 kHz (with a 56.12 dB SPL threshold). This is likely due to the species' evolutionary adaptation to predators (Greenfield 2014). For example, multiple bat species are known predators of a sympatric species of cricket, *Teleogryllus oceanicus*. These bats emit ultrasonic clicks in the range of 20-60 kHz (Fullard et al. 2005), which overlaps with the peak sensitivity of *T. commodus* in this study. This sensitivity to ultrasonic frequencies is also present in other gryllid species, with frequency sensitivities ranging from 25-40 kHz (Moiseff et al. 1978; Farris and Hoy 2002; Howard et al. 2008).

The findings of this study demonstrate that *T. commodus* is sensitive to both ultrasonic and sonic frequencies in the airborne channels. Previous research has shown that crickets exhibit categorical perception by dividing sound frequencies into attractive and repulsive sounds (Wytenbach et al. 1996; Fullard et al. 2005). Frequencies below 16 kHz trigger positive phonotaxis, causing individuals to turn toward the sound, while frequencies above 16 kHz result in negative phonotaxis, causing individuals to move away from the sound. The sensitivity of *T. commodus* to multiple airborne ranges suggests a similar mechanism of categorical perception, whereby sounds in the sonic range may be specific to conspecific signals, while sounds in the ultrasonic range may be used to detect predatory threats. The ability to distinguish between predator and conspecific signals and elicit distinct behavioral responses could significantly contribute to the species' survival and evolution.

While the previous experiments on the airborne channel showed only single sensitivity peaks for both sonic and ultrasonic channels, the crickets in this study showed multiple sensitivity peaks in the lower frequency range for substrate-borne vibrations (50-500 Hz). The frequencies that were found to have a low threshold were 159 Hz (0.74 mm/s), 200 Hz (0.65 mm/s), and 400 Hz (0.52 mm/s). This may be a consequence of the manner in which signals propagate through substrate as opposed to air. In one study conducted on *T. neglectus*, which produce courtship and post-copulatory signals, cricket substrate-borne signals ranged from 30 Hz on elm bark, between 80-110 Hz on spruce bark and moss, and around 40 Hz on rock (Stritih and Čokl 2014). Thus, the substrate plays a major role in the frequency of the signal. The substrate-dependent frequency of the signal could be due to two potential reasons, neither of which was discriminated in the study. Either the crickets could have produced different signals depending on the substrate, or the signal could have been the same, but altered by the substrate itself (Elias

et al. 2004). Signals that propagate through a given substrate are often distorted by that substrate. Many signals with substrate-borne components take the form of refraction waves (Michelsen et al. 1982), and the frequencies disperse at speeds dependent on the substrate. The higher-frequency components of the signal will arrive at the receiver prior to the lower-frequency components of the signal (Mortimer 2017). Thus, the same signal may be changed by the time it reaches the receiver depending on the substrate through which it propagates. Regardless of whether different frequencies of the signal are attributed to the sender, or to the substrate, multiple sensitivity peaks may be evolutionarily beneficial due to the broad frequency range of substrate-borne signals.

In the higher frequency range for substrate-borne vibrations (500-1600 Hz) there were no observed single-frequency sensitivity peaks. Frequencies ranging from 635-1600 Hz exhibited a sensitivity threshold of <0.45 mm/s, indicating greater sensitivity compared to the lower substrate-borne frequencies mentioned earlier. Although no specific narrow frequency peak was detected within this range, the results suggest that the entire frequency range is sensitive to detecting substrate-borne vibrations. The detection of frequencies from 500-1,000 Hz is carried out by the subgenual organ, which is located on the foreleg, and which is the most sensitive organ for the detection of substrate-borne vibrations (Dambach 1972). The frequencies below 500 Hz are detected by campaniform sensilla located in the legs of the cricket (Young and Ball 1974). The subgenual organ may be used for long-range detection of substrate-borne vibrations, such as an approaching predator, whereas the campaniform sensilla may be used for close-range communication such as courtship displays; however, the use of substrate vibrations during *T. commodus* courtship displays has yet to be investigated. A closely related gryllid species, *T. oceanicus*, produces vibratory signals coupled to airborne signals during courtship displays with

peak frequencies ranging from 32-176 Hz (Broder et al. 2021). Due to the frequency sensitivities between 159-200 Hz, it is possible that *T. commodus* produces vibratory signals with frequencies below 200 Hz.

Research into understanding the frequency sensitivities of the auditory sensory systems of insects has broad applications, ranging from pest control, conservation, and bioinspired technology. In the field of pest control, acoustic signals can be used to attract and trap insects, manipulate their behavior, or interrupt intraspecific communication using either airborne sounds or substrate-borne vibrations propagated through plant leaves or stems (Mankin 2012). To determine the optimal sounds to broadcast, whether airborne or substrate-borne, identification of the most sensitive frequency thresholds of the auditory sensory system is a critical first step. In the field of conservation biology, historically, efforts have focused on environmental factors such as temperature, vegetation, and rainfall to identify key components in an ecosystem needed for species survival and reproduction. However, this does not consider sensory stimuli such as sound. Traditionally, vegetation density and type have been used to define songbird distribution, but recent research has identified variation in the acoustic environment as a better indicator of breeding distributions (Kleist et al. 2017). With many species in decline, characterizing the auditory sensory system may aid in identifying sounds that facilitate species' interactions with their environment and lead to informed management strategies.

Finally, insect auditory systems are a useful model in the field of biomimicry, which uses natural biological mechanisms to inspire and improve engineering and technology (Lurie-Luke 2014). Insects are incredibly efficient at identifying and locating sound sources in noisy environments, and the simplistic organization of their auditory sensory system makes them an effective model for modern computing and communication systems (Ma and Krings 2009). One

such example of bioinspired technology is the development of a directional microphone for hearing aids inspired by insect auditory systems (Miles and Hoy 2006). To utilize insect auditory sensory systems for biotechnology, understanding and characterizing the auditory sensory system is a critical first step.

Moving forward, it is crucial to consider the multimodal role of sound in sensory ecology rather than treating airborne and substrate-borne vibrations as independent factors. These sensory channels have evolved to work together (e.g., the act of stridulation creates both an airborne and substrate-borne component of the signal, Caldwell 2014). Future research should focus on how the auditory sensory systems integrate signals simultaneously from airborne and substrate-borne channels.

Results from this research were the first to identify the frequency sensitivities of *T. commodus* in the airborne ultrasonic range and substrate-borne vibrations. Peak sensitivities in the airborne channel provide support for the evolution of matched filters for the detection of conspecific and predator signals. Multiple sensitivities for substrate-borne vibrations highlight the variation in substrate-borne signals and the use of different sensory organs for detection. Overall, understanding the auditory sensory system of insects is vital for gaining insights into their behavior, ecology, and survival and has various practical applications.

**CHAPTER 2: THE IMPACT OF DIFFERENT TYPES OF NOISE ON THE
PHONOTACTIC BEHAVIOR OF FEMALE AUSTRALIAN BLACK FIELD CRICKETS
(*TELEOGRYLLUS COMMODUS*).**

Abstract

Many animals rely on acoustic signals to extract biologically important information from the environment such as the locations of mates and predators. Elevated background noise has the potential to disrupt the detection and assessment of the signal, leading to decreased reproductive success. While many animals have evolved the capability to detect sounds beyond the frequencies in which they produce signals, most noise studies focus on noise that overlaps with the signal of interest. This study investigates how noise from varying acoustic modalities (ultrasonic sound, sonic sound, vibrational sound) affects female phonotaxis in the Australian black field cricket, *Teleogryllus commodus*. Acoustic playback trials were conducted to determine how ambient noise in three biologically relevant bandwidths (ultrasound 25-45 kHz; sonic 1-20 kHz, & substrate-borne vibrations 100 Hz-1,000 Hz) influences phonotaxis in *T. commodus*. Female movements towards a speaker broadcasting male calling songs were assessed under the different noise treatments. The presence of noise, regardless of type, increased the distance the female traveled and the time the female spent searching. The female departed the starting position more quickly when high-level ultrasonic noise was broadcast. Travel velocity significantly increased in response to all noise types; however, the change in velocity did not occur at all noise levels within each noise type. Two different mechanisms of masking are proposed that may be affecting female behavior: energetic masking and informational masking.

This study expands our knowledge of the effects of noise on understudied taxa and highlights the importance of considering the sensory sensitivity of animals when investigating the impact of noise on animal behavior.

Introduction

Communication signals facilitate animal interactions and convey information that affects the receiver's behavior (Bradbury and Vehrencamp 2011). For example, acoustic signals play a critical role in evaluating and localizing potential mates. Often, in acoustically orienting species, localization is facilitated through phonotaxis, in which individuals use acoustic signals to orient toward a potential mate until they encounter one another (Gerhardt, Huber, & Simmons, 2003). Signals that advertise an individual's location to potential mates are especially important for solitary or widely dispersed species (Gerhardt, Huber, & Simmons, 2003).

Effective signaling requires the receiver to be able to detect and discriminate the signal from other sounds to extract relevant information such as the caller's location; sensory pollutants can interrupt this process. For instance, Lusitania toadfish (*Halobatrachus didactylus*) are unable to detect the courtship sounds of conspecifics in the presence of noise from shipping activity (Vasconcelos et al. 2007). Acoustic noise is a sensory pollutant that is ubiquitous in most ecosystems and constrains signal transmission across the landscape while also interfering with an animal's ability to detect non-communicative cues. Acoustic noise, defined as unwanted sound, interferes with the receiver's ability to detect and discriminate different signals and/or cues, which may result in receiver mistakes (Brumm and Slabbekoorn 2005b). It can span broad frequencies of sound across an individual's range of detection (Halfwerk and Slabbekoorn 2015). Impaired signal localization in the presence of noise can lead to consequences for both senders and receivers such as increased predation risk and energetic output. Senders must spend more

time signaling, which increases their energetic output and makes them more conspicuous to predators or parasitoids; receivers may increase their search time and take a more circuitous route which is energetically costly and increases predation risk (Naguib 2013).

There are three main sources of noise: organisms (biotic), the physical environment (abiotic), and anthropogenic mechanisms (Pijanowski, Farina, et al. 2011). With multiple sources of noise present throughout most environments, noise often spans a broad bandwidth of frequencies and multiple acoustic modalities. Acoustic modalities are defined as acoustic sounds detected by different sensory channels (i.e., airborne sound and substrate-borne vibrations). The presence of noise in multiple sensory channels creates tradeoffs: animals need to be alert for cues associated with predators or other risks while also maintaining sufficient attention for detecting signals related to mating and/or foraging opportunities (Lima and Bednekoff 1999). It's well established that airborne noise interferes and energetically masks relevant signals likely reducing the ability of a receiver to detect relevant sounds and extract information (Brumm and Slabbekoorn 2005b), but also may reduce overall responsiveness to sounds leading to consequences for the receiver. Many aerial prey species rely on ultrasonic cues from predators such as bat echolocation signals to determine the presence and direction of potential predators (Greenfield 2016); terrestrial prey rely on substrate-borne vibrations to detect predators (wolf spiders, *Lycosidae*; termites, *Coptotermes acinaciformis*; moth larvae, *Semiothisa aemulataria*; treefrog embryos, *Agalychnis callidryas*; Virant-Doberlet et al., 2019). When noise interferes with an individual's ability to detect and assess an approaching predator, they become more susceptible to predation. Studies often highlight the energetic masking effects of noise, where noise energetically overlaps with the focal animal's signal (Naguib 2013) while omitting the potential impact from elevated ambient sound outside the energetic masking bandwidth.

Regardless of noise source, noise acts as a general stressor on internal processes that can lead to changes in performance and decision-making (e.g. rats, brown shrimp, *Crangon crangon*; hens, *Gallus gallus domesticus*; humans; Kight & Swaddle, 2011) and disrupt attention and cognitive ability (e.g. rats; Cui, Wu, & She, 2009). Even noise that does not energetically overlap with an animal's signal can indirectly affect communication and cause informational masking (Rosa and Koper 2018). Unlike energetic masking, informational masking does not occur due to the inability to detect signals but occurs due to the central auditory system not being able to process the features of the signal (Shinn-Cunningham 2013). While there is little experimental data identifying the effects of informational masking, Bee and Gupta (2022) determined that informational masking can constrain acoustically guided mating behavior in treefrogs (Gupta and Bee 2022).

Animals rely on sensory input from multiple sources to assess their environment and respond accordingly; individuals must be able to detect and assess relevant signals while simultaneously engaging in activities such as foraging, mate localization, and social communication. The presence of noise in an environment can shift attention away from relevant signals, causing distraction. Attention is often divided across different activities, animals receive input from visual cues, predator vocalizations, and conspecific signals (Parasuraman 1984). Caribbean hermit crabs (*Coenobita clypeatus*) allowed a simulated predator to approach closer in the presence of noise (Chan and Giraldo-Perez 2010). Distraction can lead to increased predation or missed mating opportunities.

To understand how noise induces informational masking, the type of noise stimuli used must be expanded to include stimuli that do not energetically overlap with acoustic signals. Studies on noise effects disproportionately address airborne noise and its impact on airborne

signals, even though vibratory signals are widespread (Cocroft and Rodríguez 2005). Airborne ultrasound and substrate-borne vibrations (or infrasound) are rarely included in studies of noise impacts on animals although 90% of animals rely on some form of substrate-borne vibrations (Hill 2008). While the use of substrate-borne vibrations is widespread (Mammalia, Aves, Reptilia, Amphibia, Osteichthyes, Arthropoda, Nematoda; Hill, 2008), ultrasonic hearing is most common in mammals for sound localization and communication for some small mammals (Heffner and Heffner 2008). While invertebrates primarily rely on substrate-borne vibrations, some insects have evolved organs for the detection of airborne sound in both the sonic and ultrasonic range (Orthoptera, Lepidoptera, Coleoptera, Dictyoptera, Neuroptera; Hoy & Robert, 1996). Organs to detect airborne sounds have evolved independently 19 times in 7 different orders of insects with more likely to be identified (Fullard and Yack 1993). The detection of airborne sound and substrate-borne vibrations evolved independently of each other in invertebrates and lead to different physiological responses.

