HOW WILDLIFE RESPOND TO NATURAL NOISE

by

Dylan G.E. Gomes

A dissertation

submitted in partial fulfillment

of the requirements for the degree of

Doctor of Philosophy in Ecology, Evolution, and Behavior

Boise State University

May 2021

BOISE STATE UNIVERSITY GRADUATE COLLEGE

DEFENSE COMMITTEE AND FINAL READING APPROVALS

of the dissertation submitted by

Dylan G.E. Gomes

Dissertation Title: How Wildlife Respond to Natural Noise

Date of Final Oral Examination: 16 February 2021

The following individuals read and discussed the dissertation submitted by student Dylan G.E. Gomes, and they evaluated the student's presentation and response to questions during the final oral examination. They found that the student passed the final oral examination.

Jesse R. Barber, Ph.D.	Chair, Supervisory Committee
Jennifer S. Forbey, Ph.D.	Member, Supervisory Committee
Ian C. Robertson, Ph.D.	Member, Supervisory Committee
Clinton D. Francis, Ph.D.	Member, Supervisory Committee
Akito Y. Kawahara, Ph.D.	Member, Supervisory Committee

The final reading approval of the dissertation was granted by Jesse R. Barber, Ph.D., Chair of the Supervisory Committee. The dissertation was approved by the Graduate College.

DEDICATION

To the Rocky Mountains and the wonderful woman that I found there: may you both stay wild and free

ACKNOWLEDGMENTS

I specially thank Jesse R. Barber for being an amazing mentor, colleague, and friend who intimately contributed to all parts of this dissertation from funding and writing to fieldwork and analysis.

I thank my clam, Laura Grace Barta and Hunter J. Cole, for making a wonderful family and giving me personal support. Laura Grace Barta is the most amazing partner I could ever ask for and gives life its purpose. Hunter J. Cole is the most amazing fieldworker I could have ever asked for and inspires me to do better. I thank my twin sister, Justine Gomes, for always believing in me and being there when I need her; my brother, Brayden Gomes, for helping me realize the endless possibilities; my father, Tony Gomes, for teaching me to work hard and to not procrastinate; and my mother, Jennifer Gomes, for her unconditional love and her reading to me as a child.

I thank Hunter J. Cole, Laura Grace Barta, Cory A. Toth, Elizeth Cinto-Mejia, Krystie Miner, Charlotte Cumberworth, Christine Petersen, Amanda Emmel, Nicholas Carlson, Blair Boyt, Kate Sweet, Ben Sweet, Yael Lehnardt, William Prum, Will McDonald, and Connor Burgin for their help with logistics and/or fieldwork, Paula Cushing and the Denver Museum of Nature and Science for help with spider identification, Juliette Rubin for assistance with detection of bat calls in noise, Jake

Anderson for recording the infrasonic components of Figure 1.3, and Robert Hennefer for leading the pack mule team during our 2017 field deployment.

I thank Jennifer Forbey, Ian Robertson, Clinton Francis, and Akito Kawahara for serving on my committee and offering support and feedback on the various components of the dissertation work presented here.

I thank Brian and Kathleen Bean for allowing us access to their land, Lava Lake Ranch, where most of this research took place.

I thank the National Science Foundation (NSF), the Colorado Mountain Club Foundation, the American Arachnological Society, James A. Redfield and the Ecology, Evolution, and Behavior program at Boise State University for funding.

Lastly, I thank Laura Grace Barta, Hunter J. Cole, and Jesse R. Barber for many philosophical conversations about what we think knowledge, truth, and uncertainty are, issues within the sociological structure of scientific culture, and what scientific progress ought to look like.

ABSTRACT

Animal sensory systems have evolved in a natural din of noise since the evolution of sensory organs. Anthropogenic noise is a recent addition to the environment, which has had demonstrable, largely negative, effects on wildlife. Yet, we know relatively little about how animals respond to natural sources of noise, which can differ substantially in acoustic characteristics from human-caused noise. Here we review the noise literature and suggest an evolutionary approach for framing the study of novel, anthropogenic sources of noise. We also push for a more quantitative approach to acoustic ecology research.

To build a better foundation around the effects of natural noise on wildlife, we experimentally and continuously broadcast whitewater river noise across a landscape for three summers. Additionally, we use spectrally-altered river noise to explicitly test the effects of masking as a mechanism driving patterns. We then monitored bird, bat, and arthropod abundance and activity and assessed predator-prey relationships with bird and bat foraging assays and by counting prey in spider webs.

Birds and bats largely avoided high sound levels in noisy environments. Bats also avoided acoustic environments dominated by high frequency noise while birds avoided noise that overlapped with their song, the latter trend suggesting that communication is impaired. Yet, when sound levels were high overlapping noise was not any more disruptive than non-overlapping noise, which suggests that intense noise interferes with more than communication. Avoidance of noise that overlapped in frequency with song was stronger for low-frequency singers. Bats that employ higher frequency echolocation were more likely to avoid high sound level noise; we explore potential explanations for this pattern. Most arthropod Orders responded to noise, yet the directions of effects were not consistent across taxa. Some arthropods increased in abundance in high sound level areas – perhaps in response to the absence of bird and bat predators. Reinforcing this possibility, visually foraging birds and passively listening bats decreased foraging effort beyond what was expected based on declines in abundance and activity. Orb-weaving spiders increased dramatically in high sound level areas, which could be due to a release from predation, an increase in prey capture, or direct attraction to high sound level river noise.

Overall, we demonstrated significant changes to many vertebrate and invertebrate taxa during playback of whitewater river noise. We were able to parse out the effects of sound pressure level and background frequency on these individual taxa and predator-prey behaviors. Our results reveal that animals have likely long been affected by particular characteristics of noise, which may help explain contemporary responses to anthropogenic noise. As the spatial and temporal footprint of anthropogenic noise is orders of magnitude greater than intense natural acoustic environments, the insights provided by our data increase the importance of mitigating noise pollution impacts on animals and their habitats. It is clear that natural noise has the power to alter animal abundances and behavior in a way that likely reverberates through entire communities and food webs. Future work should focus on strengthening the relationships between these potential predators and prey and highlight how the structure of the system changes under such noise treatments.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF ABBREVIATIONS

SPL	Sound pressure level
dB	decibels
dBA	A-weighted decibels; also written as dB(A)
kHz / Hz	kilohertz / hertz

INTRODUCTION

Animal sensory systems have evolved in natural noise since the evolution of sensory organs. Anthropogenic noise is a recent addition to the environment, which has had demonstrable, largely negative, effects on wildlife. Yet, we know relatively little about how animals respond to natural sources of noise. It is likely, however, that a more nuanced understanding of how animals deal with natural sources of noise (and over evolutionary timescales) will enable us to be better poised to understand how animals will respond to novel sources of anthropogenic noise.

In the first chapter we review the noise literature and suggest an evolutionary approach for understanding natural noise and framing the study of novel, anthropogenic sources of noise. We also push for a more quantitative approach to acoustic ecology research, such as measuring sound pressure levels and frequency components of acoustic environments (rather than categorizing; *e.g.* anthropogenic or natural), which we then demonstrate in later chapters.

To build a better foundation around the effects of natural noise on wildlife, we experimentally and continuously broadcasted whitewater river noise across a landscape for three summers and monitored bird, bat, insect and spider abundance, activity, and behavior in Chapters 2 – 4. The second chapter focuses on the effects of this whitewater river noise experiment on bird and bat abundance and activity, respectively, and foraging behavior of both groups. The third chapter focuses on the effects of this same experiment on orb-weaving spider abundance, behavior, and body condition. The fourth chapter concentrates on the effects that experimental noise plays on arthropod abundance more broadly.

We set out in the Pioneer Mountains of Idaho with nearly four tons of gear to understand how natural noise shapes the demographics and behavior of these taxa. Over the three years (2017-2019) that the experiment took place, we relied on our own backs to both deploy and take down all of this gear each year before blizzards, wind-blown trees, and avalanches had the opportunity to destroy it. The one exception to this was during our 2017 deployment of the Fish Creek drainage. Flooding snowmelt had washed-out the Fish Creek road, so we employed a packer and a team of mules to help get our gear to sites within this drainage. We carried solar systems, batteries, speakers, recording units, and miscellaneous other equipment into these mountains to broadcast river noise 24-hours a day, seven days a week for three months each year.

We generally deployed the gear in the late spring (May), often during periods of intense snowmelt, but sometimes during snowfall – before our study taxa were present or active in the area. Similarly, we packed out our gear in late July after most songbirds had left on their fall migration, and after most bat activity in the area. By broadcasting noise in such a way, most habitat selection decisions (i.e., where to take up residence) likely occurred during noise playback. This design allowed our experiment to closely follow what animals might experience when they encounter an actual whitewater river during migration or spring emergence. The alternative of broadcasting noise later in the year (e.g., when birds have established breeding territories) is that we are then asking questions about what components of river noise make animals leave when they’ve already made a habitat selection decision – which is a far less likely scenario in the real world (although might be relevant for areas just below a dam spillway).

Why did we use an experimental approach? Instead, why not simply monitor different streams with varying degrees of noise? Streams that are considered to have high sound levels (i.e., are interpreted as loud by humans) are also likely larger and run through steeper terrain. This increased streamflow and steepness might make soils, and thus, vegetation quite different – all confounding variables that are difficult to deal with logistically and statistically. The power of the experiment is that we turned relatively slow-moving streams into raging whitewater rapids, without any of these confounds – we simply altered the acoustic environment to mimic fast-flowing water. Importantly, this experimental design also allowed us to manipulate an essential component of those acoustic environments – background frequency.

Using spectrally-altered river noise (as well as unaltered river noise), we were able to explicitly test the effects of frequency on the demographics and behavior of our study taxa. Specifically, we were able to test masking as an underlying mechanism of noise avoidance. The prevailing hypothesis of why birds and bats avoid noisy places is that important signals (bird song) and cues (bat prey) are difficult to hear. This hypothesis relies on a term called masking, whereby noise that overlaps in frequency with a signal (or cue) of interest interferes with the auditory perception of such a signal. Few have begun to test questions like these in the lab. Researchers can broadcast noise that either does or does not overlap with signals or cues and ask how a focal animal’s ability to hear or respond to these signals or cues might change. If only overlapping noise treatments interfere with the behavior of interest for the species of interest, the researcher might conclude that masking indeed appears to be the mechanism at play. The novelty of our experiment is that we did this across a landscape and were able to simultaneously ask this question about many individual species at once.

We also begin to assess the indirect effects of noise. Noise, like any perturbation, likely affects many taxa at once. It can disturb predator-prey relationships (which we assessed here), which can alter food webs and ultimately shape entire communities of organisms. The bats, birds, insects and spiders within our system in the Pioneer Mountains of Idaho were studied extensively for three years by a large team of researchers. The data presented here build the foundation for future analyses that link connections across taxa and trophic levels to build a deeper understanding of how wildlife respond to natural noise.