Insects use airborne sound in multiple contexts including, detection, avoidance, and deterrence of predators, prey localization, and conspecific communication (Greenfield 2016). Airborne noise can disrupt male advertisement calls, interfering with the female's ability to accurately assess mate quality and use phonotaxis to locate signaling males (Romer 2013b). Airborne noise may also increase predation risk. Most studies to date have focused solely on energetic masking as the source of these effects but many insects use a broad range of frequencies of sound to accurately assess their environment; it is important to investigate airborne noise beyond the frequencies that mask male signals to fully understand the impact noise has on behaviors crucial for survival and reproductive success.

Substrate-borne vibrations are used to collect information about the environment, conspecific communication and cooperation, the detection of prey, avoidance of predation, and promote symbiotic relationships (Raboin and Elias 2019). The detection and production of substrate-borne vibrations are widespread amongst insects, but little is known about how substrate-borne vibrational noise impacts the detection and assessment of airborne signals. Although substrate-borne vibrations have largely been overlooked as a source of noise, researchers have identified potential impacts on invertebrate behavior. Past studies have found that substrate-borne vibrations disrupt mating and predator-prey dynamics (Wilcox et al. 1996; Wignall et al. 2011; Gordon and Uetz 2012); however, these studies focus solely on how substrate-borne vibrations impact vibratory signals, very little is understood about how insects that detect both airborne and substrate-borne sounds respond when presented with noise from different modalities and frequencies. Studies of noise on animal behavior that focus exclusively on noise that energetically overlaps with the focal animal's signal fail to account for the complexity of both noise and animal sensory systems, which prevents a full understanding of the impact of environmental noise.

This project aims to identify the effects of airborne sonic (20 Hz-20 kHz; hereafter “sonic”), airborne ultrasonic (20 kHz-45 kHz; hereafter “ultrasonic”), and substrate-borne vibration (100-1,000 Hz; hereafter “substrate-borne vibrations”) on a female's ability to locate a signaling male. The Australian black field cricket (*Teleogryllus commodus*) was chosen as a suitable model system to address this question because orthopterans have a complex sensory system that is sensitive to multiple types of sound and has been extensively studied. *Teleogryllus commodus* males produce long-range advertisement signals that females rely on to navigate to potential mates (Evans 1983). *T. commodus* detect airborne sounds and substrate-borne

vibrations via independent organs and then integrate the signals in the neurological system, extracting different information depending on the frequency of the sound. Different frequencies provide information about conspecifics, aerial predators, and terrestrial predators.

To test how different types of noise affect phonotactic behavior, females were exposed to three different noise stimuli: sonic, ultrasonic, and substrate-borne vibrations. Within each treatment, the female was exposed to different intensities of noise to determine whether intensity, the presence of noise, or a combination of the two affected female behavior. If localization of a calling male is affected by only energetic masking and not information masking, there should be a shift in behavior only during the sonic noise treatment; if noise is disrupting attention via distraction and informational masking, then there should be a shift in behavior with all three forms of noise.

Methods

To assess how effectively *T. commodus* females localize male calls in noisy environments, single-speaker behavioral trials were conducted on 150 virgin females. All study subjects were from an established colony reared and maintained at the University of New Hampshire. The crickets were kept on a 14/10 light/dark cycle with food and water *ad libitum*.

Behavioral Arena

A circular behavioral arena was set up in a semi-anechoic chamber (Figure 5). Acoustically transparent fabric in which airborne sounds did not reflect off the surface was stretched across a 50 cm diameter wooden ring. The arena was surrounded by 15 cm high walls of plastic to keep the crickets in the arena. The arena was placed on an air table to prevent excess

vibrations from interfering with the playback trials. Two speakers (OrbAudio) were positioned 180° apart at the arena perimeter and pointed to the arena center to broadcast male calls. For non-directional noise treatment, airborne noise was broadcast from a speaker (OrbAudio) suspended 1m above and pointed toward the center of the arena. For the substrate-borne vibration treatments, an electromagnetic shaker (TMS 2004E powered by an ART SLA-2 amplifier connected to a PC) was in contact with the underside of the stretched fabric that constitutes the arena floor at the arena center.

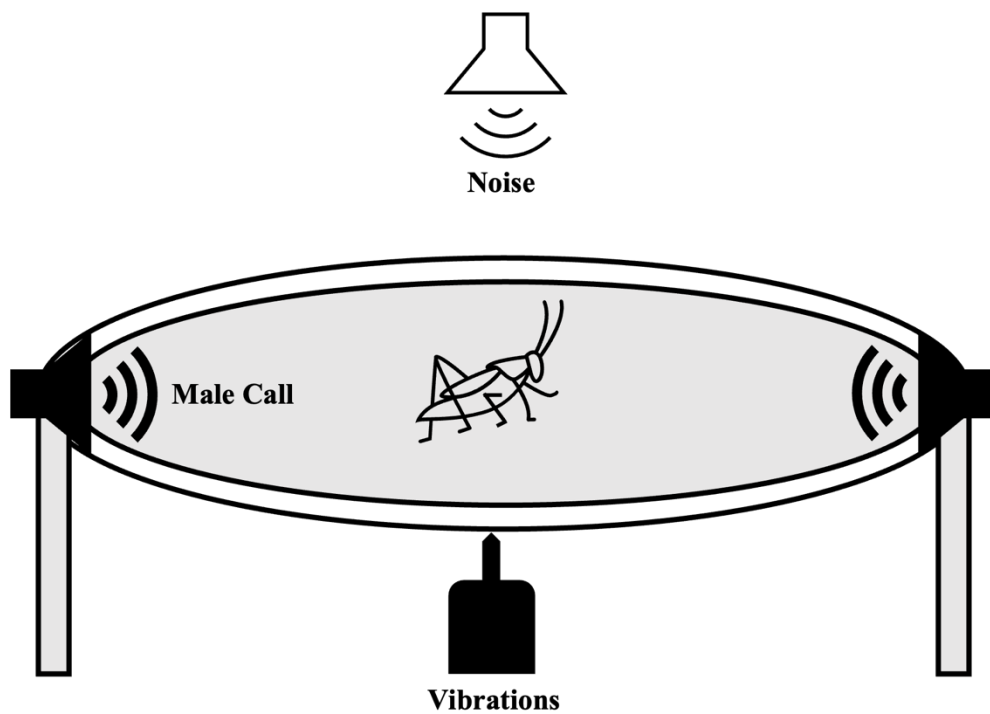


Figure 5: A circular behavioral arena (50 cm diameter) was used to test the effects of noise on phonotaxis in female *T. commodus*. Two speakers were set up 180° apart pointing to the center of the arena in which one speaker broadcasts male calling songs during trials. A speaker was placed 1m above the center of the arena to broadcast ultrasonic and sonic noise.

Behavioral Trials

Male calling songs were recorded in a semi-anechoic chamber. Male subjects were from the same laboratory-reared population. To record male songs, a microphone coupled to an audio

recorder (Tascam DR-100mkII) was positioned above a small enclosure (30 cm x 20 cm) containing a single male; the process was repeated on 25 different males. Each male was recorded for approximately 12 hours. The exemplar male calling song was generated by manually extracting high-quality songs in Adobe Audition, with the final exemplar representing songs from five different males stitched together for a 3-minute file (Figure 6A). For each behavioral trial, the stimulus was played back at 73 dB (L_{max} , 6 Hz-20 kHz, re 20 μ Pa) calibrated at the center of the behavioral arena.

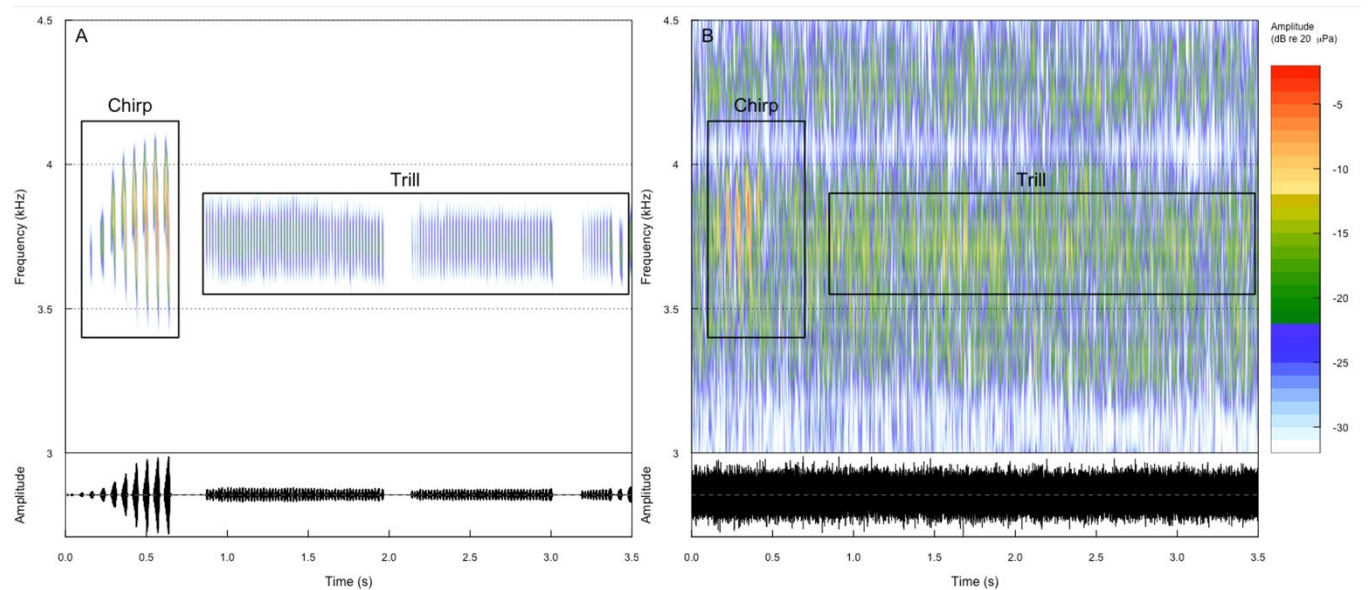


Figure 6: **A.** Spectrogram and oscillogram of a male *T. commodus* calling song. Male calling songs are characterized by two elements, an amplitude-modulated chirp followed by a longer trill. A three-minute exemplar of a male calling song was created and broadcast to females during behavioral trials to elicit phonotaxis. **B.** The male calling song played simultaneously with the 67 dB sonic noise treatment.

Treatments were divided into ultrasonic, sonic, and substrate-borne vibrational noise (described below). All noise stimuli were created in Adobe Audition. There were three ultrasonic noise stimuli based on one of the following intensities: 70, 75, and 80 dB (L_{max} re 20 μ Pa).

Ultrasonic noise was calibrated using a calibrated sonic reference tone, whose voltage was measured on an oscilloscope. The ultrasonic tone was then calibrated to the same voltage on the oscilloscope. Each ultrasonic noise treatment consisted of a broadband (25-45 kHz) 1-second pulse with a 1-second inter-pulse interval repeated for 3 minutes.

There were five sonic noise stimuli based on one of the following intensity levels: 67, 70, 73, 76, and 79 dB (L_{\max} re 20 μ Pa). Since Gryllid sensory systems exhibit high sensitivity to sound intensities of 1dB or less, it was concluded that females could biologically distinguish between the different noise trials at steps of 3 dB (Hedwig and Poulet 2005; Schöneich and Hedwig 2010). The sonic noise was calibrated using a sound level meter (Brüel & Kjaer Type 2250). Sonic noise was constant broadband (20 Hz-20 kHz) white noise.

There were three substrate-borne vibration stimuli: low (1 mm/s), medium (5 mm/s) and high (15 mm/s) intensity. The substrate-borne vibration was calibrated with a Polytec PDV 100 laser Doppler vibrometer. Each substrate-borne vibration stimulus consisted of a 1-second pulse with 1-second inter-pulse intervals repeated for 3 minutes with a frequency range of 100 Hz-1,000 Hz. These intensities were determined from previous experiments conducted in the laboratory (Abate 2018, unpublished) to elicit a behavioral response from gryllids. All signals were calibrated at the center of the arena.

Each female was randomly assigned to one of the three treatment groups (ultrasonic noise, sonic noise, and substrate-borne vibration) with 50 females tested per treatment group, for a total of 150 females. Each female was exposed to all the intensity levels within the assigned treatment. The first trial always started with a control stimulus, where a male calling song was randomly broadcasted from one of the two arena speakers to prevent bias to one side. The control was broadcasted without noise to collect baseline behaviors and ensure the female was receptive

and exhibited phonotaxis. In the subsequent trials, the female was exposed to the control playback plus the broadcast of the noise stimulus and the order of noise levels was randomized (Figure 2b). Therefore, females assigned to ultrasonic noise and substrate-borne vibration underwent four distinct trials (trial 1- control only, trials 2-4 control plus one of the three intensity level treatments). Females assigned to sonic noise underwent six distinct trials (trial 1- control only, trials 2-6 control plus one of the five intensity level treatments).

Using a clear plastic cup, a female was placed in the center of the arena. Once the broadcast began, the cup was lifted, and the female was allowed to move freely about the arena. Trials lasted until the female located the speaker broadcasting the male call or after 3 minutes had elapsed. There was a 1-minute break between trials. The process was repeated until the female was exposed to all the stimuli within her treatment group. Each playback experiment was recorded using HD video and analyzed in Ethovision XT software (Noldus Information Technology) to determine the female's response and path structure (distance, velocity, duration, latency to start, and meander; see definition of variables in Table 1) An example of path analysis in Ethovision can be found in Figure 7A-B.