CHAPTER ONE: USING PAST TO UNDERSTAND PRESENT: COPING WITH NATURAL AND ANTHROPOGENIC NOISE

The final version of this article has undergone full peer review and has been accepted for publication. Please refer to the Version of Record. Please see: https://doi.org/10.1093/biosci/biaa161 (Gomes, Francis & Barber, 2021)

Introduction

In less than two decades, the literature on the effects of anthropogenic noise on wildlife has transformed from a handful of studies to a vast body of knowledge (Shannon et al., 2016). Traffic (e.g. automobile, shipping, airplane), energy extraction activities, and marine sonar are all modern, and ‘unnatural’, sources of noise that are drastically altering acoustic environments on a global scale (Buxton et al., 2017). Researchers have nearly unanimously shown negative impacts of noise on animal behavior, such as communication (reviewed in Brumm 2013) and foraging (Purser & Radford, 2011; Siemers & Schaub, 2011; Wale, Simpson & Radford, 2013a), and have demonstrated changes in risk assessment (Chan et al. 2010, Morris-Drake et al. 2017), oxygen consumption (Wale, Simpson & Radford, 2013b), stress levels (reviewed in Kight and Swaddle 2011), olfactory response (Morris-Drake, Kern & Radford, 2016), sleep (Connelly et al., 2020), reproductive success (Halfwerk, Holleman & Slabbekoorn, 2011), and survival (Simpson et al., 2016). More limited research has gone beyond the individual level and has shown that local abundance (e.g., Cinto Mejia et al. 2019), community structure (e.g., Francis et al. 2011), and ecological services, such as seed dispersal and pollination (Francis et al., 2012a) can be shaped by anthropogenic noise.

The impacts of natural sources of noise, on the other hand, have been studied intensely in animal behavior research only, with a near-exclusive focus on animal communication (Brumm, 2013; Wiley, 2015) and echolocation (Corcoran & Moss, 2017). Natural noise has, however, received commensurately little attention in the ecological and evolutionary literature as an ecological niche axis and a force that can shape animal populations or communities. Yet, some sources of natural noise are as pervasive as anthropogenic noise. Snapping shrimp noise, for example, dominates some marine acoustic environments (Hildebrand, 2009). Recent work has shown that abiotic natural noise can detrimentally affect communication and foraging to a similar degree as anthropogenic noise. Crashing surf noise negatively affects song performance in sparrows comparable to effects from anthropogenic noise (Davidson et al., 2017). Foraging bats experience larger deficits hunting in noise generated from wind blowing through rushes, than they experience when foraging in roadway traffic noise (Schaub, Ostwald & Siemers, 2008). However, natural acoustic environments not only disrupt the transmission of information, but can itself be used as a source of information about habitat quality (Zhao et al., 2017), approaching predators (Haff and Magrath 2010), or the location of prey (Goerlitz, Greif & Siemers, 2008). Since the origins of hearing organs animals have likely been under strong selective pressures to pay attention to information-based habitat cues and to avoid the negative consequences of noise (Barber, Crooks & Fristrup, 2010). This likely makes the acoustic environment an essential niche axis that shapes animal communities. Yet, perhaps because of the perceptual biases of human researchers (Van Dyck, 2012), this niche axis is underappreciated in ecology – an effect that is exacerbated within the infrasonic and ultrasonic ranges of acoustic ecology, which are particularly unexplored. This is problematic given that other taxa do not share our perceptual worldview – or *umwelt* (von Uexküll, 1909).

Swaddle et al. (2015) outlined a framework for understanding rapid evolution from novel introductions of anthropogenic noise (and light). Their framework highlights differences in how animals respond to anthropogenic noise via immediate behavioral response to noise, developmental plasticity from maturing in noise, and evolutionary changes to populations. Yet, our understanding of evolutionary responses to anthropogenic noise is likely to be incomplete without knowing how animals have evolved in response to natural noise over much longer periods of time. Although it is possible that some animals have and are evolving strategies to respond to anthropogenic noise *de novo*, many already have pre-existing behavioral flexibility, developmental plasticity, or potentially useful coping traits, due to a long evolutionary history within a naturally noisy world, upon which contemporary selection is now acting (Figure 1.1).

We argue that natural noise is a niche axis that can drastically alter animal behavior and shape communities, and that an emphasis on studying the effects on populations is needed. We hypothesize that this niche axis has led to the evolution of mechanisms to maintain hearing tasks in a naturally noisy world, some of which could be co-opted to deal with anthropogenic noise. Many behaviors other than communication are affected by noise, yet the state of the literature is severely biased in this direction (Jerem & Mathews, 2020). Thus we do tend to focus on examples taken from this communication-heavy literature, but emphasize the future need for a broader understanding of noise impacts. We argue that a deeper understanding of how animals use and deal with natural sources of noise will give us insights into how animals may respond to the further expansion of anthropogenic noise exposure (Buxton et al., 2017). The response an animal has to noise likely depends on the acoustic characteristics of that noise source, features that are independent of whether that source is anthropogenic or natural. Thus, we need to quantify acoustic environments, rather than broadly categorize them into anthropogenic or not.

Why pay attention? – the acoustic environment as an under-appreciated niche axis

The many abiotic and biotic sounds present in an environment constitute a collective "soundscape," or acoustic environment, that holds an abundance of information, which can be extracted by listening animals (Pijanowski et al., 2011). This sensory axis is of critical importance for survival and reproduction (Bradbury and Vehrencamp, 1998) and can be used as information in habitat selection decisions (Dominoni et al., 2020). The sounds of chorusing birds (Ward & Schlossberg, 2004; Nocera, Forbes & Giraldeau, 2005) and calling frogs (Buxton, Ward & Sperry, 2015) may act as cues of habitat quality for conspecific or heterospecific animals that require similar habitat or resources. Analogously, abiotic noise may encode information about habitat quality. Torrent frog females prefer males that call near high-intensity waterfall noise (Zhao et al., 2017).

The difficulty of extracting information from an acoustic environment increases when background sound levels rise (Brumm, 2013). Chorusing frogs, insects, and birds each have a harder time hearing each other over the noise from their own, loud aggregations (Aubin and Jouventin, 1998; Gerhardt and Huber, 2002; Bee and Micheyl, 2008). Wind-generated noise makes it more difficult for cetaceans and birds to communicate, and for bats to hear the sounds of their prey, which can lead to avoidance of noisy areas (Lengagne et al., 1999; Schaub et al., 2008; Dunlop et al., 2010).

However, local avoidance and attraction to noise do not necessarily translate to population-level effects. Thus, noise is not necessarily beneficial simply because a species is more commonly found in those noisy areas. Hennigar et al. (2019), for example, found that some songbirds are attracted to traffic noise during the breeding season, although other research shows clear negative consequences for bird populations near roads (Reijnen, Foppen & Meeuwsen, 1996; Benítez-López, Alkemade & Verweij, 2010). If animals have evolved to be attracted to habitat cues (such as waterfall noise, e.g. Zhao et al., 2017), they may also be attracted by similar anthropogenic noise that acts as a sensory trap (West-Eberhard, 1984; Christy, 1995; Dominoni et al., 2020). Similarly, animals that avoid noise do not inevitably suffer negative consequences of exposure. It is possible that they find other, less degraded, habitat. However as anthropogenic noise expands, animals will likely find fewer quiet refuges. Additionally, the absence of noise avoidance is not proof of a lack of biological impact. Some birds fail to respond to noise in nest placement, yet they experience higher rates of hatch failure and increased stress hormone dysregulation (Kleist et al., 2018), whereas other birds that stay in noisy places experience reduced body condition (Ware et al., 2015). Thus, we need to be careful when drawing conclusions about the effects of noise. In future research we should strive to understand noise impacts on populations, which are the unit of conservation concern, and are currently under-represented in noise studies (Jerem & Mathews, 2020).

How animals deal with natural noise

There are numerous examples of response mechanisms that animals have evolved for communicating in a noisy world (reviewed in Brumm and Slabbekoorn, 2005; Brumm and Naguib, 2009; Brumm, 2013). Some crickets that deal with higher levels of competition for acoustic niche space have more finely-tuned auditory neuronal filters, which filter communication calls from noise (Schmidt, Riede & Römer, 2011). The extent to which other aspects of hearing have been targets of selection from variation in natural sounds is an avenue of research ripe for exploration. For instance, does population-level variation in exposure to naturally noisy backgrounds correlate with an animal's ability to detect a signal or cue in noise (i.e. critical ratios; see Dooling and Popper, 2007 for details). Such hearing adaptations might facilitate living with novel sources of human-caused noise in a manner similar to pre-adaptation of birds with high-pitched vocalizations to anthropogenic acoustic environments (e.g., Rheindt, 2003; Hu and Cardoso, 2009; Cardoso et al., 2018, 2020).

Many behaviors that likely evolved in response to hearing in naturally noisy conditions might help animals deal with anthropogenic noise (see Table 1.1). However, behavioral responses can be neutral, negative, or positive in relation to fitness (Read, Jones & Radford, 2014). Most research in the field has stopped after finding a behavioral response, thus a crucial next step is determining whether these behavioral changes actually impact survival or fitness (Francis & Barber, 2013). If populations that evolved particular traits to deal with natural noise are able to innately deal with anthropogenic noise, those traits, or the natural acoustic context in which they live, might inform, or help us predict, other animals' responses to anthropogenic noise (i.e. guild-, trait-, habitat-specific responses). However, first, we must understand the differences between anthropogenic and natural sources.

What is the difference between natural and anthropogenic noise?

Natural sources of noise can alter animal behavior to a similar degree as anthropogenic sources (see Introduction), yet empirically testing the difference in responses between categorical 'natural' and 'anthropogenic' sources is often not a genuine comparison. Any distinction between them is muddied if we consider how humans have altered the geographical and temporal patterns of natural noise.

The damming of a river turns the rushing rapids upstream of the dam into a slow-moving, quiet river, and then a placid lake. While just below the dam the noise from the spillway can be intense during periods of high flow. This anthropogenic change to a natural acoustic environment can also vary in daily or seasonal temporal cycles, as humans alter the flow at different times of the year for agricultural irrigation (Zeng and Cai, 2014) and at different times of day to optimize delivery of energy from hydro-electric dams to meet demand (Cushman, 1985; Kern et al., 2011). Even more subtle changes are clearly human-driven. Changes to climate are leading to altered snowfall (Verzano and Menzel, 2009) and snowmelt rates (IPCC, 2007) - and consequently, changes in streamflow (Alcamo et al., 2007; Schneider et al., 2013) and, thus, background sound levels.

Similarly, the contribution of animal vocalizations to the acoustic environment are expected to change as phenological patterns shift the timing of migration and reproductive behavior, and as animal distributions expand and contract due to human-induced climate change (Sueur, Krause & Farina, 2019). Recent reports have highlighted large declines in insects (Montgomery et al., 2020; van Klink et al., 2020) and birds (Rosenberg et al., 2019), many of which vocalize. Thus, natural noise from biotic choruses may be declining due to human activity, yet it is not clear what downstream consequences this anthropogenic "silencing" will lead to. Alternatively, acoustic environments might become dominated by other species, as introduced and invasive species compete for acoustic niche space (Tennessen et al., 2016; Medeiros et al., 2017).

These altered sources of noise are arguably more 'natural' than automobile traffic noise, yet they are clearly not free from human influence. Boundaries begin to fall apart for terms that have been defined in the soundscape literature to describe noise sources as either being generated by humans (anthrophony), geological processes (geophony), or non-human animals (biophony, Pijanowski et al., 2011). Considering humans can influence all three of these terms on spatial and temporal scales, the distinction between them can become quite difficult to logistically, or theoretically (as above) distinguish. A more quantitative approach is necessary.

Quantifying the effects of noise characteristics

There are three main characteristics of noise – frequency (perceived as pitch), amplitude (perceived as loudness), and temporal patterns, which can be used to describe any acoustic environment regardless of source (see **Appendix 1** for guide to quantification). Quantifying noise can help us better tease apart actual effects of noise exposure on wildlife – as opposed to broad categorization (see Pater et al., 2009; Gill et al., 2015). That is, it is likely the characteristics (frequency, amplitude, and temporal patterns) of noise that animals are responding to, not the source itself. If an animal evolved to deal with intense whitewater rapids, that same animal should be able to deal with anthropogenic noise of similar characteristics as whitewater rapids. Thus, future research should focus on questions such as which noise frequencies make hearing tasks difficult for various taxa, how intense must a source be before we see negative consequences to populations, what temporal patterns of noise are the most (and least) disruptive to wildlife, and how much animals' abilities to hear in noise varies within and among populations and species that inhabit environments with very different noise characteristics (Figure 1.2). This latter question can be tackled with a better understanding of critical ratios. Critical ratios are a measure of the detectability of a tone, calculated as the difference (in sound level) of the background sound level and the just detectable tone. Understanding critical ratios for biologically relevant signals, such as alarm calls, predator sounds, or mate attraction songs, which have very different spectral profiles than artificial tones, is an important step towards ecological relevancy. Quantifying noise effects will allow more effective mitigation of noise and point towards species-specific targets of least harmful noise characteristics (*sensu* Dominoni et al., 2020).

To better understand individual characteristics of noise on wildlife, researchers can alter the amplitude (Siemers & Schaub, 2011; Bunkley & Barber, 2015), frequency (Gomes et al., 2016), or temporal patterns (Neo et al., 2014; Bee & Vélez, 2018) of noise playback experiments. Some researchers, for example, have used white noise at various intensity levels to measure the effects of amplitude alone, while others use pure tones to separate the effect of frequency (Table 1.1). While the use of altered noise profiles can be quite artificial, it has served as a useful way to tease apart precisely which characteristics of noise relate to the behavioral shift of interest. We suggest that researchers using noise with artificial characteristics in experiments also try to include ecologically-relevant noise, both natural and anthropogenic, for direct comparison, placing artificial stimuli in context.

Responding to frequency:

Not all noise equally disrupts hearing tasks because animal hearing is sensitive to different frequencies. That is, noise that overlaps in frequency (i.e. spectral overlap) makes hearing a signal or cue of interest more difficult (Lohr, Wright & Dooling, 2003; Dooling & Popper, 2007). For example, low frequency noise that overlaps with prey sounds decreases foraging efficiency of frog-eating bats, while higher, non-overlapping frequencies do not (Gomes et al., 2016).

Many have proposed that communicating animals can avoid being masked by shifting the frequency of their vocalizations such that they do not overlap with background noise (Patricelli & Blickley, 2006; Roca et al., 2016). Slabbekoorn and Peet (2003) argue, for example, that great tits (*Parus major*) have songs of higher minimum frequencies in urban environments (relative to forest birds) to avoid low-frequency urban noise. Frequency shifts due to anthropogenic noise could be due to real-time behaviorally flexibility (reviewed in Brumm and Zollinger, 2013), altering song frequency during learning or development (Rabin & Greene, 2002; Moseley et al., 2018), or rapid evolution at the population level (Luther and Baptista, 2009; Swaddle et al., 2015). Recent evidence suggests that population level changes might be more likely (Zollinger et al., 2017), but most work to date has focused on individuals.

Including the seminal paper by Slabbekoorn and Peet (2003), many of the real-time minimum frequency shifts reported are exaggerated by measurement errors

(Zollinger et al., 2012; Brumm et al., 2017), thus future researchers should avoid manually measuring minimum frequency within a spectrogram. Additionally, few have actually tested whether or not these frequency shifts are biologically relevant, and those that have tested relevancy suggest that frequency shifts are actually not beneficial (Luther & Magnotti, 2014; Luther, Phillips & Derryberry, 2016). Luther and Magnotti (2014), for example, showed that territorial males actually respond less to songs with upward shifted minimum frequencies, making this behavioral change appear maladaptive. Nevertheless, shifting frequencies to avoid spectral overlap should, in theory, help animals avoid the effects of masking (Lohr et al., 2003; Parris and McCarthy, 2013; see Dooling and Popper, 2007; Barber et al., 2010 for an overview of masking). While the effect can be quite small (Nemeth & Brumm, 2010), a change in minimum frequency affects bandwidth, which can substantially impact vocal performance (Derryberry et al., 2020). Thus, we urge researchers to ask the question of whether or not frequency shifts incur any communication, and thus reproductive, benefit and actually enable populations to persist in unnaturally noisy environments, rather than continuing to lengthen a list of species that behaviorally shift communication frequencies in noise.

Avoiding frequency overlap in acoustic space is not novel, but rather appears to be an ancient strategy. In undisturbed natural systems, vocalizations of sympatric species tend to not spectrally overlap with abiotic noise sources (Narins et al., 2004; Brumm & Slabbekoorn, 2005; Feng et al., 2006). Echolocating bats shift their sonar frequency perhaps to avoid overlap with conspecifics (termed jamming avoidance response; Ulanovsky et al., 2004; Gillam et al., 2007; Bates et al., 2008), although recent evidence suggests that this behavior is not widespread in the wild (Cvikel et al., 2015; Götze et al.,

2016) and modeling efforts indicate that it lacks efficacy (Mazar & Yovel, 2020). These patterns are often presumed to be the result of an evolutionary divergence in communication frequency driven by masking avoidance (Nelson and Marler, 1990; Brumm and Naguib, 2009). In contrast, Both and Grant (2012) played back a novel frog call to tree frogs, which immediately shifted their calls upwards in frequency, presumably to avoid spectral overlap. Thus, understanding which traits are behaviorally flexible or developmentally plastic, rather than requiring many generations of evolution, will better inform us as to which species can more quickly respond to anthropogenic noise exposure.

Is it possible that animals that have evolved in environments that are more variable, including acoustic variability, could have more flexibility or plasticity to deal with novel anthropogenic sources of noise? Evidence hinting at this possibility comes from a small comparative study where intra-individual variation in song was positively correlated with environmental seasonality (Medina and Francis, 2012). Seasonal sources of noise, such as swollen rivers from snowmelt or acoustically-active breeding animals provide intuitive links between seasonality and variability in the sound frequencies of acoustic environments, yet more work is needed to quantify whether such links are common.

Responding to amplitude:

Background sound levels are the most commonly measured metric of acoustic environments (see supplement). Likely for good reason, increasing sound levels from both cicada and river noise leads to increased ground squirrel vigilance, and some parasitoid flies have trouble localizing calling host crickets with increased levels of both traffic and crashing surf noise (Phillips et al., 2019). Although these and other studies have begun to identify analogous behavioral response to natural and human-made noise, whether natural sounds causes similar patterns of avoidance remains a key question for future research.

The Lombard effect, whereby animals vocalize more intensely in noisy environments (Lombard, 1911), is a widespread response that animals use to increase signal-to-noise ratios in background noise during communication and foraging via echolocation (reviewed in Brumm and Zollinger, 2011; Zollinger and Brumm, 2011; Luo et al., 2018). Recent evidence suggests that the Lombard effect evolved some 450 MYA (Luo, Hage & Moss, 2018) in vertebrate ancestors (Figure 1.1). Understanding ancestral states of such behaviors is key to predicting how more of the tree of life will deal with anthropogenic noise stressors. Yet, it is important to note that the Lombard effect is not always a solution as there is a physical limit to the signal intensity animals can produce, and some taxa may already vocalize at this limit (Brumm & Zollinger, 2011, 2017; Schwartz & Bee, 2013). Once background noise levels exceed an individual's limit, the Lombard effect is no longer a useful strategy to deal with noise. Further, there are costs to calling louder, such as increased energy use (Holt et al., 2015; but see Oberweger and Goller, 2001; Zollinger et al., 2011), and attraction of predators (Gomes et al., 2017), which might outweigh any signal-to-noise ratio benefit that an organism receives.

Responding to temporal patterning:

If noise is not consistent over time, animals might be able to benefit by shifting timing of behavior. In other words, animals may avoid intense noise by being active during periods of the day that are less busy. Birds shift chorus timing to avoid temporal overlap with airplane noise (Gil et al., 2014) and urban noise (Nordt and Klenke, 2013).

Yet, these strategies are not new. In naturally noisy choruses, birds produce signals in a way that reduces the timing of acoustic overlap (Cody & Brown, 1969; Ficken, Ficken & Hailman, 1974; Brumm, 2006; Luther, 2008). Intermittent noise can provide gaps in background noise over much shorter timescales. Animals can listen within these windows of lower-amplitude noise, often referred to as ‘gap-listening’ or ‘dip-listening’ (Vélez and Bee, 2011). That is, if background noise energy is reduced for long enough, animals can discriminate signals amongst the noise. However, non-consistent noise is not always beneficial.

Noise that is less predictable, or regular, is likely more distracting (Glass & Singer, 1972; Matthews et al., 1980; Kjellberg et al., 1996), and noise that is intermittent may be more likely to be stressful than continuous noise (Neo et al., 2014; Debusschere et al., 2016). Greater sage-grouse more strongly avoid intermittent, rather than continuous, roadway noise (Blickley, Blackwood & Patricelli, 2012). Fish that exhibit a stress-induced change in swimming depth take longer to recover to a normal depth in intermittent (compared to continuous) noise, which the authors suggest is due to the difficulty of habituating to intermittent noise (Neo et al., 2014). The onset and the duration of noise exposure also play a role in disturbance. Crab oxygen consumption increases and fish are startled by brief exposures to noise, but neither show increased responses to prolonged noise exposure (Purser & Radford, 2011; Wale, Simpson & Radford, 2013b). Squid showed behavioral habituation to repeated noise exposure over a five-day period (Mooney et al., 2016), yet over multiple months, prairie dogs showed no signs of habituation to roadway traffic noise in their activity levels (Shannon et al., 2014).

Based on studies focused on anthropogenic sources, it is not clear if intermittent or continuous noise is more detrimental to wildlife. Some animals may be able to communicate in intermittent gaps (see above), but others might be less likely to habituate to such noise profiles. To further complicate the matter, noise can have temporally-modulated frequencies or amplitudes that make hearing tasks *more* difficult if these modulations are similar to a signal of interest - termed modulation masking (Vélez et al., 2012). That is, the background noise in a busy pub is more likely to make human speech indiscernible because that noise is amplitude-modulated more similar to the signal of interest (because it is human speech) than other sources of noise that contain the same frequencies and are just as loud overall (Bacon & Grantham, 1989; Kwon & Turner, 2001). Thus, oddly enough, gaps in noise can make communication either more or less difficult depending on the overall temporal structure of the acoustic environment. While it would be useful to be able to predict what amplitude-modulation rate of noise would help (dip-listening) or hinder (modulation masking), existing evidence suggests there are no concrete rules. For instance, grey tree frogs (*Hyla chrysoscelis*) can dip-listen while green tree frogs (*Hyla cinerea*) cannot (Vélez and Bee, 2011; Vélez et al., 2012). These *Hyla* species are very closely related but incapable of the same strategy. To speculate, it is possible that *H. chrysoscelis* evolved the ability to dip listen because they have historically dealt with more acoustic niche competition. If heterospecifics call at similar frequencies, there may be significant pressure to alter temporal structure of calling or listening effort. In this case, understanding how their recent past has allowed them to diverge in this way will be crucial for trying to predict anthropogenic noise ‘survivors.’

Infrasound and ultrasound

Domesticated rock pigeons can detect infrasound (Kreithen and Quine, 1979), and possibly use these cues for navigation (Quine, 1982; Hagstrum, 2000). Concave-eared torrent frogs produce calls that contain harmonics with considerable energy in the ultrasonic range, above much of the energy of white-water rivers (Narins et al., 2004; Feng et al., 2006). While many taxa produce ultrasonic harmonics as a byproduct of vocalization, electrophysiological recordings of these frogs confirm their ability to hear these frequencies, and playback studies confirm behavioral responses to such frequencies (Feng et al., 2006).