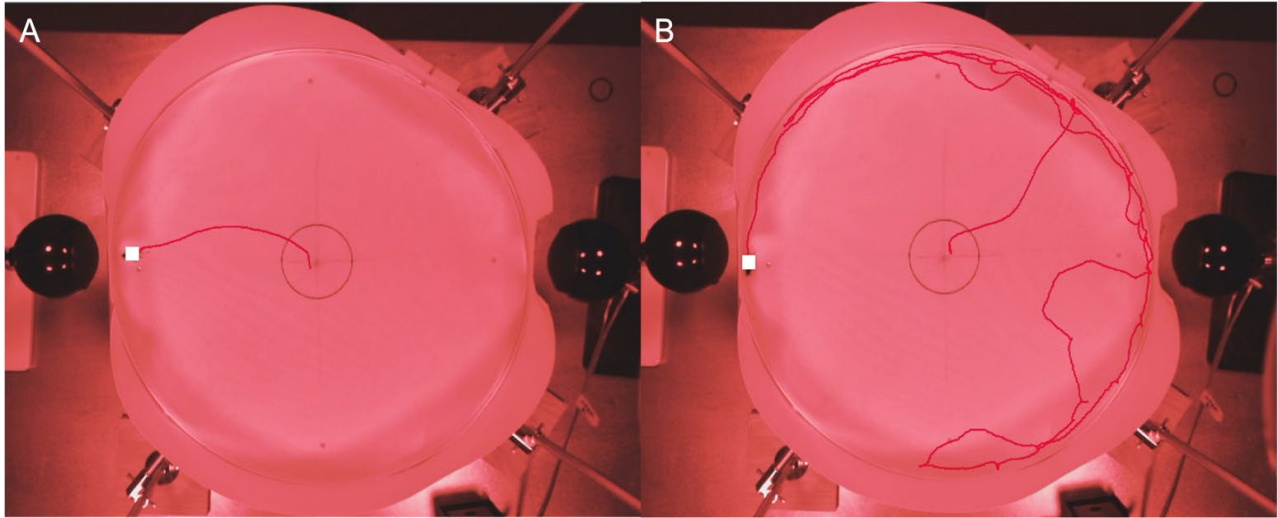


Figure 7: The path of female *T. commodus* while locating the male signal was analyzed in Ethovision. **A.** An example of the path a female traveled to locate the male signal during the control trial in which only the male call was broadcast at 73 dB. **B.** This picture shows the change in the female's path structure when searching for the male call while 73 dB sonic noise was broadcast from a speaker located directly above the arena.

Generalized linear mixed-effects models were built to test the relationship between female search behavior and noise intensity, with individual as a random effect to control for individual variation. This was followed by a Tukey's post-hoc test with a Bonferroni correction. Variables that did not meet the assumption of normality were log-transformed (.001 was added to account for zeroes). To confirm there was no habituation as the trials progressed, residuals were visually analyzed.

To test the relationship between female search behavior and airborne noise type, ultrasonic and sonic noise, the three ultrasonic intensities (70, 75, and 80 dB L_{max} re 20 μ Pa) were compared to three of the closest sonic intensities (70, 76, and 79 dB L_{max} re 20 μ Pa). The data were binned into low (70dB ultrasonic and sonic), medium (75dB ultrasonic and 76dB sonic), and high (80dB ultrasonic and 79dB sonic) intensities. Generalized mixed-effects models were built to test the relationship between female search behavior, the type of airborne noise,

noise intensity, and the interaction of noise type and intensity, with individual as a random effect. Followed by a Tukey’s post-hoc test with a Bonferroni’s correction. Statistical analyses were performed on R version 2022.07.1 (R Development Core Team, 2022).

Table 1: Movement variables measured from the path females traveled to locate a speaker broadcasting a male calling song. Measurements were taken by uploading videos of noise trials and analyzed using Ethovision XT software.

| Variable | Unit | Description |
|------------------|-------------|--|
| Distance | cm | Total path distance followed by a cricket in the arena |
| Velocity | cm/sec | The mean speed at which a cricket traveled |
| Duration | sec | The time it took for a cricket to travel to the broadcasting speaker |
| Latency to Start | sec | The time it took for a cricket to move from the starting position |
| Meander | deg/cm | The change in direction of a cricket relative to the distance moved |

Results

Ultrasonic Noise

Distance traveled was significantly higher when ultrasonic noise treatments were applied compared to the noise-free control ($F_3=14.76$, $p<0.0001$, Table 2, Figure 8A). There was no difference between noise levels (Table 2, Figure 8A). The duration of time spent searching was significantly higher when ultrasonic noise was broadcast compared to the control ($F_3=9.20$, $p<0.0001$, Table 2, Figure 8B). There was no significant change in search duration between the three noise levels (Table 2, Figure 8B). The female’s velocity was on average 1.35 cm/s higher at

the 75 dB, noise levels compared to the control (95% CI=1.10-1.67 cm/s, Table 2, Figure 8C). Velocity did not significantly increase when the 70 dB or 80 dB noise levels were applied (Table 2, Figure 8C). When the female was released from the plastic cup, the noise level significantly affected how much time she spent at the starting position before moving. At noise levels of 70 dB, the female spent on average 4.25 s more at the starting position compared to the 80 dB noise level (95% CI=1.62-11.16 s, Table 2). Meaning the female moved more quickly from the starting position when exposed to higher levels of ultrasonic noise. Meander did not significantly change when ultrasonic noise was applied (total, $F_3=0.33$, $p=0.8$; mean, $F_3= 1.12$, $p=0.34$).

Table 2: Results of a pairwise test for a one-way ANOVA to assess the movement of females when exposed to ultrasonic noise of different intensities. Bold denotes significance ($\alpha=0.05$).

| Intensity (dB) | | Distance (cm) | | Velocity (cm/s) | | Duration (s) | | Latency to Start (s) | |
|----------------|------|---------------|-------------------|-----------------|-------------|--------------|------------------|----------------------|-------------|
| | | t_{147} | p value | t_{147} | p value | t_{147} | p value | t_{147} | p value |
| Control | 70dB | -4.76 | <0.0001 | -0.781 | 1 | -4.428 | <0.001 | -0.417 | 1 |
| Control | 75dB | -4.826 | <0.0001 | -2.871 | 0.02 | -2.927 | 0.02 | 0.833 | 1 |
| Control | 80dB | -6.212 | <0.0001 | -2.505 | 0.08 | -4.661 | <0.001 | 2.544 | 0.07 |
| 70 | 75dB | -0.066 | 1 | -2.09 | 0.22 | 1.501 | 0.81 | 1.25 | 1 |
| 70 | 80dB | -1.452 | 0.9 | -1.724 | 0.52 | -0.233 | 1 | 2.961 | 0.02 |
| 75 | 80dB | -1.386 | 1 | 0.366 | 1 | -1.734 | 0.51 | 1.711 | 0.53 |

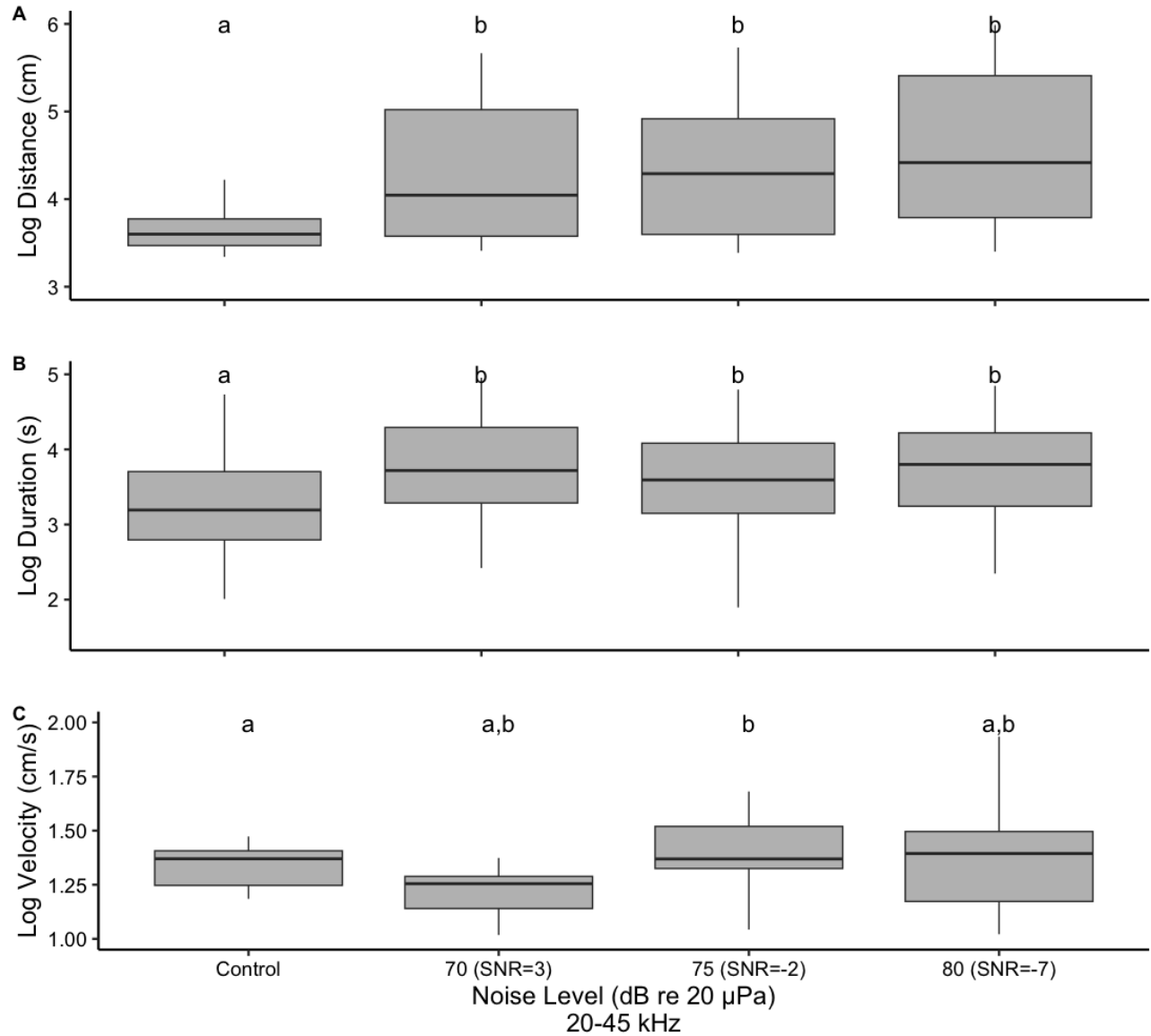


Figure 8: The phonotactic response of female *T. commodus* to a male advertisement signal played simultaneously with different levels of ultrasonic noise. **A.** The distance females traveled while locating the calling male, **B.** the duration of time females spent searching for the male caller, and **C.** the velocity at which the females traveled while searching for the male.

Sonic Noise

Females traveled a significantly greater distance when sonic noise treatments were applied compared to the control with no noise ($F_5=13.15$, $p<0.0001$, Table 3, Figure 9A). There were no significant differences in distance traveled among the noise levels (Table 3, Figure 9A).

Time spent searching increased when sonic noise treatments were applied ($F_5=7.17$, $p<0.0001$, Table 3, Figure 9B). There was no significant difference between the sonic noise levels (Table 3, Figure 9B). The velocity at which females traveled was significantly higher when sonic noise treatments of 70 dB and 76 dB were applied ($F_5=2.63$, $p=0.02$, Table 3, Figure 9C). There was no significant difference between the sonic noise levels (Table 3, Figure 9C). Meander (total, $F_5=1.37$, $p=0.23$, mean, $F_5=1.79$, $p=0.12$), and latency to move from the starting position ($F_5=1.17$, $p=0.32$) did not significantly change when exposed to sonic noise.

Table 3: Results of a pairwise test for a one-way ANOVA to assess the movement of females when exposed to sonic noise of different intensities. Bold denotes significance ($\alpha=0.05$).

| Intensity (dB) | | Distance (cm) | | Velocity (cm/s) | | Duration (s) | |
|----------------|------|---------------|------------------|-----------------|-------------|--------------|-------------------|
| | | t_{245} | p value | t_{245} | p value | t_{245} | p value |
| Control | 67dB | -5.622 | <0.001 | -2.551 | 0.17 | -3.766 | 0.003 |
| Control | 70dB | -6.76 | <0.001 | -3.201 | 0.02 | -4.321 | 0.0003 |
| Control | 73dB | -5.353 | <0.001 | -2.502 | 0.19 | -3.52 | 0.0077 |
| Control | 76dB | -5.883 | <0.001 | -2.93 | 0.05 | -3.712 | 0.0038 |
| Control | 79dB | -7.182 | <0.001 | -2.24 | 0.39 | -5.71 | <0.0001 |
| 67 | 70dB | -1.054 | 1 | -0.65 | 1 | -0.555 | 1 |
| 67 | 73dB | 0.27 | 1 | 0.049 | 1 | 0.246 | 1 |
| 67 | 76dB | -0.261 | 1 | -0.379 | 1 | 0.054 | 1 |
| 67 | 79dB | -2 | 1 | 0.311 | 1 | -1.944 | 0.7963 |
| 70 | 73dB | 1.323 | 1 | 0.698 | 1 | 0.801 | 1 |
| 70 | 76dB | 0.793 | 1 | 0.271 | 1 | 0.609 | 1 |
| 70 | 79dB | -0.505 | 1 | 0.961 | 1 | -1.388 | 1 |
| 73 | 76dB | -0.53 | 1 | -0.428 | 1 | -0.192 | 1 |
| 73 | 79dB | -1.829 | 1 | 0.263 | 1 | -2.189 | 0.4428 |
| 76 | 79dB | -1.2 | 1 | 0.69 | 1 | -1.998 | 0.7031 |

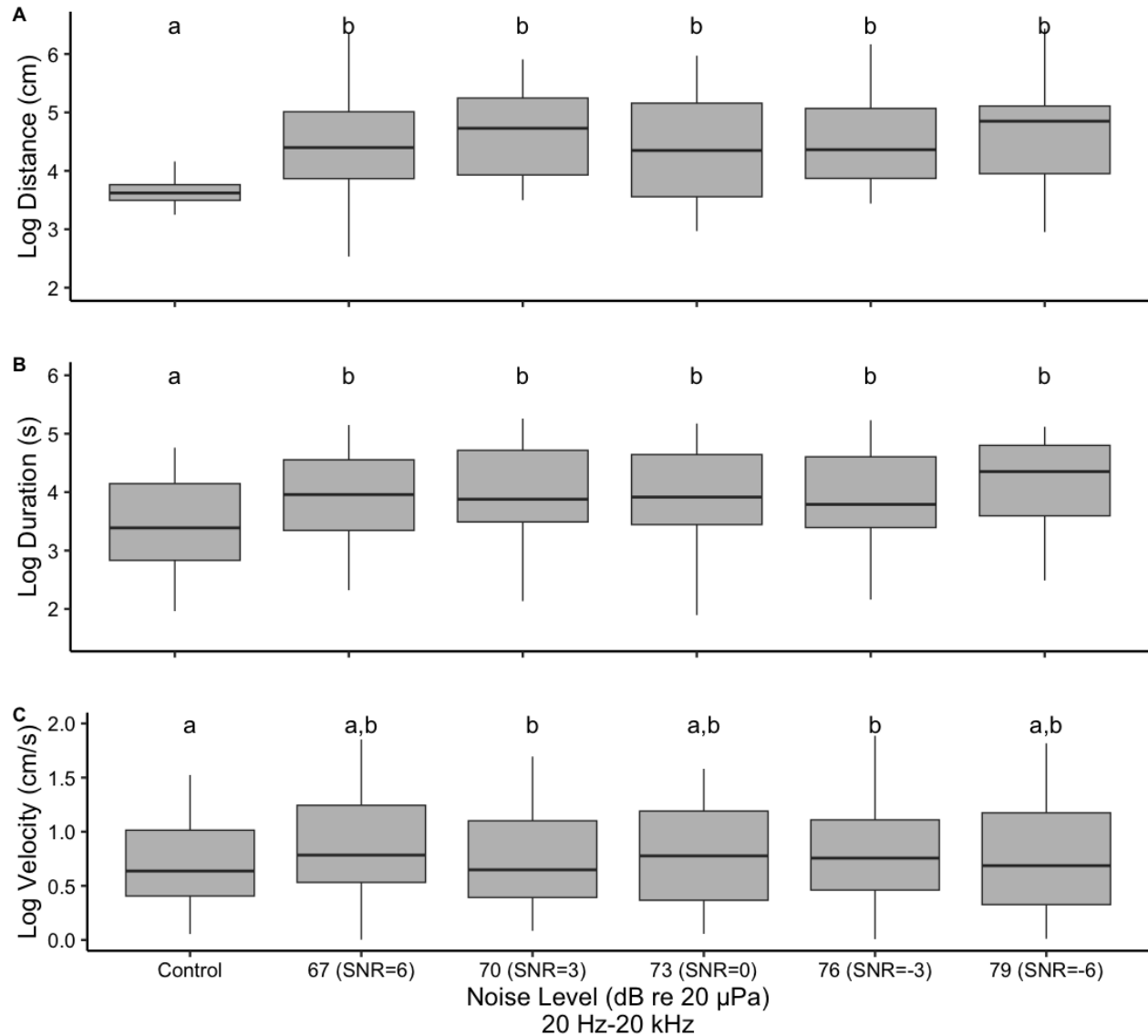


Figure 9: The phonotactic response of female *T. commodus* to a male advertisement signal played simultaneously with different levels of sonic noise. **A**. The distance females traveled while locating the calling male, **B**. the duration of time females spent searching for the male caller, and **C**. the velocity at which the females traveled while searching for the male.

Substrate-Borne Vibrations

Distance traveled significantly increased when substrate-borne vibrations were broadcast compared to the control ($F_3=14.08$, $p<0.0001$, Table 4, Figure 10A). There was also a significant difference in distance traveled between noise levels (Table 4, Figure 10A). At noise levels of 1

mm/s, distance traveled was on average 1.39 cm higher than the distance traveled at 5 mm/s (95% CI=1.08-1.79). At noise levels of 15 mm/s, the distance traveled was on average 1.44 cm higher than the distance traveled at 5mm/s (95% CI=1.12-1.85 cm). Duration significantly increased with substrate-borne vibration levels of 1 mm/s and 15 mm/s compared to the control with no noise present ($F_3=5.03$, $p=0.002$, Table 4, Figure 10B). There was no significant difference between the noise levels (Table 4, Figure 10B). The velocity at which the female traveled was significantly higher when substrate-borne vibration levels were at 1 mm/s and 15 mm/s compared to the control ($F_3=9.35$, $p<0.0001$, Table 4, Figure 10C). Velocity was on average 1.30 cm/s higher when substrate-borne vibration levels were 15mm/s in comparison to 5 mm/s levels (95% CI=1.11-1.53, Table 4, Figure 10C). Latency to move from the starting position ($F_{3,147}=0.40$, $p=0.75$) and meander (total, $F_{3,147}=1.25$, $p=0.29$; mean, $F_{3,147}=0.33$, $p=0.80$) did not significantly change when exposed to substrate-borne vibrations.

Table 4: Results of a pairwise test for a one-way ANOVA to assess the movement of females when exposed to substrate-borne vibrational noise of different intensities. Bold denotes significance ($\alpha=0.05$).

| Intensity (mm/s) | | Distance (cm) | | Velocity (cm/s) | | Duration (s) | |
|------------------|------|---------------|-------------------|-----------------|------------------|--------------|--------------|
| | | t_{147} | p value | t_{147} | p value | t_{147} | p value |
| Control | 1 | -5.402 | <0.0001 | -3.215 | 0.009 | -3.744 | 0.001 |
| Control | 5 | -2.774 | 0.03 | -1.808 | 0.43 | -1.81 | 0.43 |
| Control | 15 | -5.676 | <0.0001 | -5.105 | <.0001 | -2.706 | 0.04 |
| | 1 5 | 2.628 | 0.05 | 1.408 | 0.96 | 1.933 | 0.33 |
| | 1 15 | -0.274 | 1 | -1.89 | 0.36 | 1.038 | 1 |
| | 5 15 | -2.902 | 0.02 | -3.297 | 0.007 | -0.895 | 1 |

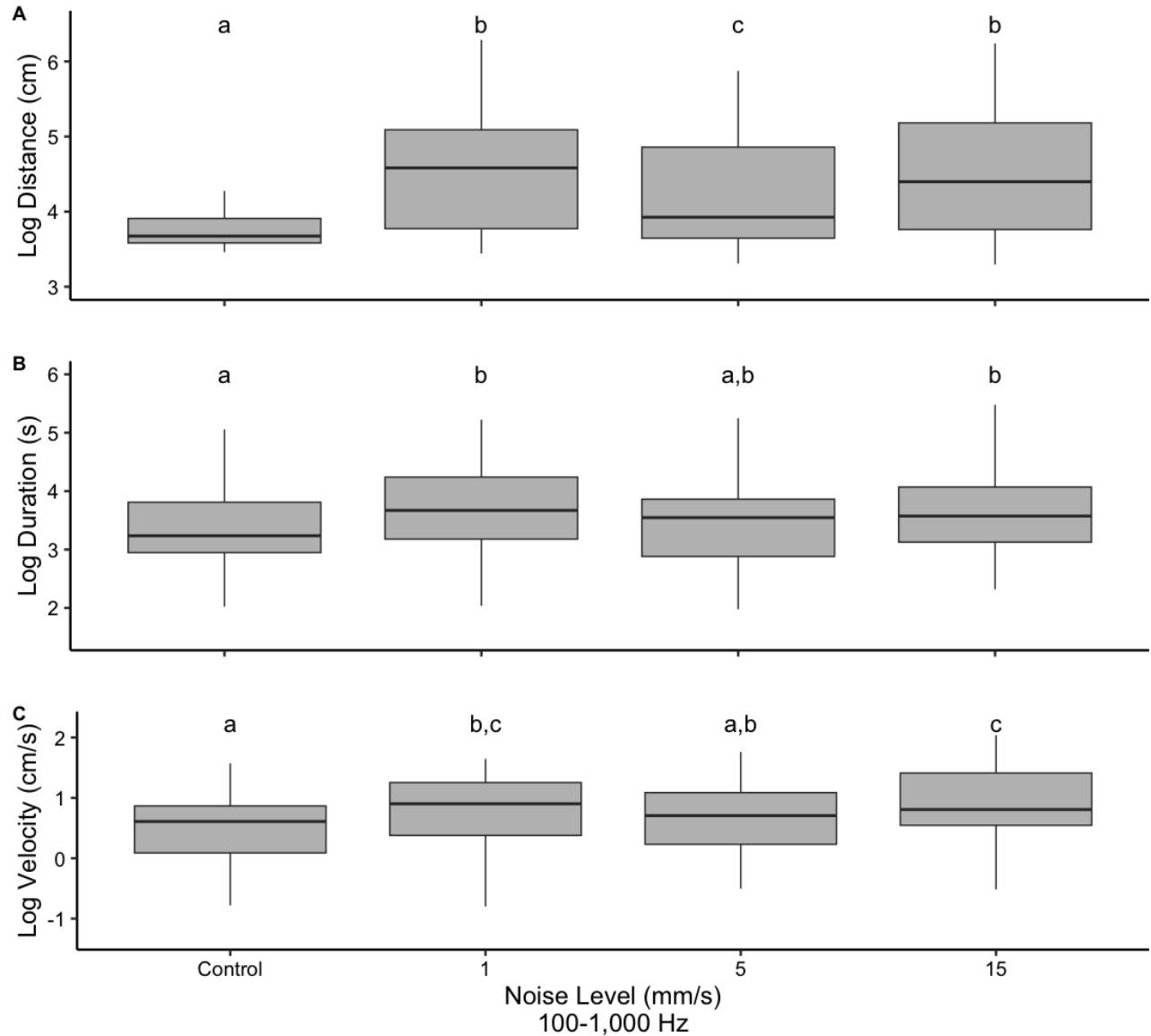


Figure 10: The phonotactic response of female *T. commodus* to a male advertisement signal played simultaneously with different levels of substrate-borne vibrations. **A.** The distance females traveled while locating the calling male, **B.** the duration of time females spent searching for the male caller, and **C.** the velocity at which the females traveled while searching for the male.

Comparison of Ultrasonic and Sonic Noise

In a comparison of the two airborne noise types, ultrasonic and sonic, we were able to compare similar noise levels binned into three categories (low, medium, and high). Noise type and level did not significantly affect the distance the female traveled ($F_{1,98}=2.43$, $p=0.12$).

Velocity did not significantly vary between the airborne noise type or levels ($F_{1,98}=0.51$, $p=0.48$). The duration of time spent searching did not significantly differ based on noise type ($F_{1,98}=3.83$, $p=0.06$) but did vary by noise level ($F_{1,98}=6.48$, $p=0.04$). The time the female spent searching was on average 1.29s longer when exposed to high-intensity (79dB) sonic noise than when the female was exposed to medium-intensity (75dB) ultrasonic noise (95% CI=.98-1.70 s; $t_{98}=3.22$, $p=0.02$). Latency to start did not significantly differ between levels ($F_{2,196}= 2.20$, $p= 0.11$) but latency to start did vary by noise type ($F_{2,196}=3.78$, $p= 0.02$). When exposed to high-level sonic noise, the time the females spent at the starting position was on average 3.05 s longer than when exposed to the high-level ultrasonic noise (95% CI=1.14-8.15 s, $t_{98}=3.36$, $p=0.02$, Figure 11).

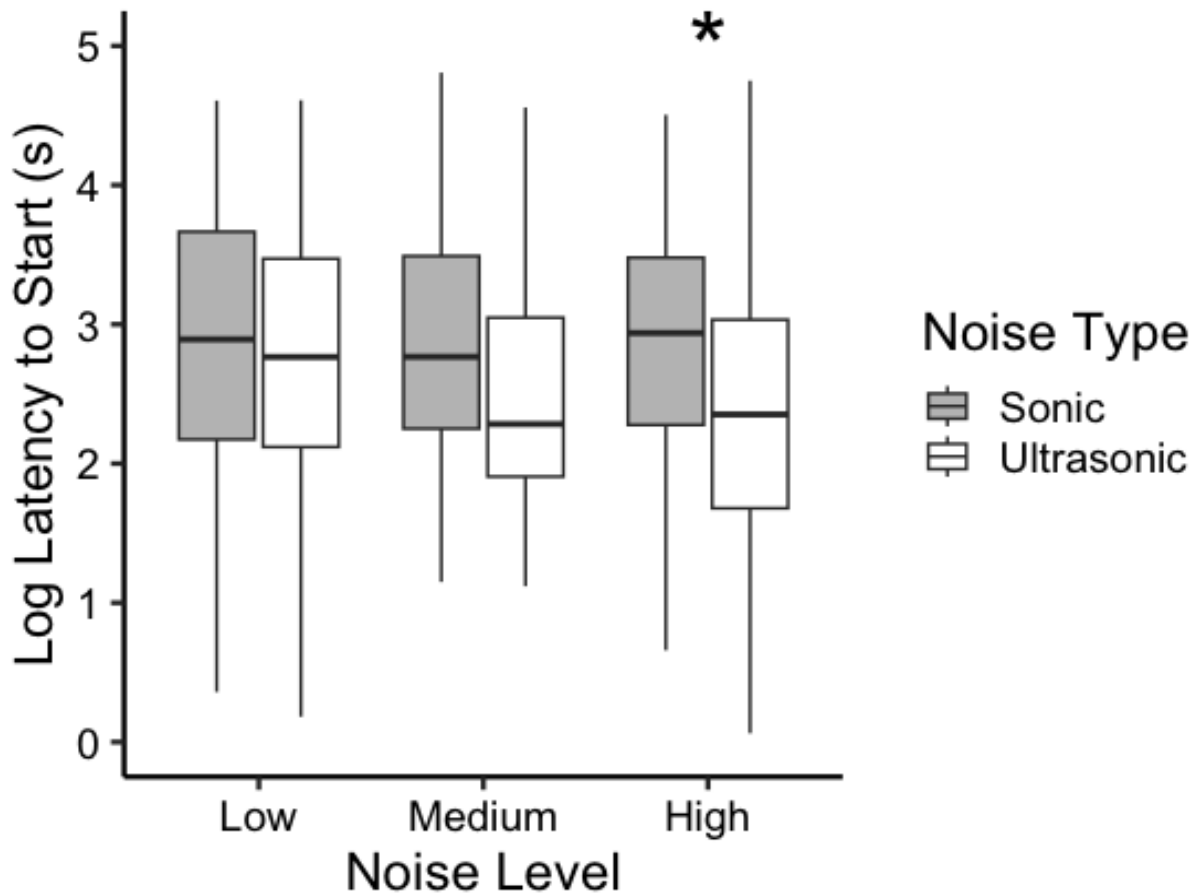


Figure 11: Box and whisker plot representing the response of female *T. commodus* to airborne sonic and ultrasonic noise. The female spent more time at the starting position when exposed to high levels of sonic noise compared to exposure to high levels of ultrasonic noise ($t_{98}=3.36$, $p=0.02$). Asterisks denote significance ($\alpha=0.05$).