Animals as small as crickets and as large as elephants use infrasound in communication (Kämper and Dambach, 1979; Garstang, 2004) while ultrasound is used in both communication or echolocation of a variety of taxa (Jones, 2005; Sales, 2012) such as anurans (as mentioned above; (Feng et al., 2006), rodents (Sewell, 1970; Nyby & Whitney, 1978; Wilson & Hare, 2004), moths (Spangler, Greenfield & Takessian, 1984; Jang & Greenfield, 1996; Nakano et al., 2008), katydids (Bailey & Gwynne, 1988; Morris et al., 1994), shrews (Buchler, 1976; Tomasi, 1979), bats (Griffin, Webster & Michael, 1960), cetaceans (Norris et al., 1961; Evans, 1973), canids, and felids (Heffner & Heffner, 2008). Yet, both infrasonic and ultrasonic frequencies often go unmeasured in acoustic ecology or ‘soundscape’ research. This is perhaps due to human perceptual bias (Van Dyck, 2012) along with constraints in recording and production technology.

Importantly, both anthropogenic and natural sources can contain considerable infrasonic and ultrasonic energy (Figure 1.3). Many natural sources of noise such as weather patterns or storms, volcanoes, and ocean wave activity can generate infrasound

(Arrowsmith and Hedlin, 2005; Johnson and Ripepe, 2011), and rain noise generates ultrasonic energy that can disrupt timing of animal activity (Geipel et al., 2019). It is still largely unclear what effects these components of the acoustic environment (from both anthropogenic and natural sources) have on wildlife.

Conclusions

Natural noise is an under-appreciated niche axis that has the power to alter animal behavior, change distributions, filter communities and, potentially, shape population trajectories. Yet the question '*how does noise affect animal populations?'* remains unexplored. Past selection from natural sources is likely responsible for the growing list of behavioral responses to anthropogenic noise. That is, animals have evolved a diversity of ways of dealing with natural noise, with some taxa likely using multiple strategies at once. *Are animals that evolved in naturally noisy situations pre-adapted to deal with anthropogenic noise?* We still lack a deeper understanding of how phylogeny might constrain, or give opportunity for, co-opting these strategies for modern selective pressures. Thus more information about both shared evolutionary history and more recent selective pressures are needed to understand how noise shapes extant behavioral responses. *Do we see population-level variation in noise exposure which might be linked to behavioral coping mechanisms?* This knowledge should provide testable hypotheses about interspecific variation in responses to changing acoustic conditions with expanding urbanization, as responses are agnostic to the source of sound provided that it has similar frequency, amplitude and temporal characteristics. Thus, if we are to understand how animals have evolved in response to noise, we must focus on quantification, not categorization, of acoustic environments.

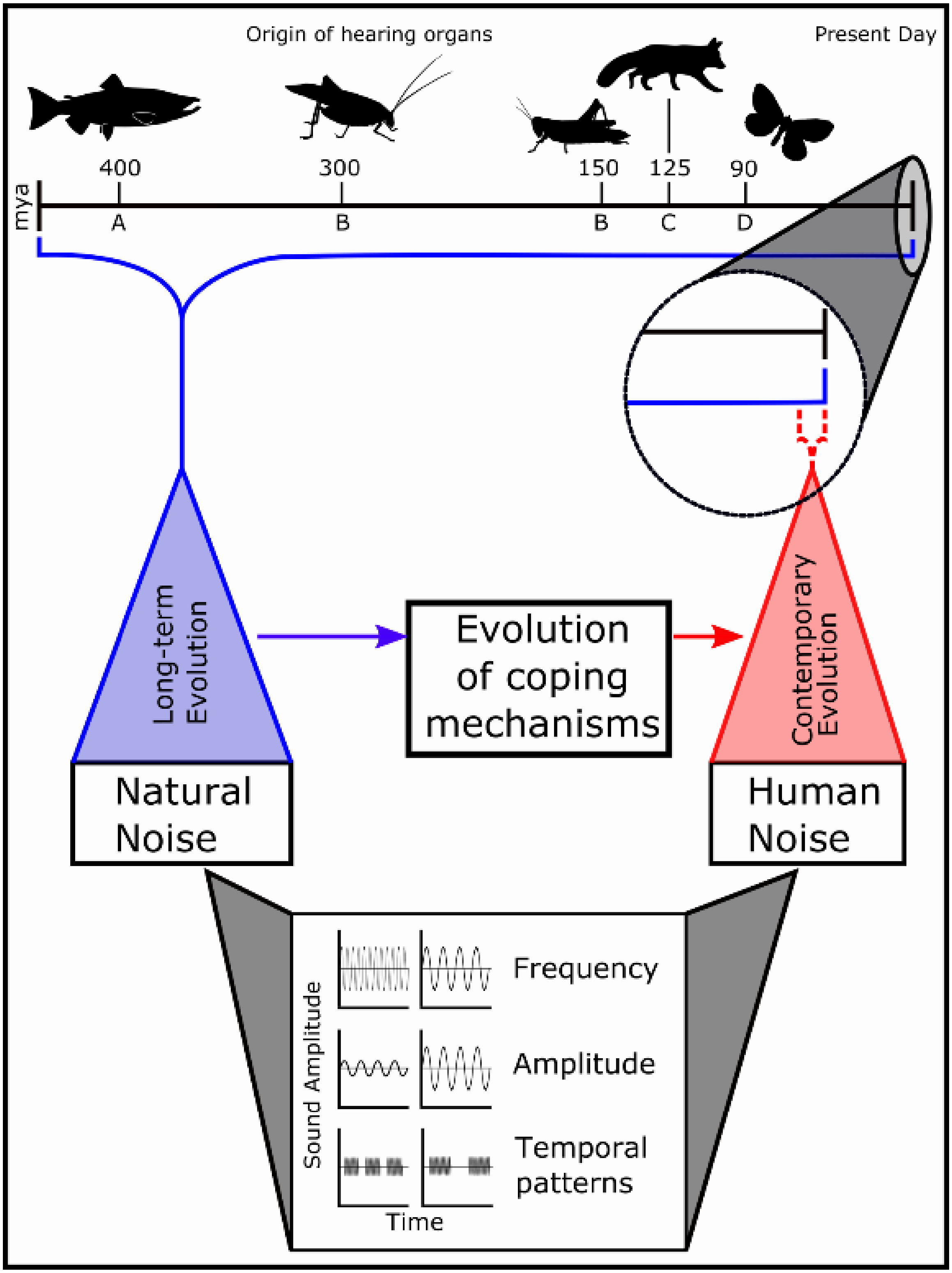


Figure 1.1 How evolution in naturally noisy situations can lead to the co-option of coping mechanisms in novel anthropogenic acoustic environments.

Natural sources of noise have been around since the origin of hearing organs (respective to any individual taxa, see silhouettes and references below), while anthropogenic noise is a young phenomenon. Both natural and anthropogenic sources share characteristics that can be quantified (frequency, amplitude, and temporal patterns). This quantification (rather than categorization of ‘anthropogenic’ or ‘not’) is important for understanding the effects of noise on wildlife. References for phylogenetic timing of hearing organs: A = vertebrate inner ear (Popper, Platt & Edds, 1992), B = Orthopteran ears (Song et al., 2020), C = modern mammalian cochlea (Manley, 2012), D = Lepidopteran ears (Kawahara et al., 2019).

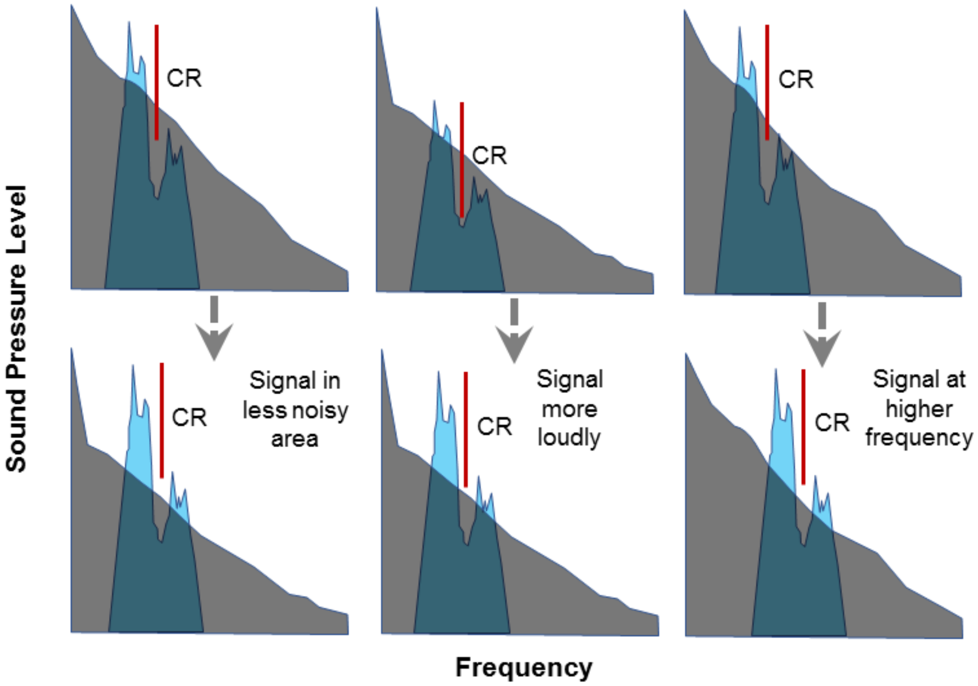


Figure 1.2 Power spectra of a signal and background acoustic environment.

The red line indicates the critical ratio, defined as the signal to noise ratio necessary for a pure tone to be detectable above background noise, specifically the energy per hertz in the background noise. We diagram the signal (blue) and noise (grey) as power spectra, which indicate sound pressure level at each frequency. In the top row, the critical ratio is overlapping with noise, and thus the signal cannot be detected. In the bottom row, the signaler has escaped the masking effects of noise by either signaling in a less noisy area (indicated by a sound pressure level decrease in the grey power spectra), signaling with greater intensity (indicated by a sound pressure level increase in the blue power spectra), or signaling at a higher frequency (indicated by an upward shift in frequency in the blue power spectra). Critical ratios for biologically relevant sounds deserve further attention (see main text).