Table 5: Pathways of *T. commodus* females were measured using Ethovision XT software. The means and standard deviations were calculated for each measured variable while females tried to locate a simulated calling male under three noise types and different intensities: ultrasound (25-45 kHz), sonic (20 Hz-20 kHz), and substrate-borne vibrations (100-1,000 Hz).

| Noise Stimuli | Distance (cm) | | Velocity (cm/s) | | Duration (s) | |
|-------------------------|----------------------|--------|-----------------------|----------|------------------------|------------|
| Ultrasound(n=50) | Mean | SD | Mean | SD | Mean | SD |
| Control | 41.04 | 14.61 | 1.79 | 0.99 | 32.66 | 25.46 |
| 70 dB | 119.66 | 135.5 | 1.97 | 1.04 | 69.57 | 65.7 |
| 75 dB | 113.7 | 116.78 | 2.58 | 1.72 | 55.52 | 51.62 |
| 80 dB | 141.03 | 118.96 | 2.62 | 1.73 | 68.22 | 61 |
| Sonic(n=50) | | | | | | |
| Control | 42.29 | 15.31 | 1.58 | 1.05 | 43.19 | 32.48 |
| 67 dB | 117.18 | 102.66 | 2.19 | 1.47 | 69.48 | 52.88 |
| 70 dB | 125.53 | 79.11 | 2.25 | 1.53 | 72.36 | 51.12 |
| 73 dB | 113.12 | 88.19 | 2.08 | 1.21 | 66.2 | 47.2 |
| 76 dB | 117.97 | 93.01 | 2.16 | 1.38 | 67.51 | 48.68 |
| 79 dB | 143.06 | 116.3 | 2.06 | 1.36 | 84.03 | 53.07 |
| Substrate(n=50) | | | | | | |
| Control | 50.24 | 27.78 | 2.01 | 1.45 | 36.54 | 31.96 |
| 1mm/s | 119.04 | 95.81 | 2.54 | 1.29 | 62.62 | 74.78 |
| 5mm/s | 83.41 | 68.24 | 2.26 | 1.3 | 46.71 | 42.9 |
| 15mm/s | 135.88 | 126.7 | 2.94 | 1.77 | 56.58 | 68.51 |
| Noise Stimuli | Latency to Start (s) | | Meander mean (deg/cm) | | Meander Total (deg/cm) | |
| Ultrasound(n=50) | Mean | SD | Mean | SD | Mean | SD |
| Control | 22.34 | 22.08 | 275.97 | 2554.37 | 65023.14 | 2042036.42 |
| 70 dB | 24.93 | 24.8 | 477.67 | 2210.18 | 610203.48 | 2448929.23 |
| 75 dB | 19.38 | 22.88 | -106.37 | 2560.25 | 334500.87 | 4202715.71 |
| 80 dB | 19.74 | 29.55 | -238.29 | 2111.67 | 116812.39 | 3831648.56 |
| Sonic(n=50) | | | | | | |
| Control | 30.26 | 26.39 | 21008.92 | 12080.17 | 2843728.02 | 28842598 |
| 67 dB | 33.51 | 38.49 | 18649.18 | 13205.14 | 40168366 | 50554687.4 |
| 70 dB | 31.36 | 33.9 | 16325.17 | 9020.77 | 36091937 | 33628164.2 |
| 73 dB | 33.66 | 34.83 | 19966.54 | 12914.27 | 40758034.9 | 43616505.8 |
| 76 dB | 25.96 | 29.21 | 17354.61 | 9769.12 | 35541196 | 36179884.4 |
| 79 dB | 28.8 | 29.02 | 17266.99 | 11312.83 | 43712607.6 | 45139159.5 |
| Substrate(n=50) | | | | | | |
| Control | 24.57 | 29.24 | 154.1 | 3217.28 | 126781.4 | 3547423.54 |
| 1mm/s | 31.42 | 69.86 | 195.17 | 1415.38 | 322457.18 | 2505557.05 |
| 5mm/s | 25.45 | 33.12 | 454.19 | 1757.59 | 1088747.07 | 3334236.82 |
| 15mm/s | 17.98 | 20.08 | 33.73 | 2121.71 | -130341.65 | 3737291.99 |

Discussion

This research demonstrates exposure to ultrasonic, sonic, and substrate-borne vibrational noise affects the behavior of female *T. commodus* mate-searching behavior. The results of this study suggest noise does not need to overlap with the male's acoustic signal to influence female behavior. Crickets exposed to noise, regardless of noise type, had a statistically significant increase in the time they spent searching, the distance traveled, and the velocity they traveled. This means the females traveled less efficiently in their search for the signaling male. These findings support prior research that shows exposure to noise affects mate-searching behavior. In one study, female *Gryllus bimaculatus* exhibited a decrease in preference for the speaker broadcasting the male signal in the presence of noise; however, the authors were not able to conclude this was caused by a decrease in the effectiveness of phonotaxis (Schmidt et al. 2014). Male grasshoppers showed a reduction in the turning responsiveness towards female calls in the presence of noise (Reichert 2015). The previous studies heavily emphasize energetic masking but this is an incomplete picture. In studies on the impact of noise on communication, energetic masking is commonly used to explain the negative effects of noise on auditory perception and the resulting behaviors with little attention being paid to informational masking. Since noise studies primarily focus on energetic masking, little is known about the impacts of informational masking.

In the treatment where crickets were exposed to ultrasonic noise, females responded by increasing the time spent searching and increasing the distance traveled. This response is consistent with informational masking. The male signal (4 kHz) was energetically separated from the ultrasonic noise (20- 45 kHz). While the tympanal organ detects airborne sound, the neurons for detecting ultrasound and sonic noise are independent of each other; therefore, ultrasonic noise

should not interfere via energetic masking with the female's ability to detect the male signal. The results suggest the female's ability to process salient information from relevant acoustic signals may be hindered. Past research on multisensory integration showed that auditory signals interfered with a cat's (*Felis catus*) ability to navigate to a visual signal only if the auditory signal was broadcast from a location different from the visual signal (Stein et al. 1989). Like the crickets in this study, the cats were still able to detect the signal of interest, but their localization ability was hindered by a different sensory input indicating neurons responsible for multisensory integration may interfere with cognitive processes.

There are two context-specific behaviors of hearing in insects, the detection and localization of mates and rivals and the detection and localization of predators and parasitoids (Greenfield 2016). For gryllids, the frequency of the sound determines the context and ultimately affects the behavioral response (Schildberger and Hörner 1988). Informational masking could potentially lead to distraction while the female tries to extract different information from two separate sounds. Female crickets use ultrasonic perception to extract information about potential predators (Wytenbach et al. 1996) while the male signal is produced in the sonic range and provides information about their location and mate quality. When these two signals co-occur the female's attention may become divided between searching for and assessing the male signal and assessing information about potential predators. In this study, this manifested as prolonged searching for the male.

Females exposed to high ultrasonic noise levels were quicker to move from the starting position than when low levels of ultrasonic noise were present. This could be an attempt to counter potential predation as previous studies have shown; animals act more quickly to a perceived predator in the presence of noise. Prairie dogs and California ground squirrels

increased vigilance as background noise levels increased and were quicker to respond to a predator either through alarm calls or returning to their burrow (Le, Garvin, Barber, & Francis, 2019; Rabin, Coss, & Owings, 2006; Shannon, Angeloni, Wittemyer, Fristrup, & Crooks, 2014). The females in this study may be attempting to quickly find shelter and calling males may provide an honest indicator of such shelter. One study demonstrated that crickets under stronger predation pressure spent more time inside refuge and acted more quickly to find shelter (Hedrick and Kortet 2006). Another study found female crickets, *Gryllus bimaculatus*, were quicker to move from the starting position in the presence of noise (Bent et al. 2018). The decrease in the latency to start may represent a shift in the female's priority from mate searching to predator avoidance. Prairie dogs have been shown to flee and seek shelter more quickly in the presence of noise, indicating this may be a possible response amongst prey species in the presence of noise (Shannon, Crooks, et al. 2016). Mistakes in effectively gleaning information about a potential predator hold greater consequences than mistakes in extracting information about conspecifics; the behavioral response to predators may override the behavioral response to conspecifics.

When the results of the two airborne noise treatments (sonic and ultrasonic) were compared, females spent less time at the starting position when exposed to high-intensity ultrasonic noise compared to high-intensity sonic noise. This response to ultrasonic noise may represent a context-specific anti-predator response, triggered by the frequency of the sound. These two sounds of different frequencies, each trigger different and opposing neurological responses. Ultrasonic sounds trigger a negative phonotactic response and sonic sounds trigger a positive phonotactic response (Schildberger and Hörner 1988). These results suggest the female's response to ultrasonic noise may be an anti-predator response since she is quicker to move from the starting position than when presented with sonic noise. When two signals of different

frequencies compete, each presenting important information and triggering different opposing neurological signals, the female's behavior may be negatively impacted and could result in increased predation risk and increased energetic output. The slower response time in the sonic noise may also be the female's response to energetic masking in which she is not initially able to detect the male signal and spends more time trying to detect the signal to avoid potential mistakes.

In the presence of substrate-borne vibrational noise, the detection of the male signal was not impeded by energetic masking, but female phonotaxis was still impacted. Females traveled a greater distance and took more time in locating the calling male, indicating constraints on the female's attention. The detection of substrate-borne vibrations is widespread in invertebrates and the receivers used to detect substrate-borne vibrations are distinct from those of the auditory system (Stumpner and Von Helversen 2001). The noise stimulus is separated energetically from the male signal and detected by the subgenual organ independent of the tympanal organ; vibrational noise does not interfere with the female's ability to detect the male signal. Gryllids rely on substrate-borne vibrations to detect approaching terrestrial predators; the female response to substrate-borne vibrational noise may illustrate the tradeoff between mate searching and predator detection. While distance traveled was significantly higher at all the levels and showed more variability than the control, the distance traveled at 5 mm/s was significantly lower than the distance traveled at 1 and 15 mm/s. That difference may show that there are different behaviors in response to the information contained in the signal. Substrate-borne vibrations show nearness of a predator and that may influence the animal's response. Increasing velocity could represent an anti-predator response. Vibrations are used to determine the direction and distance from the source (Shadley and Hill 2001); the signal's intensity may indicate the threat's magnitude. When

individuals increase their mobility they become more susceptible to predation (Heller 1992). To counter being more conspicuous, increasing their velocity may help individuals avoid predation especially if the threat is perceived to be nearby due to the intensity of the signal. While these tactics may help avoid predation, they may reduce the female's ability to assess male signals and result in females choosing lower-quality mates.

Unfortunately, very little attention has been paid to substrate-borne vibrations as a noise source, even though most arthropods are sensitive to vibrations of less than 1kHz (Virant-Doberlet et al. 2019). It is not yet understood what the indirect consequences of substrate-borne vibrational noise is. Previous studies have found that introduced substrate-borne vibrations reduce the mating frequency of leafhoppers on plant hosts; however, that research focused on disrupting vibrational communication (Eriksson et al. 2012). Thus, it is not known if the change in mating frequency was due only to energetic masking or if informational masking also played a role in the individual's inability to locate a signaling mate.

In the sonic noise treatment, the female altered her search behavior ultimately increasing the distance and duration of her path to locate the signaling male. The increased time and movement may represent the female's attempt to separate the signal of interest from background noise. While the female response to ultrasonic and substrate vibrational noise are consistent with informational masking, the female response to sonic noise supports previous studies on the effects of energetic masking negatively affecting mate searching behavior on acoustically localizing species. When female *G. bimaculatus* were exposed to traffic noise, there was a reduction in the female's ability to detect and approach a signaling male (Bent et al. 2018). The phonotactic path of female bushcrickets, *Conocephalus brevipennis*, orienting toward a speaker broadcasting male signals, became more random as the background noise increased (Bailey and

Morris 1986). While these results support energetic masking, informational and energetic masking are not mutually exclusive and it may not be possible to definitively determine if only energetic masking is causing the behavioral shifts; it could be a combination of both.

Noise affects female phonotaxis in an acoustically localizing species and can have consequences on survival and reproductive success. The negative effects of noise on mate searching can have direct impacts on both males and females. Changes to search behavior impose fitness costs to the sender and receiver such as increased predation risk and energetic output. The increase in female mobility and time spent searching, increases the risk of predation on the female (Gwynne 1987; Heller 1992). When females increase their search time, males must increase the time they spend calling making them more conspicuous to predators and increasing their energetic output (Prestwich 1994; Zuk and Kolluru 1998; Mowles 2014). Changes to reproductive success could have bottom-up ecological consequences. Insects are a crucial component of all ecosystems and perform many critical ecosystem services such as pollination, decomposition, and nutrient cycling, and are an important food source for many animals (Mulder et al. 1999).

There is sufficient evidence that noise affects phonotaxis; however, it is still unknown how these changes in search behavior may affect other behaviors such as mate choice. Females rely on the accurate assessment of the male's signal to determine the quality of a potential mate. The presence of noise resulting in informational or energetic masking may hinder the female's ability to accurately assess the quality of a potential mate or detect the male signal. Disrupting the detection or assessment of male signals will lead to mistakes that could ultimately decrease individual fitness and reproductive success (Naguib 2013).

Many studies have focused on an animal's ability to overcome energetic masking via both evolutionary and behavioral mechanisms (Romer 2013b). Informational masking has the potential to act as a strong selection factor in acoustically communicating animals. Animal sensory systems have evolved to detect sounds beyond the frequency of sounds individuals can produce; however, studies of noise have narrowly targeted noise that overlaps with the focal animal's signal (Dominoni et al. 2020). By not considering the full scope of sounds animals are sensitive to, there is a limited understanding of the impacts of noise present in the environment and selection pressures that could influence future conservation efforts.

The effects of noise on animals are far-ranging with impacts extending from individual fitness to community-level processes. The results of this study highlight the need to expand noise research to include substrate-borne vibrations and frequencies beyond the human audible range. The diversity of animal sensory systems and how different types of sound inform how animals interact with their environment need to be accounted for to better understand the constraints and adaptations of living in an increasingly noisy world.

CHAPTER 3: NOISE DISRUPTS MATE CHOICE BY AUSTRALIAN BLACK FIELD CRICKETS (*TELEOGRYLLUS COMMODUS*)

Abstract

Mate choice requires individuals to accurately assess signals from potential mates to make an informed decision. Successful decisions require receivers to detect and properly assess signals; however, sensory pollutants can disrupt this process. Environmental noise can affect acoustic signals and impact mate choice, leading to negative effects such as reduced reproductive output or decreased fitness. This study tested whether different types of noise (ultrasonic, sonic, and substrate-borne vibrations) impacted females' ability to choose between two male acoustic phenotypes in *Teleogryllus commodus*. The two acoustic phenotypes represent high-quality males with a higher chirp rate and low-quality males with a lower chirp rate. Two-speaker tests were conducted by broadcasting high-quality and low-quality male signals from speakers placed on opposite sides of a circular behavioral arena. One of three types of noise was broadcast simultaneously with the male signal, either from overhead speakers for airborne noise or below the arena for substrate-borne vibrations. For each noise type, there were three intensities plus a control with no noise broadcast with the signals. During the ultrasonic noise treatment (20-45 kHz), the probability of females choosing the high-quality male significantly decreased at all tested noise intensities. Similar results were seen for the substrate-borne vibration trials (1 Hz-1,000 kHz). The probability of females choosing the high-quality male significantly decreased during all treatments, 1mm/s, 5 mm/s, and 15 mm/s. During the sonic treatments (1-20 kHz), the likelihood of choosing the high-quality male significantly decreased only during the 67 dB SPL

re 20 μ Pa and 73 dB SPL re 20 μ Pa trials compared to the control. There was no effect during the 70 dB SPL sonic trial. The findings suggest that noise disrupts the process of female mate choice, and it can have a considerable impact on female behavior regardless of acoustic modality.

Introduction

Accurate assessment of potential mates is crucial to many sexually reproductive organisms; this decision impacts individuals, populations, and communities. At the individual level, selecting the appropriate mate can increase survival, number of offspring, and viability, translating to direct and indirect fitness benefits for choosier individuals (Candolin 2019). Mate choice can also affect the structure, and distribution of a species, affecting abundance, distribution, and interspecific interactions within an ecological community (Candolin and Wong 2019). Organisms base their reproductive decisions on a wide range of species-specific signals, that convey some measure of quality in potential mates. A potential mate's quality can be communicated via different sensory modalities to communicate a given individual's quality, such as visual, chemical, auditory, tactile, or electrical. These types of signals can be used alone (unimodal) or in combination (multimodal) (Partan and Marler 1999). For mate choice to be successful, individuals must detect a measure of quality in potential mates, and thus assess the signal and respond accordingly. This requires that the intended receiver must be able to detect and perceive the signals to obtain reliable information leading to informed mating decisions (Rosenthal 2017). Thus, disruptions to the mate choice process can have vast consequences for an individual's and a population's survival.

The mate choice process can be disrupted when environmental conditions constrain the signal's transmission, detection, or assessment. Disruptions can come in many forms, depending on the type of signal, and can lead to maladaptive responses. For example, the broad-nosed

pipefish (*Syngnathus typhle*) uses visual signals to guide mate choice when selecting a mate. Increasing water turbidity can interfere with the ability of males to visually assess potential mates. Under low visibility conditions, males spend less time making an assessment, and fewer choose larger females (Sundin et al. 2010). This maladaptive response is known as relaxed mate choice (Candolin 2019). Female palmate newts (*Lissotriton helveticus*) rely on chemical cues from males to assess male immune response, but when exposed to waterborne chemicals from exotic eucalyptus plantations, the females changed their mate choice preference (Iglesias-Carrasco et al. 2017). Other disruptions might increase the cost of choosing mates such as increases in search time, leading to an increased risk of predation. Other disruptions might cause individuals to relax mate choice decisions and choose suboptimum mates potentially causing a decrease in fitness. While animals may adapt or evolve different signaling behaviors to counter disruptive environmental factors (Ord et al. 2010; Preininger et al. 2013), many now live in environments where disruptions such as environmental acoustic noise are increasing rapidly.

Environmental noise, in particular, can disrupt the mate choice process by interfering with the capabilities of the auditory sensory system to detect and process relevant acoustic signals. Impeding the reception and perception of information about a potential mate can alter the receiver's response (Wiley 2013). Environmental noise arises from three sources: biological (biophony), geological (geophony), and anthropogenic (anthrophony) (Pijanowski, Farina, et al. 2011). Regardless of the source of noise, all three types are known to affect mate choice across various taxa. Crickets (*Gryllus bimaculatus*) exposed to traffic noise are less likely to discriminate between high-quality and low-quality males (Bent et al. 2021). Increased chorus noise changes females' discrimination of male treefrog (*Hyla ebraccata*) calls and alters female preference (Wollerman and Wiley 2002). When noise overlaps energetically with the male's

signal, energetic masking occurs. In instances of energetic masking, males often change their call to try to overcome the masking effects of elevated noise; however, the change may not be in line with female preference and may lead to a reduction in mating opportunities. Male birds often increase the frequency of their call in urban areas to avoid the masking effect of noise, but females strongly prefer low-frequency male calls (Slabbekoorn et al. 2012).

Energetic masking, in which noise energetically overlaps with the acoustic signal, can prevent a receiver from detecting a signal. Energetic masking can make the signal difficult to distinguish from the ambient noise and lead to missed mating opportunities. To counter the impact of missed signals, individuals may need to exert more signaling effort and shift the frequency of their call or the timing which may not be favorable (Barber et al. 2010). Energetic masking can also distort the information contained in the signal by masking parts of the signal. For example, noise that masked only the low-frequency portion of birdsong, distorted information received by the female (Halfwerk, Bot, et al. 2011). If signals are distorted by noise, females cannot make informed mating decisions based on unreliable information, leading to consequences such as a decrease in reproductive success and individual fitness. The reproductive success of great tits (*Parus major*) was negatively affected by high levels of noise, females laid smaller clutches in noisier areas. Furthermore, the presence of elevated noise levels was also associated with reduced fledgling numbers, regardless of clutch size (Halfwerk, Holleman, et al. 2011).

The growing body of research on the effects of environmental noise on animal behavior and communication has focused primarily on the effects of energetic masking and airborne noise (Naguib 2013). This bias has left researchers with an incomplete picture of how noise affects animals as many animals can detect sounds from different auditory frequencies and different

acoustic modalities. Acoustic modalities are defined as acoustic sounds detected by different sensory channels (i.e., airborne sound and substrate-borne vibrations). More focus needs to go to noise that does not energetically overlap with the animal's signal, because environmental noise beyond the frequency range or acoustic modality of the animal's signal may nevertheless impact an individual's ability to properly assess a signal by dividing the receiver's attention or interfering with sensory processes via informational masking. Informational masking occurs when background noise or competing sounds do not overlap in energy with a signal but still interfere with an animal's ability to extract relevant information. Such interference can lead to errors in signal processing and interpretation, and can ultimately impact the animal's ability to communicate, navigate, or find food (Wiley 2013).

An individual's attention is often divided between assessing a conspecific signal and monitoring for incidental sounds in the environment, such as the approach of a predator. Distraction associated with informational masking significantly affects an animal's ability to make appropriate mate choice decisions. The inability to attend fully to signals emitted by potential mates can lead to errors in mate choice and result in individuals choosing mates that are less favorable in terms of reproductive success or genetic quality (Wiley 2013).

While most studies have focused on energetic masking, a few have investigated informational masking. Informational masking occurs when noise does not energetically overlap with a signal. In *Hyla chrysoscelis*, females show a reduced phonotactic response and *Gryllus bimaculatus* females show a decrease in preference for a signaling male (Schmidt et al. 2014; Gupta and Bee 2022). While these studies demonstrate that informational masking occurs in noisy environments, they solely focus on noise in the same acoustic modality (i.e., the impact of

airborne noise on an airborne signal) and phonotaxis. It is still unclear how noise from different auditory modalities affects mate choice.

The aim of this research is to determine how three different noise types, sonic (1-20 kHz), ultrasonic (25-45 kHz), and substrate-borne vibrations (100 -1,000 Hz), affect the mate choice process in the Australian black field cricket (*Teleogryllus commodus*). Female *T. commodus* readily respond to and locate chirping males, preferring males with higher chirp rates (Brooks et al. 2005). They can detect both airborne sounds and substrate-borne vibrations. The female's ability to discriminate between a high and low-quality male in the presence of the three noise types: sonic, ultrasonic, and substrate-borne vibrations, was assessed to determine how different types of noise affect female mate choice. I tested the hypothesis that exposure to noise will impair females' ability to discriminate between preferred (high chirp rate) and non-preferred (low chirp rate) male acoustic phenotypes.

Methods

Animals

Two-choice speaker trials were conducted on 150 virgin females of *T. commodus* derived from crickets originally located in New South Wales, Australia. All study subjects were reared and maintained at the University of New Hampshire. Females and males were reared in the same room. Once sex could be determined, females were separated into different containers from males. The crickets were kept on a 14/10 light/dark schedule at 26°C with food and water *ad libitum*.

Behavioral Arena

A circular behavioral arena was constructed in a semi-anechoic chamber (Figure 12). The arena consisted of a 50 cm wooden ring in which acoustically transparent fabric was stretched. A 15 cm high hard plastic wall surrounded the arena to prevent escape. Male calls were broadcast from two speakers (OrbAudio) positioned on opposite sides of the arena and directed toward its center. Speakers were suspended 1 m above the arena which broadcast non-directional sonic and ultrasonic airborne noise. Substrate vibrations were transmitted via an electromagnetic shaker (TMS 2004E powered by an ART SLA-2 amplifier connected to a PC) placed below the arena and in contact with the center of the fabric arena floor.

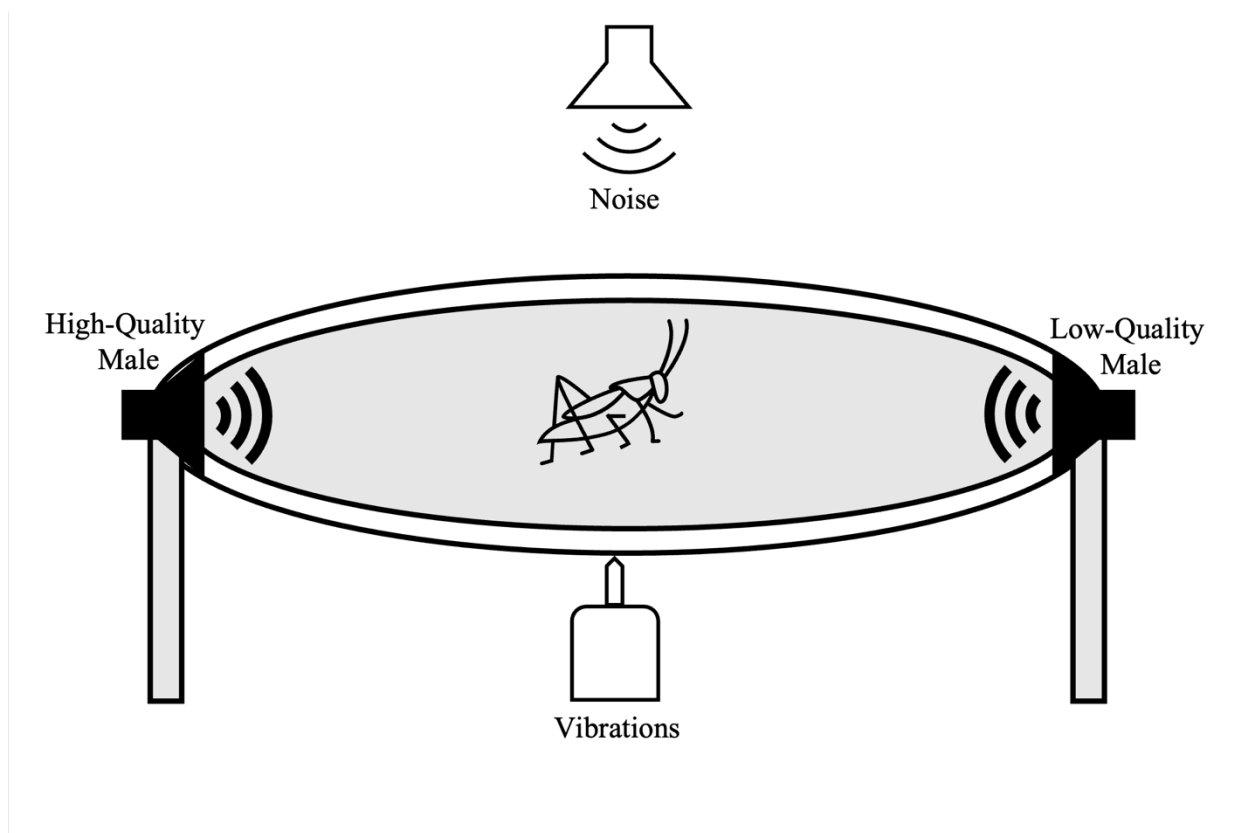


Figure 12: A circular behavioral arena (50 cm diameter) was used to test the effects of noise on female mate choice in *T. commodus*. Two speakers were set up 180° apart pointing to the center of the arena to broadcast male calls. A speaker was placed 1m above the center of the arena to broadcast ultrasonic and sonic noise while a shaker was positioned beneath the arena to produce substrate-borne vibrations.

Behavioral Trials

The advertisement call of male *T. commodus* consists of a short, amplitude-modulated chirp followed by a longer trill sequence; each call element is comprised of a series of pulses (Figure 2) (Bentley and Hoy 1972; Hill et al. 1972). To create two male acoustic phenotypes, samples of the male *T. commodus* calls were manipulated using sample calls that came from recordings previously done for a different playback experiment with the same population of crickets (Chapter 2). The following parameters were manipulated in Adobe Audition: pulses per chirp, pulses per trill, time between pulses (interpulse interval), and time interval between chirp and trill (chirp/trill interval) (Figure 13). Females prefer a higher pulse rate (Brooks et al. 2005); so the pulse rate was decreased to create a low-quality male. To achieve the reduction in pulse rate in the chirp and trill series, every other pulse was replaced by silence; silence was also added to the interval between the chirp and trill series to increase the time them. A high-quality male acoustic signal was created by reducing the interpulse interval in both the chirp and trill series (Table 6). Three-minute recordings were created for both phenotypes.