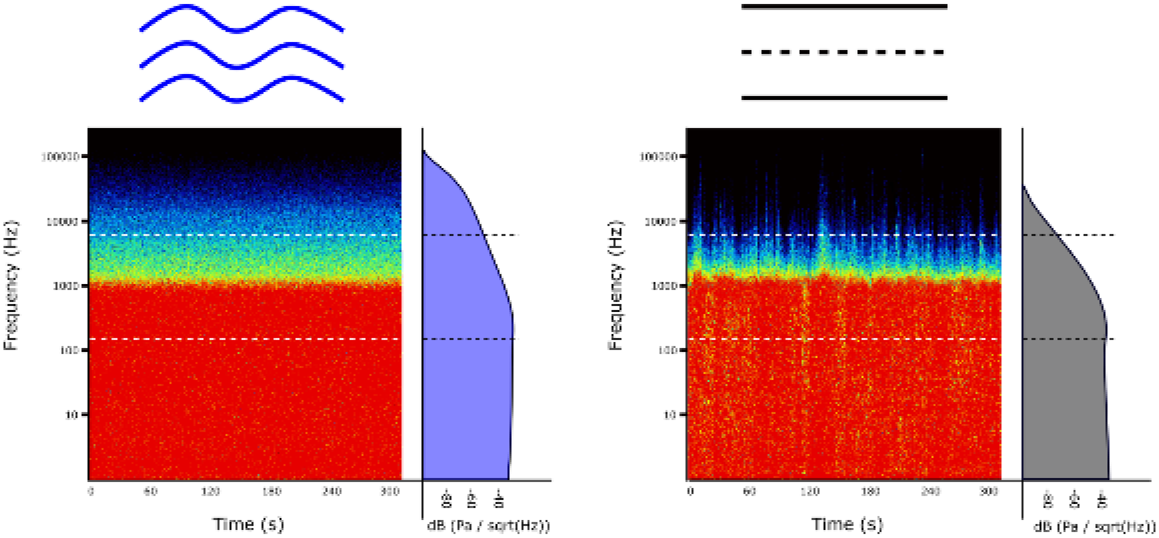


Figure 1.3 Spectrogram and power spectra of river and road

Spectrograms are 5-minute recordings of rivers (left) and roads (right), created with 3 different sets of microphones. Dotted lines indicate boundaries in spectrograms and power spectra where data originate from infrasonic (custom build; J. Anderson), sonic (NT1-A; RØDE Microphones), and ultrasonic microphones (CM16/CMPA; Avisoft-Bioacoustics). Power spectra (blue and black shaded for rivers and roads, respectively) are calibrated spectral density plots of all three recordings combined. Symbols above each spectrogram indicate a river (left), and a road (right).

Table 1.1 **Example response mechanisms from noise studies with natural, anthropogenic and artificial noise sources.**

Table is not intended as a comprehensive representation of the literature. Primary research is cited in many cases, whereas influential reviews are cited in others to highlight the vast breadth of knowledge on that particular component of the table. Acronyms: AM = amplitude-modulated; BLN = band-limited noise; WN = white noise; TOD = Time of day.

Noise characteristic	Response	Natural noise ex:	source	Anthropogenic noise ex:	source	Artificial noise ex:	source
Frequency	Change call frequency	Douglas and Conner 1999	Ocean surf	Reviewed in Patricelli and Blickley 2006	Many	Tressler and Smotherman 2009, Hage et al. 2013	BLN
Frequency	Freq. syllable selection	?		Wood and Yezerinac 2006, Nemeth et al. 2013	Urban	?	
Amplitude	Lombard effect	Reviewed in Brumm and Zollinger 2011	Many	Brumm 2004, Parks et al. 2011	Urban; shipping	Tressler and Smotherman 2009, Hage et al. 2013	BLN
Amplitude	Loud syllable selection	?		Nemeth et al. 2013	Urban	Brumm and Zollinger 2017	BLN
Amplitude	Spatial release from masking	Schwartz and Gerhardt 1989, Bee 2007	Frog chorus; rainforest	?		Hine et al. 1994, Turnbull 1994, Dent et al. 1997	Tones; WN
Temporal patterning	Increase call duration	Lengagne et al. 1999, Love and Bee 2010	Wind; frog chorus	Foote et al. 2004, Bunkley and Barber 2015	Boat; urban; gas compressor	Luo et al. 2015, Brumm and Zollinger 2017	BLN; WN
Temporal patterning	Increase call redundancy (repeat calling)	Lengagne et al. 1999, Brumm and Slater 2006, Thode et al. 2020	Wind; waterfall	Sun and Narins 2005, Thode et al. 2020	Airplane & motorcycle; seismic air gun	Luo et al. 2015, Gomes et al. 2016, Brumm and Zollinger 2017	BLN
Temporal patterning	Dip listening	Vélez and Bee 2011, Lee et al. 2017	Frog chorus	Sills et al. 2017	Seismic air gun	Ronacher and Hoffmann 2003	AM BLN

Temporal patterning	Dip calling	Douglas and Conner 1999, Brumm 2006, Herrick et al. 2018	Ocean surf; bird chorus; frog chorus;	Vargas-Salinas and Amézquita 2013, 2014	Traffic	Zelick and Narins 1982, 1983	Tones
Temporal patterning	Change TOD active	Ficken et al. 1974, Greenfield 1988	Bird chorus; Katydid chorus	Fuller et al. 2007, Gil et al. 2014	Urban; airplane	?	
Depends on shift	Shift focus (same modality)	Dunlop et al. 2010, Rhebergen et al. 2015	Wind; frog chorus	Halfwerk et al. 2019	Urban	Gomes et al. 2016	BLN
NA	Shift sensory modality	Reviewed in Partan 2017	Many	Partan et al. 2010	Urban	?	

CHAPTER TWO: PHANTOM RIVERS FILTER BIRDS AND BATS BY ACOUSTIC NICHE

This article has undergone full peer review and has been accepted at Nature Communications.

Abstract

Natural sensory environments, despite strong potential for structuring systems, have been neglected in ecological theory. Here, we test the hypothesis that intense natural acoustic environments shape animal distributions and behavior by broadcasting whitewater river noise in montane riparian zones for two summers. Additionally, we use spectrally-altered river noise to explicitly test the effects of masking as a mechanism driving patterns. Using data from abundance and activity surveys across 60 locations, over two full breeding seasons, we find that both birds and bats avoid areas with high sound levels, while birds avoid frequencies that overlap with birdsong, and bats avoid higher frequencies more generally. We placed 720 clay caterpillars in willows, and find that intense sound levels decrease foraging behavior in birds. For bats, we deployed foraging tests across 144 nights, consisting of robotic insect-wing mimics, and speakers broadcasting bat prey sounds, and find that bats appear to switch hunting strategies from passive listening to aerial hawking as sound levels increase. Natural acoustic environments are an underappreciated niche axis, a conclusion that serves to escalate the urgency of mitigating human-created noise.

Introduction

Animals surveil the environment to extract information important for decision making. Bats alter roost emergence in the presence of rain noise (Geipel et al., 2019) and bees use ultraviolet (Giurfa et al., 1995) and electromagnetic (Clarke et al., 2013) signals created by flowers to learn the location of nectar rewards. The information an animal can extract from the world, its umwelt (von Uexküll, 1909), has long been appreciated as important for explaining animal behavior (Bradbury & Vehrencamp, 1998), yet we often fail to account for the filtering effects of these umwelten when explaining larger ecological patterns. Despite recent advances in understanding the role that anthropogenic noise and artificial light play on wildlife (Barber, Crooks & Fristrup, 2010; Kight & Swaddle, 2011; Francis & Barber, 2013; Swaddle et al., 2015; Dominoni et al., 2020), it is surprising that natural sensory environments, such as gradients of light and sound, are rarely used in ecological analyses (Gomes, Francis & Barber, 2021). In one of the few exceptions, noise from nearby streams had the most power in explaining where frogs chose to call relative to other habitat variables (Goutte, Dubois & Legendre, 2013). Recent experimental evidence further supports a potentially widespread role of sensory environments in shaping animal behavior and ecology. Playback of river noise alters spider abundance (Gomes, Hesselberg & Barber, 2020), healthy coral reef sounds increases fish settlement on degraded reefs (Gordon et al., 2019b), and stream noise, paired with male advertisement calls, attracts more female torrent frogs (Zhao et al., 2017).

The cacophony of an insect chorus and the thunder of a mountain river are examples of intense acoustic sources that characterize many environments. There are 150,000 km of marine shoreline (NOAA, 2014) and 5.6 million km of rivers and streams in the United States alone (US EPA, 2014) that expose adjacent environments to the sounds of moving water. We hypothesize that such intense natural acoustic sources have the power to structure habitat use (Gomes, Francis & Barber, 2021). To test this hypothesis, we selected 60 locations within 20 sites, matched for elevation and riparian vegetation, along streams in the Pioneer mountain range of Idaho (Figure 2.1A) and monitored two taxonomic groups dependent upon the acoustic environment (Bradbury & Vehrencamp, 1998) that are abundant, diverse, and widespread across our system – birds and bats. Ten sites remained acoustically unaltered (controls) and spanned a natural range of sound levels; from quiet, slow-moving streams to loud, whitewater rapids (30.6 – 73.8 dBA, 24-hour L50). We broadcast whitewater river noise from speaker arrays powered by solar panels and banks of batteries at five additional, naturally quiet streams using acoustic recordings taken from the highest sound level control sites. These phantom rivers thus presented the amplitude and spectral profiles of raging, whitewater rapids (avg. median frequency ± SD: 2.1 ± 1.3 kHz). To understand the mechanisms underlying responses to the acoustic environment, we also created a gradient of background spectra by broadcasting shifted river noise of an identical temporal profile, but shifted upwards in frequency (4.8 ± 1.3 kHz) at five additional quiet-stream sites (Figure 2.1B). We created these files so that the average broadcast energy, weighted by birds' hearing thresholds, was the same (see supplement for details; Figure 2.1C).

Energetic masking occurs when there is spectral overlap between the signal and background noise. Masking of vocalizations, like birdsong, can drive distributional shifts of animals in areas exposed to anthropogenic noise (Francis, 2015). Similarly, the masking of prey cues is suggested to be a primary mechanism structuring the space use of acoustically-mediated predators, such as gleaning bats (Schaub, Ostwald & Siemers, 2008; Gomes et al., 2016). We predicted that overlap between song and background noise would be an important predictor of bird distributions if masking of birdsong is underlying noise effects (Figure 2.1D). Because most bat echolocation is higher frequency than the acoustic environments we created, we did not expect changes in bat activity to be related to sonar frequency, yet we did predict that gleaning bats would avoid sites with energy in higher frequencies (>3 kHz; Fuzessery et al., 1993) due to masking of prey-generated sounds (Figure B.11; Schaub, Ostwald & Siemers, 2008; Gomes et al., 2016). Our experimental design allowed us to explicitly test the effects of sound level separately from those of background spectra.

Results and Discussion

Leveraging data from 2,969 point counts (~150 count hours), we found bird abundance declined by 7.0% (95% CI: 3.4 – 10.5%) for each 12 dB increase in sound level (Figure 2.2A; Table B.1). High-intensity noise makes detection and discrimination of acoustic signals and cues more difficult, either because of energetic masking at the periphery of the auditory system, or because of limited central attentional resources (Dominoni et al., 2020). To explore masking of communication, we took the difference between the median background frequency and individual bird species' peak vocalization frequency as a measure of spectral overlap with the acoustic environment. Birds with a peak vocalization frequency closer to the median of the background spectrum showed lower abundances, with declines of 10.0% (5.1 – 15.3%) for each 2 kHz increase in spectral overlap (Figure 2.2B). However, these overlap-mediated effects interact with sound level in a diminishing way (Table B.1): higher amplitude background noise resulted in weaker relationships between spectral overlap and bird abundance. It seems that when acoustic environments are intense, masking of specific vocalizations is no longer the primary mechanism underlying distributional changes (Figure B.14).

Individual species models (Table B.2) combined with phylogenetically-informed, trait-based analyses indicate that birds with lower-frequency songs avoid noise with similar spectra, while birds with higher frequency vocalizations do not ($t = -3.73$; $p < 0.01$; Figure 2.2C). Previous work (Francis, Ortega & Cruz, 2011) found that lower-frequency vocalizers more strongly avoid high sound levels. Here, no distributional patterns related to song frequency emerged in response to the sound level or median frequency of the acoustic environment (Table B.3).

Animals that remain in anthropogenic noise can bear costs, such as reduced body condition (Dominoni et al., 2020). To examine one potential behavioral cost of exposure to natural noise, we placed 720 clay caterpillars across our sites (Figure B.8). While controlling for bird abundance, the odds of a caterpillar being depredated by a bird decreased by 37.2% (95% CI: 22.7 – 49.1%) for each 12 dB increase in sound level (Figure 2.2D; Table B.4). As this task was entirely visual, it seems likely that cross-modal attentional limitations underlie this effect (Halfwerk & Slabbekoorn, 2015). Birds that persist in high sound-level environments will likely suffer negative foraging consequences under noise exposure and such effects may have indirect consequences for arthropods (Gomes, Hesselberg & Barber, 2020).

The direct effects of the acoustic environment are a potential driver of bat distributions. Limited evidence suggests that space-use by bats is shaped by anthropogenic noise (Bunkley et al., 2015), and laboratory work has shown that gleaning bats have difficulty hunting in both anthropogenic and natural noise (Schaub, Ostwald & Siemers, 2008; Gomes et al., 2016). Using ~100,000 identified bat call sequences, we found that overall bat activity decreased 8.2% (95% CI: 4.8 – 11.4%) for each 12 dB increase in sound level, and decreased 19.5% (16.1 – 22.8%) for each 2 kHz increase in median background frequency (Figure 2.3A-B; Table B.5). Individual-species models reveal consistently similar inferences (Table B.6). Bats likely perceive higher frequency noise as louder (Koay, Heffner & Heffner, 1997), yet masking of echolocation is an improbable explanation for these results as bat sonar does not spectrally overlap with the acoustic environments we studied (although see Bunkley et al. (2015) for frequency shifts in non-overlapping noise). Phylogenetically controlled trait-based analyses revealed that bats with increasingly high-frequency sonar exhibited increasingly lower activity with rising sound levels ($t = -5.39$; $p < 0.001$; Figure 2.3C), further counter to masking as an explanatory mechanism. This finding may reflect indirect drivers if small insects disproportionately avoid noise, as these are most accessible to high-frequency echolocators (Houston, Boonman & Jones, 2004). Alternatively, high-frequency echolocators (and listeners Koay, Heffner & Heffner, 1997) experience a reduced sensing area, since high-frequencies attenuate quickly, which may compromise risk assessments in a noisy world.

While these data suggest that masking of echolocation is not responsible for patterns of bat activity, they do indicate that limited attentional resources available for sonar processing and perhaps masking of lower frequency environmental cues (Goerlitz, Greif & Siemers, 2008) might be two underappreciated drivers of bat distributions. We used additional trait-based analyses to test a component of the latter hypothesis and found that bats capable of hunting via passive-listening are not more likely to avoid noise (Table B.8). This result is at odds with previous laboratory work (Schaub, Ostwald & Siemers, 2008), and might indicate that wild bats are behaviorally flexible enough to cope with noise (Gomes et al., 2016). Indeed, those bats that are obligate aerial hawkers are more likely to avoid higher-frequency acoustic environments ($t = -4.1$; $p < 0.01$).

To quantify bats' use of passive listening and active sonar strategies, and to explore if bats employ flexibility in hunting techniques to circumvent the costs of noise, we deployed custom-designed assays at 36 locations across our sites. We placed small speakers playing insect walking and orthopteran mating sounds on the ground to evaluate bats' attraction to prey-generated cues (Figure B.13). To query bats' use of sonar-mediated aerial hawking we used a motor-driven synthetic wing (Lazure & Fenton, 2011) placed at 1 m above the ground to echo-acoustically mimic the wingbeat frequency of insect prey (250 Hz, e.g., Diptera (Dudley, 2002); Figure B.12). We focused our analysis on bat species that employ both strategies (i.e., behaviorally flexible bats; including *Corynorhinus townsendii, Myotis evotis, Myotis lucifugus,* and *Myotis thysanodes*; see supplement for more information) and predicted that high sound-level acoustic environments would hinder bats' use of passive listening (which requires processing of lower-frequency sounds) and result in heightened use of sonar (Lazure & Fenton, 2011;

Gomes et al., 2016). Indeed, while controlling for changes in bat abundance, for every 12 dB increase in sound pressure level and 2 kHz increase in median background frequency, bat activity at speakers playing prey cues decreased by a factor of 0.58 (95% CI: 0.38 – 0.87; Figure 2.3D; Table B.7), while aerial hawking activity increased by a factor of 8.1 (95% CI: 1.5 – 44.1) at simultaneously deployed robo-insects. This strategy switching only seemed to occur at sites with relatively higher frequency acoustic environments, likely because the bulk of the energy of prey-generated sounds are within these frequencies (Goerlitz, Greif & Siemers, 2008). The ability to behaviorally switch is unlikely to be universal, which may allow flexible bat species to persist where others cannot (Gomes et al., 2016).

We experimentally show that natural noise can have strong effects on animal abundance, activity, and behavior, yet our findings are dependent on the probability of detecting vocalizing animals in noise (Pacifici, Simons & Pollock, 2008; Ortega & Francis, 2012). For birds, we controlled for this potential problem using four approaches. We turned off speakers during counts so that most observations occurred below sound levels known to interfere with detection (Ortega & Francis, 2012) (Figure B.6). To implement imperfect detection into our models, we both directly measured observer detection in noise with a birdsong playback experiment (Figure B.7), and estimated bird detection probabilities with a noise-informed removal model (Table B.11). We wore earplugs and earmuffs during a duplicate set of point counts so that observations were visual-only (Table B.12), which suggest similar inferences as above (Table B.1). For bats, a laboratory test verified acoustic recording units were triggered similarly in a gradient of noise levels. Further, we validated that identification software correctly classified bats by experimentally adding noise to files (see supplement).

Our results demonstrate that natural acoustic environments represent an underappreciated dimension of the niche and are clearly important in shaping animal behavior and distributions. Incorporating this axis into our understanding of the natural world will provide stronger inference for both basic and applied questions (Gomes, Francis & Barber, 2021). Because the spatial and temporal footprint of human-generated noise is orders of magnitude greater than loud natural acoustic environments, it is critical to understand that the insights provided by our data increase the importance of mitigating noise pollution impacts on animals and their habitats. Our results reveal age-old strategies for dealing with the long-standing problem of noise and help explain contemporary responses to anthropogenic noise. A renewed focus on animal umwelten will redefine our understanding of ecological niche axes that have been canalized by our own sensory biases (Gomes, Francis & Barber, 2021).

Methods

IACUC approval: All work described below was approved by the Boise State Institutional Animal Care and Use Committee: AC15-021

Site layout

We selected twenty sites, across five drainages, within the Pioneer Mountains of Idaho and matched them for elevation and riparian habitat. We split these 20 sites into 10 noise playback sites, and 10 control sites (Figure B.1). The control sites ranged from quiet, slow-moving streams to relatively loud whitewater torrents. Noise playback sites, on the other hand, were relatively quiet (not whitewater) sites, where we broadcast loud whitewater river recordings with speaker arrays hung from towers (see supplementary information for more details on noise file creation, playback equipment, and experimental setup). At five of the noise playback sites we broadcast normal river noise (hereafter referred to as 'river noise' sites), and at the other five noise sites we broadcast spectrally altered river recordings (hereafter referred to as 'shifted noise' sites).

We collected data at three primary locations within each site (Figure B.1) along riparian areas: 1) roughly in the middle of the speaker tower systems, 2) at a shorter distance from the middle location (mean: 198.2 m +/- 54.5 m SD; range: 117.6 m - 384.5 m), and 3) and a longer distance from the middle location (in the opposite direction from the nearer location; mean: 312.7 m +/- 64.7 m SD; range: 249.1 m - 479.6 m). Thus, sites were approximately 510.9 m +/- 98.3 m long (range: 374.7 - 850.6 m), along the riparian corridor. All control sites were, at minimum, 1 km apart along the riparian corridor from any noise site, to maintain acoustic independence (see Figure 2.1A).

Data collection

Birds

We conducted three-minute avian point counts between one half hour before sunrise and 6 hours after sunrise (roughly 0530 – 1130 hours). During the project, we conducted 1330 point-counts from 28 May to 20 July 2017 and 1639 point-count events occurred from 7 May to 24 July in 2018.

Caterpillar deployment

We deployed a total of 720 clay caterpillars throughout the 2018 breeding season. Forty caterpillars were glued to stems and branches of trees between 1 - 2.5 m high at each site. Twenty caterpillars surrounded the middle point count location at each site (a set of 10 were placed upstream, and another set of 10 were placed downstream starting from the middle ARU location), while the other twenty were at upstream and downstream sampling locations (10 each at upstream and downstream locations). Each caterpillar was placed along the riparian corridor, at least 1 m apart from each other (Roslin et al., 2017). See appendix B for details on caterpillar predation scoring.

Bird trait analysis

We performed a trait-based analysis to understand the mechanistic patterns of bird distributions in our study paradigm. Avian vocal frequencies and body mass were collected from previous work (Hu & Cardoso, 2009; Cardoso, 2014; Francis, 2015). When multiple sources contained data, the values were averaged. There were a few cases where none of those sources contained a vocal frequency or mass measurement for species of interest. Thus, representative songs were downloaded from the Macaulay Library of the Cornell Lab of Ornithology based on recording quality and geographical relevance (MacGillivray's warbler: ML42249; dusky flycatcher: ML534684; red-naped sapsuckers: ML6956), and analyzed with Avisoft SASLab Pro to obtain a peak frequency measure. Mass measurements for these 'missing' birds were taken from the 'All about birds' webpage of the Cornell Lab of Ornithology.

Bats

Measuring and identifying bat calls

We measured bat activity using Song Meter 3 (hereafter "SM3") recording units (Wildlife Acoustics Inc., Massachusetts, USA) equipped with a single SMU (Wildlife Acoustics Inc.) ultrasonic microphone. One recording unit was used at each site and pseudo-randomly rotated between the three point-count locations so that each location was monitored for at least 21 days. Microphones were mounted on metal conduit at a height of approximately 3 m, and oriented perpendicular to the ground and to face away from the stream to ensure optimal recording conditions (Figure B.9; see supplement for more information).

Robotic insects

We used a modified version of Lazure and Fenton's (Lazure & Fenton, 2011) apparatus to present bats with a fluttering target (Figure B.12). This consisted of a 3 cm^2 piece of masking tape affixed to a metal rod [30.48 cm length x 3.25 mm diameter], which itself was connected to a 12-volt brushed DC motor (AndyMark 9015 12V, AndyMark Inc., Kokomo, IN, USA). The no-load revolution speed of these motors (267 Hz) falls within the range of wingbeat frequency measured in Chironomidae (Ogawa & Sato, 1993; Dudley, 2002), a group that is an important food source for many North American bat species (Barclay, 1991).

We attached each motor to a tripod made of PVC piping and positioned the tripod such that the target was approximately 1.2 m above the ground. Each motor was powered by a 12 V battery (35Ah AGM; DURA12-35C, Duracell) which was controlled by a programmable 12 V timer (CN101, FAVOLCANO) to automatically start and stop the motor each night. The rotors were powered for two hours following sunset.

Prey-sound speaker playback

We created a playlist composed of several insect acoustic cues to present gleaning bats: a beetle (*Tenebrio molitor*) walking on dried grass, a cricket (*Acheta domesticus*) walking on leaves, mealworm larvae (*Tenebrio molitor*) on leaves, fall field cricket (*Gryllus pennsylvanicus*) calls, and fork-tailed bush katydid (*Scudderia furcata*) calls.