Noise treatments were divided into ultrasonic (20-45 kHz), sonic (1-20 kHz), and substrate-borne vibrational noise (1-1,000 Hz), each with three different intensities. Three ultrasonic noise intensities were created: 70, 75, and 80 (dB L_{\max} re 20 μ Pa). The ultrasonic noise stimuli consisted of broadband (25-45 kHz) 1-second pulses with a 1-second inter-pulse interval repeated for three minutes. The ultrasonic noise stimuli were calibrated using a sonic reference tone, whose voltage was measured using an oscilloscope; the ultrasonic tone was then calibrated to the same voltage. The sonic noise treatment consisted of three intensities: 67, 70, and 73 dB (L_{\max} re 20 μ Pa). Sonic noise was a constant broadband (1 kHz-20 kHz) white noise and was calibrated using a sound level meter (Brüel & Kjaer Type 2250). The three substrate-borne

vibrational intensities were low (1 mm/s), medium (5 mm/s), and high (15 mm/s). Each was calibrated using a Polytec PDV 100 laser Doppler vibrometer. Each substrate-borne stimulus consisted of 1-second pulses with 1-second inter-pulse intervals repeated for three minutes with a frequency range of 100 Hz-1,000 Hz. All signals were calibrated at the center of the arena.

Each female was randomly assigned to one of the three noise treatments, with 50 females per acoustic treatment group (ultrasonic, sonic, or substrate-borne vibrations). Within each treatment group, each female was exposed to all three intensities plus a control. The control treatment was the two male acoustic phenotypes played simultaneously from different speakers with no noise. To ensure the female was receptive and exhibited phonotaxis to a calling male prior to the start of each trial, a standard male call was broadcast from one of two speakers. If the female was receptive, she would move toward the speaker broadcasting the call. Only females that showed interest in the male call were used in the trial. Once females were deemed receptive, the female was exposed to each noise treatment played simultaneously with the two male acoustic phenotypes. The male calls were each broadcast at 73 dB (L_{\max} re 20 μ Pa). The order of the trials including the control was randomized, as was the speaker broadcasting each male phenotype.

Using a clear plastic cup, a female was placed at the center of the arena. Once the playback began, the cup was lifted, and the female could freely move about the arena. The trial finished when the female moved to a speaker or three minutes elapsed without choosing a speaker. This process was repeated with one minute between each trial until the female completed all the trials in her treatment group. Each playback experiment was recorded using HD video and analyzed in Ethovision XT software (Noldus Information Technology) to measure distance traveled, duration of travel, latency to start, meander, and velocity (Table 7).

Generalized linear mixed-effects models with a logit link function were built to test the relationship between female mate choice and noise. Models were built with and without individual as a random effect; AIC values were used to determine model fit. Using a correlation matrix, it was determined that there were no correlations between the movement variables. Movement variables were assessed in individual generalized linear mixed effects models. Variables that did not meet the assumption of normality were log-transformed (.001 was added to account for zeroes). All statistical analyses were performed using R Statistical Software (v4.2.2; R Core Team 2022). Trials in which the female did not make a choice were excluded from the analysis. To confirm there was no habituation as the trials progressed, residuals were visually inspected to determine the order of the trial was not significant.

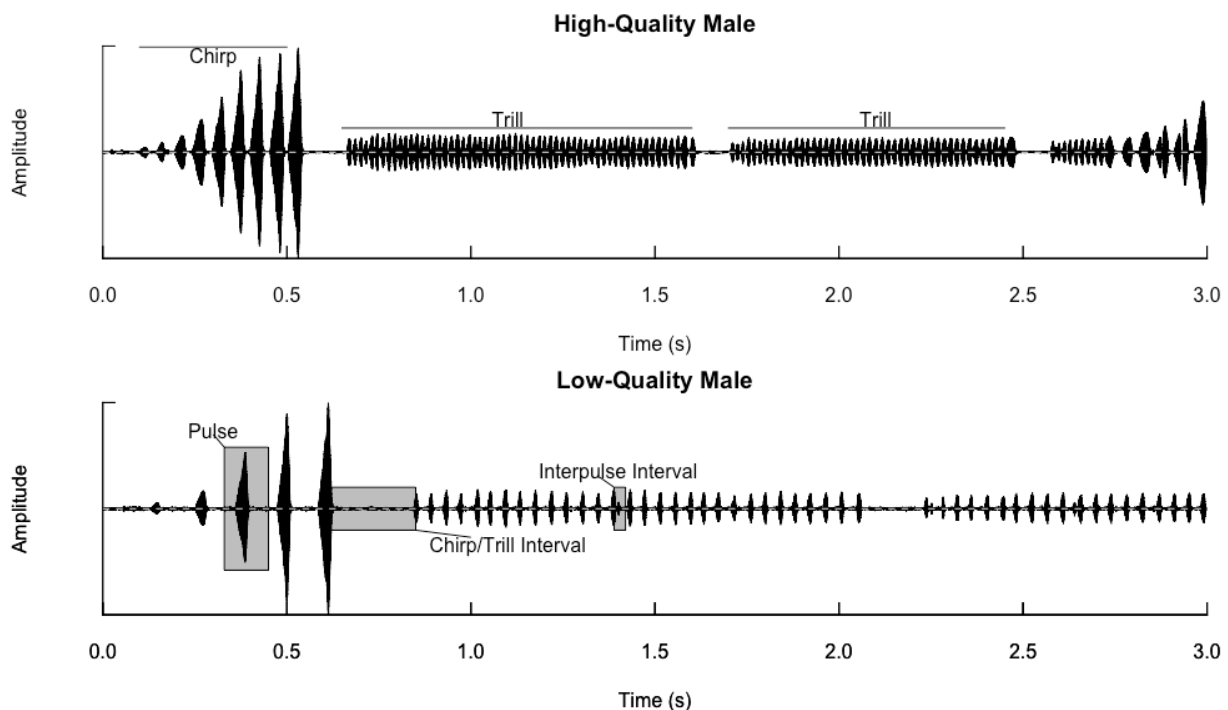


Figure 13: Two male phenotypes were created to test how noise affects female mate choice. Male *T. commodus* calling songs are made of a chirp sequence followed by multiple trill sequences with each element being comprised of a series of pulses. To create a high-quality male calling song, the pulse rate was increased by reducing the interpulse interval and the chirp/trill interval was shortened. To create a low-quality male calling song, the pulse rate was decreased by reducing the number of pulses and increasing the interpulse interval.

Table 6: Male *T. commodus* calling songs were altered to create two male phenotypes: high-quality and low-quality males. The table below reports the call parameters (mean±sd) for each acoustic phenotype.

| Male Phenotype | Chirp | | | | Chirp/Trill Interval (ms) | Trill | | | |
|----------------|----------|--------------------------|---------------|------------|---------------------------|------------|--------------------------|---------------|------------|
| | Pulses | Interpulse Interval (ms) | Duration (ms) | Pulse Rate | | Pulses | Interpulse Interval (ms) | Duration (ms) | Pulse Rate |
| High-Quality | 10±0.58 | 17±8 | 504±12 | 19.84/s | 101±25 | 47.25±8.10 | 4±1 | 786±116 | 60.11/s |
| Low-Quality | 5.5±0.71 | 74±13 | 508±78 | 10.83/s | 215±9 | 24.5±3.70 | 25±3 | 995±161 | 24.62/s |

Table 7: The movement variables were measured based on the path taken by female subjects to locate a speaker broadcasting a male calling song. Measurements were obtained by analyzing videos of noise trials using Ethovision XT software.

| Variable | Unit | Description |
|------------------|-------------|--|
| Distance | cm | Total path distance followed by a cricket in the arena |
| Duration | sec | The time it took for a cricket to travel to the broadcasting speaker |
| Latency to Start | sec | The time it took for a cricket to move from the starting position |
| Meander | deg/cm | The change in direction of a cricket relative to the distance moved |
| Velocity | cm/sec | The mean speed at which a cricket traveled |

Results

In each of the three noise treatments, 200 trials were conducted. After excluding trials in which the female made no choice, the number of trials included in the analysis was 196 ultrasonic (25-45 kHz) trials, 196 sonic trials (1-20 kHz), and 200 substrate-borne vibration (100-1 Hz) trials. Changes in odds of choosing the high-quality male are relative to the control unless otherwise stated.

Ultrasonic

During the ultrasonic control treatment, females had an 83% probability (95% CI=0.70-0.92) of choosing the high-quality male. The odds of a female choosing a high-quality male significantly decreased by an average of 68% (95% CI= 0.12-0.78) when exposed to 70 dB ultrasonic noise ($Z=-2.48$, $p=0.01$, Figure 14A). Exposure to 75 dB ultrasonic noise resulted in an average decrease in the odds of choosing the high-quality male of 60% (95% CI=0.15-0.99, $Z=-1.95$, $p=0.05$, Figure 14A). The odds of choosing a high-quality male decreased by an average of 77% (95% CI=0.09-0.55) when 80 dB ultrasonic noise was broadcast concurrently with the signal ($Z=-3.19$, $p=0.001$, Figure 14A). The movement variables were not correlated with the female's choice (Table 8).

Sonic

Under the sonic control conditions, the probability of choosing a high-quality male was 78% (95% CI=0.65-0.87). When 67 dB sonic noise was broadcast simultaneously with the signal the odds of the female choosing the high-quality male decreased by an average of 65% (95% CI=0.15-0.84, $Z=-2.1$, $p=0.02$, Figure 14B). The odds of choosing a high-quality male also decreased by an average of 68% (95% CI=0.13-0.76) when 73 dB sonic noise was broadcast simultaneously with the signal ($Z=-2.53$, $p=0.01$, Figure 14B). However, during the 70 dB sonic

noise treatment, there was only a 3% (95% CI=0.37-2.53) decrease in the odds of choosing the high-quality male, which was not a significant change ($Z=-0.05$, $p=0.96$, Figure 14B). When the three sonic noise intensities were compared, the odds of choosing the high-quality male significantly decreased by an average of 63% (95% CI=0.15-0.87) when 67 dB sonic noise was broadcast compared to when the 70 dB sonic noise was broadcast simultaneously with the signal ($Z=-2.24$, $p=0.02$, Figure 14B). The odds of choosing a high-quality male also decreased by an average of 67% (95% CI=0.13-0.78) when 73 dB sonic noise was broadcast compared to when 70 dB noise was broadcast ($Z=-2.47$, $p=0.01$, Figure 14B). The movement variables were not correlated with the female's choice (Table 8).

Substrate-borne

During the substrate-borne vibration trials, the probability of the female choosing a high-quality male during the control trials in the absence of noise was 89% (95% CI=0.76-0.95). When substrate-borne vibrations were broadcast at 1mm/s with the male signals, the odds of choosing the high-quality male decreased by an average of 83% (95% CI=0.06-0.44, $Z=-3.43$, $p<0.001$, Figure 14C). When substrate-borne vibrations were broadcast at 5 mm/s the odds of choosing the high-quality male decreased by an average of 68% (95% CI=0.10-0.87, $Z= -2.17$, $p=0.03$, Figure 14C). When substrate-borne vibrations were broadcast at 15 mm/s simultaneously with the signal, the odds of choosing a high-quality male decreased by an average of 85% (95% CI=0.05-0.40, $Z= -3.62$, $p<0.001$, Figure 14C). The movement variables were not correlated with the female's choice (Table 8).

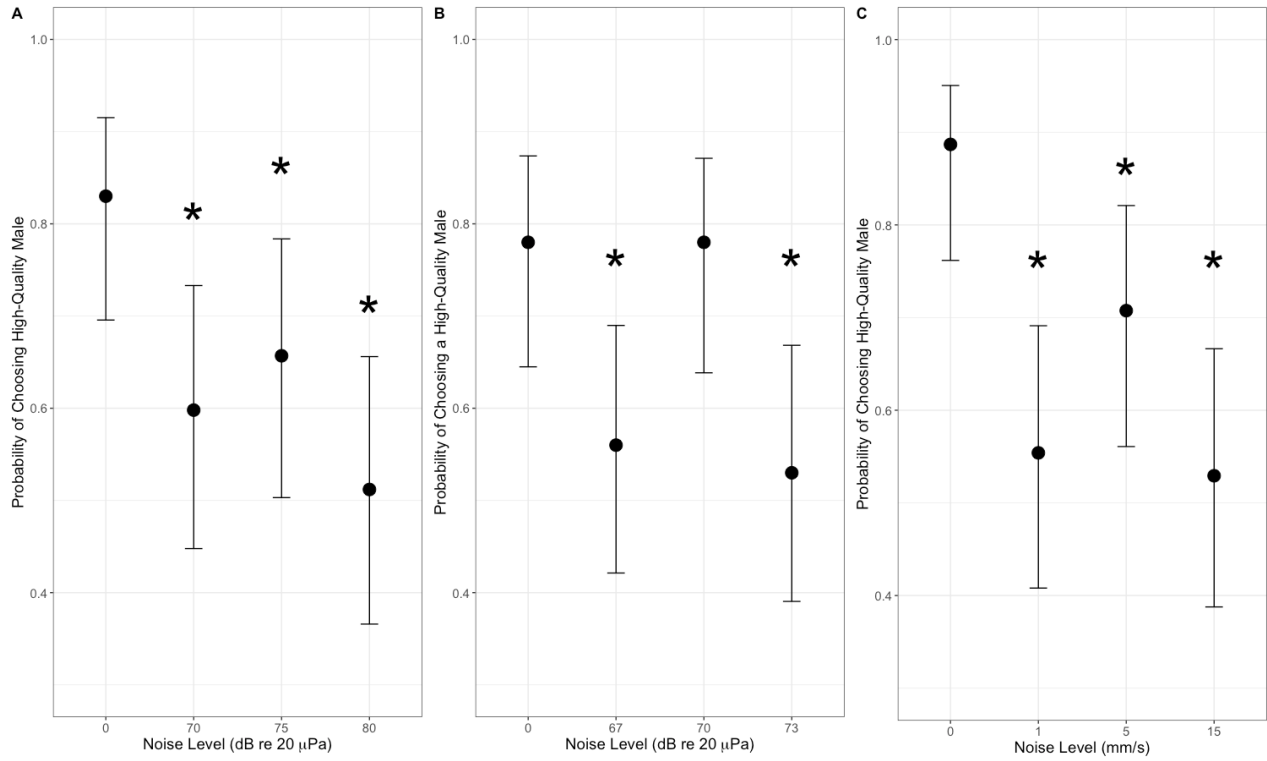


Figure 14: The modeled probability of a female *T. commodus* choosing the high-quality male acoustic phenotype in three acoustic noise environments: **A.** Ultrasonic (20-45 kHz), **B.** Sonic (1-20 kHz), and **C.** Substrate-borne vibrations (1-1,000 Hz). Asterisks show a significant difference relative to the control (0 noise level) ($\alpha=0.05$).