The cricket and katydid calls were sourced from the Macaulay Library (ML527360 and ML107505, respectively).

Experimental setup for bat foraging tests

Most sites received two rotors and two speakers: one of each at the center of the site, and one of each at approximately 125 m from the center of the site (in opposite directions in order to have tests in a range of acoustic environments), placed roughly 10 m from the edge of the riparian zone. Rotors and speakers at the center locations were separated by at least 50 m. The exception to this setup were the four positive control (loud whitewater river) sites, which only received a single rotor and speaker separated by 50 m because of logistical difficulties of accessing those sites. We paired each rotor and speaker with an SM2BAT+ bat detector equipped with an SMX-US microphone (Wildlife Acoustics Inc.; Acoustics, 2018), using tripods to elevate the microphones approximately 1 m off the ground and approximately 1 m from the speaker/rotor. We programmed the bat detectors with a gain of 36 dB and a trigger level of 18 dB to limit recordings to bats that were passing within the immediate vicinity. To allow for a comparison of activity between speakers and rotors, bat activity was only considered for the first two hours following sunset.

Bat trait analysis

We collected bat foraging behavior and peak echolocation frequency information to use as predictors in a phylogenetically controlled trait analysis (Table B.8; B.13). We based our behavioral foraging classifications on the categories of Ratcliffe et al. (Ratcliffe, Fenton & Shettleworth, 2006) and followed the classifications of Gordon et al. (Gordon et al., 2019a) where possible, and others (Kunz, 1982; Barclay, 1985; Faure &

Barclay, 1994; Ratcliffe & Dawson, 2003; Jung & Kalko, 2010; Denzinger, Tschapka & Schnitzler, 2018) where necessary. We extracted peak echolocation frequency from the 2017 and 2018 SM3 field recordings and employed two controls to decrease variability in call parameters potentially introduced via this method. First, we selected only recordings made on control sites in 2017 and 2018 (n = 740,848 calls), as echolocation call characteristics may be affected by local acoustic environments (e.g. Bunkley et al., 2015). Secondly, we averaged all call parameters per species per hour at each site to decrease the possible effects of few individuals driving measurements. This resulted in 9,538 species-hours of recordings, which themselves were averaged per species (Table B.13).

Quantifying environmental variables

We used long-term monitoring of the acoustic environment (via Roland R05 recorders) to calculate daily sound pressure level (L50 dBA) and median frequency (kHz) values for each location (see supplementary information for details on quantification of all predictor variables).

Statistics

All models of abundance, activity, and foraging transects were generalized linear mixed effects models (glmm) in R (R Core Team, 2017) using the package `lme4` (Bates, 2010, p. 4; Bates et al., 2015, p. 4) or `glmmTMB` (Magnusson et al., 2017). All distribution families were selected based on theoretical sampling processes of the data, models were checked for collinearity (VIF scores) (Lüdecke et al., 2019), and model fits were visually checked with residual plots (see supplemental R code) (Hartig, 2019).

Bird abundance and bat activity

Model predictors and covariates

Both bird and bat models had the following variables in a glmm: site and bird/bat species were random effects terms and sound pressure level (dBA L50), sound spectrum (median frequency), the interaction between sound pressure level and spectrum, elevation, percent riparian vegetation, ordinal date (and a quadratic version of this), and year as fixed effects. While year is sometimes used as a random-effect term, it is suggested to be used as a fixed effect if fewer than five levels exist for that factor, as variance estimates become imprecise (Harrison et al., 2018; Silk, Harrison & Hodgson, 2020). Additionally, moon phase was a fixed effect in the bat models (Gomes, Appel & Barber, 2020), while spectral overlap (the absolute difference between sound spectrum and bird species vocalization frequencies) and the interaction between sound pressure level and spectral overlap were fixed effects in bird models.

We attempted to fit both sound pressure level and spectrum as having random slopes for each species, yet both bat and bird models would not converge with such complex model structure. Thus, we additionally followed group models with individual species models (see supplementary information). This allowed us to model and gain inference to the nuanced differences between individual species across the study system.

Model family distribution and link function

For both bird and bat counts, we used a negative binomial distribution with a log link, rather than a Poisson distribution, because data were over-dispersed. We plotted variance-mean relationships and residuals of multiple models to select the appropriate variance structure, and compared these with AIC to select the best-fitting distribution (Harrison et al., 2018). Data and code are available at Dryad (Gomes et al., 2020).

Individual species models:

Individual species models were parameterized the same as above (except without the species term). All 12 bat species (see Table B.6; B.10) and 26 of the most common birds (see Table B.2; B.9) were modelled individually to be able to interpret model parameter estimates, with complex interactions, for each species.

Clay caterpillar predation

We modelled caterpillar predation with a glmm (binomial family; logit link function), using the number of individual scorers as weights in the model. Like the bird abundance model, we used site as a random effect and sound pressure level (dBA L50), spectral frequency (median), elevation, percent riparian vegetation, ordinal date, and year as fixed effects (Table B.4). Additionally, the predicted number of birds at a site were modelled as fixed effects to control for varying amounts of foraging birds on the landscape.

Robotic moths and prey-sound speakers

Robotic moth and prey-sound speaker models were parameterized exactly the same as the overall bat activity model. That is, the model was fit with a negative binomial family (log link) with site and species as random effects and sound pressure level (dBA L50), sound spectrum (median frequency), the interaction between sound pressure level and spectrum, moon phase, elevation, percent riparian vegetation, ordinal date (and a quadratic version of this), and year as fixed effects. Additionally, the predicted number of bats at a site were modelled as fixed effects to control for varying amounts of foraging bats on the landscape.

Trait analyses

Trait analyses were analyzed with phylogenetic generalized least squares (PGLS) to control for relatedness while predicting species responses to noise (Goutte, Dubois & Legendre, 2013). We performed PGLS analyses with the *gls* function in the R package nlme (Pinheiro et al., 2013), and accounted for error in the response variable with a fixed-variance weighting function of one divided by the square root of the standard error of the response estimate (Ives, Midford & Garland Jr, 2007; Garamszegi, 2014). We accounted for phylogenetic structure by estimating Pagel's λ (Revell, 2010). When λ estimates fell outside of the zero to 1 range, we fixed λ at the nearest boundary. For bird models, we used a pruned consensus tree from a recent class-wide phylogeny (Jetz et al., 2012). For bats, we used a pruned mammalian tree (Upham, Esselstyn & Jetz, 2019). We used initial global models with all traits as variables that explained the responses to sound pressure level (SPL; birds and bats), spectral overlap with birdsong (birds), background frequency (bats), and the interaction between SPL and each measure of frequency (birds and bats). We then used AIC model selection (Burnham & Anderson, 2004) to choose top models in explaining these patterns. Models with dAIC ≤ 4 are included in Table B.3 (birds) and Table B.8 (bats), and the top model is interpreted in the main text.

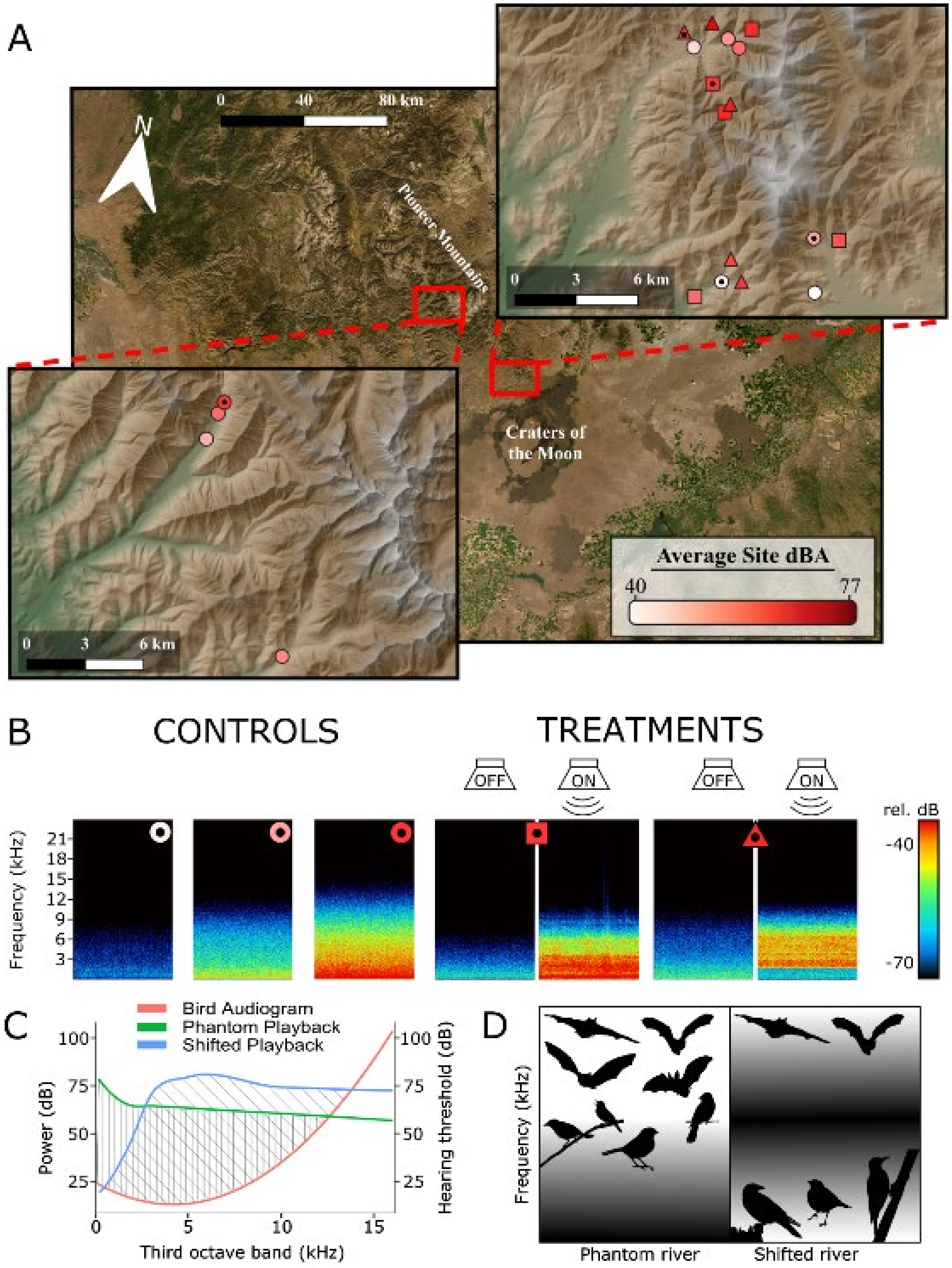


Figure 2.1 Design and predictions for phantom rivers playback experiment.

(A) Twenty sites were monitored across the Pioneer Mountains of Idaho, comprising a gradient of sound levels (indicated by color scale). Control sites are indicated by circles, phantom river playback sites by squares, and shifted-river playback sites by triangles. (B) These symbols are matched with their geographically referenced representative spectrograms (linked between A and B via black dots in center of symbols) to show the gradient of noise exposure at control sites and playback sites with speakers both on and off. (C) Both playback files were created so that the average broadcast energy, weighted by birds' hearing thresholds, was the same. (D) Predicted responses of birds and bats to the playback treatments. Silhouettes placed on frequency axis as a heuristic representation of vocalization frequency (not to scale).