Table 8: Generalized linear mixed-effects models were used to determine if female movements had an impact on mate choice. The movement variables were measured using Ethovision XT software's track analysis. The mean and standard deviation were calculated for each variable for females who chose the high-quality male (HQ) and the low-quality male (LQ). However, the results showed that none of the movement variables were significantly correlated with female mate choice ($\alpha=0.05$).

| Movement Variable | Ultrasound (20-45 kHz) | | | | Sonic (1-20 kHz) | | | | Vibrations (100-1,000 Hz) | | | |
|------------------------------|-----------------------------|-----------|--------|---------|-----------------------------|-----------|--------|---------|-----------------------------|-----------|--------|---------|
| | Mean±SD | Std Error | Z Stat | P-value | Mean±SD | Std Error | Z Stat | P-value | Mean±SD | Std Error | Z Stat | P-value |
| Total Distance (cm) | | | | | | | | | | | | |
| HQ | 69.74±40.07 | 0.004 | -1.44 | 0.15 | 69.14±35.72 | 0.004 | -1.86 | 0.06 | 60.55±35.12 | 0.004 | -1.78 | 0.08 |
| LQ | 78.43±39.87 | | | | 79.76±39.89 | | | | 70.19±36.66 | | | |
| Duration (s) | | | | | | | | | | | | |
| HQ | 54.50±60.39 | 0.17 | -0.06 | 0.95 | 49.35±45.13 | 0.20 | -0.75 | 0.45 | 39.32±29.21 | 0.21 | -0.64 | 0.52 |
| LQ | 48.42±48.49 | | | | 49.78±33.16 | | | | 42.73±36.55 | | | |
| Latency to Start (s) | | | | | | | | | | | | |
| HQ | 30.85±47.69 | 0.08 | 1.33 | 0.18 | 26.03±39.82 | 0.08 | 0.43 | 0.66 | 19.98±23.23 | 0.11 | -1.31 | 0.19 |
| LQ | 22.37±34.45 | | | | 24.03±23.29 | | | | 23.40±28.45 | | | |
| 70 Meander (deg/cm) | | | | | | | | | | | | |
| HQ | 31416466.12 ±42761702.86 | 0.09 | 0.33 | 0.74 | 22783608.94 ±30820178.51 | 0.13 | -0.38 | 0.70 | 21832317.17 ±23342979.10 | 0.11 | -0.22 | 0.83 |
| LQ | 26552135.53 ±34594373.58 | | | | 21106396.30 ±21211210.94 | | | | 24857134.81 ±33104256.60 | | | |
| Mean Meander (deg/cm) | | | | | | | | | | | | |
| HQ | 15074.43 ±9169.59 | 0.00002 | 0.32 | 0.75 | 12660.65 ±7307.21 | 0.26 | 0.33 | 0.74 | 16332.63 ±10267.29 | 0.19 | 0.24 | 0.81 |
| LQ | 14642.76 ±8875.16 | | | | 12459.29 ±7040.68 | | | | 15833.27 ±9100.75 | | | |
| Mean Velocity (cm/s) | | | | | | | | | | | | |
| HQ | 2.31±2.20 | 0.20 | -1.11 | 0.27 | 2.06±1.54 | 0.24 | -0.71 | 0.48 | 2.03±1.33 | 0.23 | -1.26 | 0.21 |
| LQ | 2.63±2.34 | | | | 2.22±1.58 | | | | 2.31±1.45 | | | |

Discussion

Noise in any acoustic modality or frequency range diminished the female's ability to discriminate between high and low-quality male phenotypes. Previous studies have cited energetic masking for the deterioration in decision-making; this research demonstrates that noise need not overlap with the animal's signal to interfere with mate choice. In fact, the reduction in the probability of the correct choice was similar across acoustic modalities. Exposure to ultrasonic noise and substrate-borne vibrations decreased the probability of choosing the high-quality male signal at all noise levels. This change in female preference may be caused by informational masking, in which the noise interferes with the female's ability to process the male's signal and extract meaningful information. Since the ultrasonic and substrate-borne noise treatments did not energetically overlap with the male's signal, only the sonic treatment supported the hypothesis that energetic masking affects behavior; however, it is not clear if the behavioral change is due solely to energetic masking or a combination of energetic and informational masking.

Sonic noise decreased the probability of correct choice at the lowest (67 dB) and highest (73 dB) noise levels, but not at 70 dB. Without further experimental evidence no conclusions can yet be drawn. This surprising result may be explained by the cricket's rearing environment which had an ambient background level of 70 dB. Females may be better able to make high-stakes decisions in an acoustic environment comparable to their rearing environment even if the conditions are less favorable than in a novel acoustic environment. If females leave their rearing environment or if acoustic conditions change, mate choice may be affected. This finding has implications for understanding the development of the sensory system and how that may affect decision-making as an adult. Changes in biological and anthropogenic activity can alter any

acoustic environment, creating new challenges for animals attempting to find and assess potential mates. Changes in the acoustic environment can have significant impacts on mate choice and reproduction in animals, especially those that rely heavily on sound for communication and mating behaviors.

Mate choice is an important behavioral process that influences reproductive success and individual fitness. Altering the mate choice process could reduce reproductive success and choosing a less preferable mate may result in a loss of fitness. While it is currently unclear how altering mate choice affects the number of offspring and viability, there is some evidence that sensory pollutants do affect viability and reproductive output. For example, when sticklebacks select less desirable mates due to a decrease in water visibility, the offspring produced have lower viability (Candolin et al. 2016). Canaries in noisy environments have a reduction in clutch size (des Aunay et al., 2017). It is important that individuals can properly assess the quality of potential mates and select those with the highest fitness, choosing high-quality mates is important for ensuring reproductive success and increasing the fitness of the individual (Bussière et al. 2008). The current study illustrates that in crickets, noise lowers the probability of selecting a high-quality mate which could lead to lower offspring viability or a decrease in reproductive output for crickets, these consequences could lead to a decline in population abundance and diversity that ultimately affects the community composition.

Invertebrates are a fundamental component of the ecosystem, alterations to invertebrate population abundance and diversity could have broad impacts on the ecosystem. Altering the mate choice process could lead to a decline in invertebrate abundance thus altering ecosystem functions (Mulder et al. 1999). Invertebrates provide ecological services such as pollination, decomposition, and nutrient release, and are a vital component in food webs (Morley et al.

2013). Environmental noise has been shown to alter invertebrate abundance and composition on the landscape (Bunkley et al. 2017). Noise-induced changes in the abundance of arthropods can have a range of effects on other organisms within the ecosystem, including those that are their prey, predators, competitors, and beneficiaries (Van Der Putten et al. 2004). Interfering with the invertebrate mate choice system can have far-reaching consequences for other organisms within the ecosystem, potentially leading to long-term alterations to the ecosystem and biodiversity.

This study provides experimental evidence that environmental noise disrupts the mate choice process by interfering with the female's ability to choose a high-quality male. These results are notable since this research looks beyond energetic masking and establishes that environmental noise from different acoustic modalities and frequency ranges has a significant impact on female behavior comparable to the impacts of environmental noise that overlaps with the male signal. Noise is complex and multifaceted and there is insufficient research looking at environmental noise outside the energetic level of an animal's signal. We thus have only a partial understanding of how noise affects invertebrates. Moving forward, research needs to focus on all components of noise especially if the noise is multimodal. This contributes to the understanding of how sensory modalities interact in noisy environments. Animal sensory systems are complex and diverse and need to be considered when identifying noise types affecting behavioral responses. Identifying how short-term responses lead to long-term effects on the individual and population will contribute to making informed conservation and management decisions.

Conclusion

Acoustic noise is a pervasive ecological issue, the impacts of which have been measured across many taxa of animals. While there are multiple types of noise, most studies on the effects of acoustic noise on animals have focused solely on airborne noise (Barber et al. 2010; Shannon, McKenna, et al. 2016). Using gryllid crickets in the *Teleogryllus* genus as a model for studying noise, this dissertation explored the impact of multiple types of noise on cricket behavior, including the often-overlooked auditory modality of substrate-borne vibrations. To determine the auditory thresholds of *T. commodus*, neurological responses to a combination of frequencies and intensities were recorded from ascending auditory neurons. Then, the impact of noise on phonotaxis was studied by measuring the female's movements while locating a signaling male in variable noise conditions. Finally, the impact of noise on mate choice was assessed by recording the female choice between two male acoustic phenotypes in variable noise conditions. The results of this dissertation highlight that noise, regardless of modality, can have consequences on many behavioral processes such as phonotaxis and mate choice.

Crickets were subjected to different combinations of frequencies and intensity of airborne sounds and substrate-borne vibrations to establish the sensitivity of their auditory system. The findings suggest that a wide range of frequencies play a role in the sensory ecology of *T. commodus*, including those used for detecting conspecifics, aerial predators, and terrestrial predators. In the airborne frequency range, sensitivity peaks at 4 kHz and 32 kHz illustrate the detection of conspecific signals, and the echolocation clicks of bats play a major role in the evolution of the auditory system. Previous research has shown other gryllid species exhibit similar sensitivities, with peak sensitivities overlapping with conspecific signals and echolocation clicks of bats (Moiseff et al. 1978; Farris and Hoy 2002; Howard et al. 2008). These

sensitivity peaks at relevant frequencies indicate the evolution of neural filters to enhance the detection of relevant signals. Insects that communicate in environments with high background noise often have neural filters that increase their sensitivity to relevant signals, thereby maximizing the signal-to-noise ratio and increasing the chances of detection (Warrant 2016). Like airborne sounds, crickets also use substrate-borne vibrations for mate localization, courtship displays, and detecting approaching terrestrial predators (Latimer and Schatral 1983; Weidemann and Keuper 1987; Broder et al. 2021); however, our understanding of their vibratory environment and their ability to differentiate between vibrations from biologically significant and insignificant sources is quite limited. The ability to differentiate between predator and conspecific signals and elicit distinct behavioral responses could greatly contribute to the survival and evolution of the species. By identifying the auditory system's sensitivities, a better understanding of biologically relevant frequencies in both auditory modalities can be established and inform future avenues of research.

Behavioral experiments sought to test how different modalities of noise across a broad bandwidth affect reproductive behaviors such as phonotaxis and mate choice. Previous studies have often focused on the effects of ambient noise that overlap with the frequency of conspecific signals and in the same airborne modality. However, the results of this dissertation demonstrate noise spanning a broad frequency range from both auditory modalities, airborne and substrate-borne, can impact reproductive behaviors. Female behavior was significantly affected by noise regardless of bandwidth, whether it was sonic, ultrasonic, or substrate-borne. Female phonotaxis was significantly affected by the presence of noise and females were less likely to choose the high-quality male acoustic phenotype regardless of noise type. Such changes are often attributed to energetic masking, where the signal overlaps with the signal of interest, preventing the

receiver from detecting the signal. Sonic noise was the only noise stimuli that energetically overlapped with the male's signal. While the results from the sonic noise trials support energetic masking, the findings from the ultrasonic and substrate-borne trials suggest that it is not the sole factor responsible for the shift in female behavior. It is possible that another type of masking is also at play. Informational masking occurs when noise does not overlap with the signal, yet still interferes with the receiver's ability to extract meaningful information (Kidd et al. 2008). Despite the considerable focus on energetic masking, our knowledge of the impact of informational masking on animal behavior is limited. However, this dissertation presents evidence that suggests informational masking may be more significant than previously believed.

Informational masking caused by noise may hinder the female's ability to accurately assess relevant signals. This can lead to mistakes in mate selection, resulting in reduced reproductive success. Additionally, informational masking can lead to distraction and can increase predation risk by diverting an animal's attention away from important environmental cues (Chan and Giraldo-Perez 2010). Noise can have significant impacts on mate choice and reproduction in animals, especially those that rely heavily on sound for communication and mating behaviors. Disrupting the assessment of male signals can lead to mistakes that could ultimately decrease individual fitness and reproductive success (Naguib 2013; Candolin and Wong 2019). Changes in insect reproductive behavior could have bottom-up consequences.

The detection of substrate-borne vibrations is widespread in insects (Hill 2008). Nevertheless, this source is often overlooked as a significant source of noise, often due to human auditory bias and a lack of access to instruments to measure substrate-borne vibrations. This dissertation has identified substrate-borne noise as a significant influence on reproductive behavior whose effects are comparable to those of airborne noise. Substrate-borne vibrations are

detected via a different auditory pathway from airborne sounds and thus do not interfere with the detection of airborne signals. Insects rely on substrate-borne vibrations to collect information and interact with their environment. By overlooking substrate-borne vibrations, we overlook the complexities of insect auditory sensory systems and therefore do not have a comprehensive understanding of the impact of noise on insects and their ecosystems.

Insects are an understudied taxon when identifying the impacts of noise on behavior. Results from this dissertation and other studies indicate the impacts of noise on insects can be vast and complex (Classen-Rodríguez et al. 2021). Future research should address the multimodal nature of noise and how the auditory system integrates different acoustic modalities. While insects are easy to study in the lab, more studies need to be conducted to seek how noise affects insects under natural conditions. Only by studying them in their natural habitat can we start to understand the broad ecological impacts of noise on insects. Field studies are important to identify how different sounds interact with the environment and ultimately affect insect behavior. Field studies need to measure all potential components of noise, including both airborne and substrate-borne noise levels to better identify sources of noise on the landscape. The results of this dissertation support reporting a more detailed characterization of noise. Raboin and Elias (2019) have suggested reporting the noise source, characteristics of the noise, the signaling environment, signaling mechanism, and types of acoustic receivers of the animals of interest (Raboin and Elias 2019). Along with identifying the acoustic receivers, it is crucial to establish the sensitivities of an insect's auditory system to determine which frequencies or modalities can have the most significant impact on their behavior. Therefore, a more comprehensive understanding of the effects of noise on insects requires a multifaceted approach that considers both the sources and the sensitivity of the auditory system.

Understanding the impact of noise on insects can be broadly applied. It can support more informed conservation and management decisions, leading to establishing thresholds for acceptable noise levels caused by human activities and identifying and protecting critical habitats. Identifying how insects respond to noise can also be used to aid in population control of many pest species that rely on acoustic signals to reproduce. Sound plays a critical role in shaping the behavior and ecology of many species, including insects, across all ecosystems. Overall, understanding how insects use sound and how noise impacts insect behavior can give crucial insights into their behavior, evolution, and ecology.

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