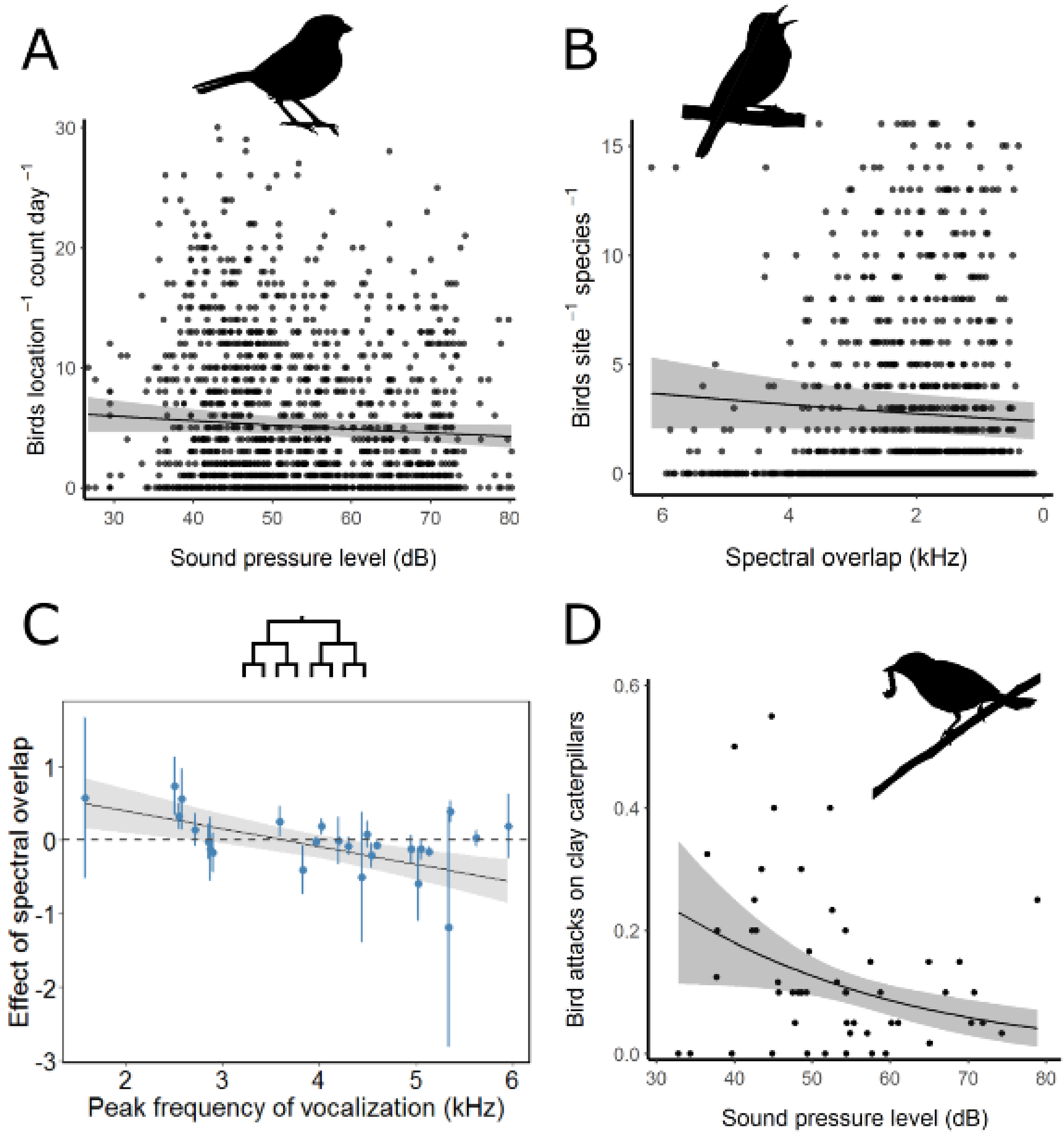


Figure 2.2 Bird responses to noise.

(A) Bird abundance declines with increasing sound levels. (B) Bird abundance declines with increasing spectral overlap with song (note reversed x axis; 0 = complete spectral overlap). (C) Phylogenetically informed trait analyses reveal that lower-frequency singers are more likely to be masked by background noise with similar spectra. (D) Bird foraging rates decrease in high sound levels. Points represent raw data, error bars represent standard errors, the plotted lines and shaded grey regions (95% confidence intervals) represent predicted values of abundance over the range of the variable on the x axis, given mean values of all other variables in the model.

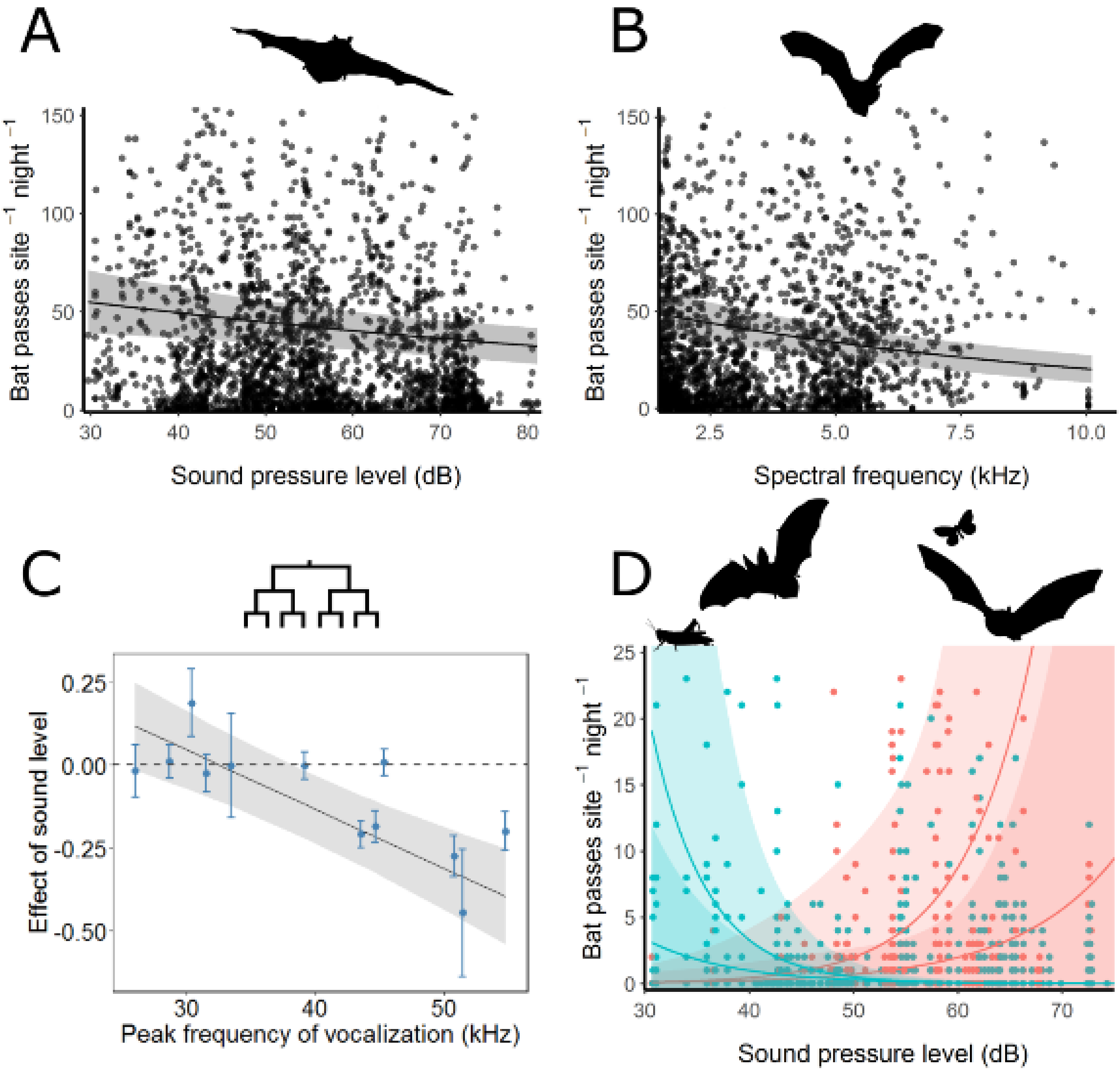


Figure 2.3 Bat responses to noise.

(A) Bat activity declines with increasing sound levels. (B) Bat activity declines with increasing frequency of the acoustic environment. (C) Phylogenetically-informed trait analyses reveal that higher-frequency echolocators are more likely to avoid high sound-level environments. (D) Foraging modality for flexible bat species appear to shift from passive-listening to aerial-hawking with variation in background sound level and frequency. Blue lines denote predicted declines in bat detections at artificial prey sounds speakers with increased sound level where top and bottom lines reflect median background frequencies at 10 and 8 kHz respectively. Red lines denote the predicted increase in bat detections at robotic fluttering insects with higher noise levels at 8 kHz (top line) and 6 kHz (bottom line). Points represent raw data, error bars represent standard errors, the plotted lines and shaded regions (95% confidence intervals) represent predicted values of abundance over the range of the variable on the x axis, given mean values of all other variables in the model (except in D).

CHAPTER THREE: PHANTOM RIVER NOISE ALTERS ORB-WEAVING SPIDER ABUNDANCE, WEB SIZE, AND PREY CAPTURE

The final version of this article has undergone full peer review and has been accepted for publication. Please refer to the Version of Record. Please cite this article as doi:10.1111/1365-2435.13739 (Gomes, Hesselberg & Barber, 2020)

Abstract

Novel anthropogenic noise has received considerable attention in behavioral ecology, but the natural acoustic environment has largely been ignored as a niche axis. Using arrays of speakers, we experimentally broadcasted whitewater river noise continuously for three summers, and monitored spider abundance and behavior across 15 sites, to test our hypothesis that river noise is an important structuring force. We find substantial evidence that orb-weaving spiders (Araneidae and Tetragnathidae) are more abundant in high sound level environments, but are not affected by background noise spectrum. We explore multiple possible mechanisms underlying these patterns, such as loss of vertebrate predators and increased prey capture, and assess spider web-building behavior and body condition in noise. Continued research on the acoustic environment will likely reveal a web of connections hidden within this neglected ecological niche axis.

Introduction

Evidence of how animals respond to anthropogenic noise and the consequences of that exposure is ever accumulating (Swaddle et al., 2015; Shannon et al., 2016; Jerem & Mathews, 2020). Just as anthropogenic noise can alter predator-prey relationships (Gomes et al., 2016; Mason, McClure & Barber, 2016), animal communities (Francis, Ortega & Cruz, 2009, 2011), and local abundance (Blickley, Blackwood & Patricelli, 2012; Bunkley et al., 2017; Cinto Mejia, McClure & Barber, 2019), it is likely that natural noise, of similar sound levels and spectra, has been doing this since the origins of hearing organs in animals. Thus, we expect intense natural acoustic environments to be a powerful and relevant ecological niche axis.

The sounds of rushing water, for example, can be used as information about habitat quality for fish (Kacem et al., 2020) and mate quality for frogs (Zhao et al., 2017). Yet it is unclear how these acoustic environments might affect downstream trophic interactions (Barton et al., 2018; Senzaki, Kadoya & Francis, 2020). Arthropods are an important food source for many vertebrate groups (Losey & Vaughan, 2006) that are known to be affected by noise (Raboin & Elias, 2019), yet have largely been ignored in the literature (Morley, Jones & Radford, 2014; Shannon et al., 2016; Jerem & Mathews, 2020). The acoustic environment can directly affect arthropod behavior, such as communication (Römer, 2013; Orci, Petróczki & Barta, 2016; Raboin & Elias, 2019), yet it may also indirectly affect arthropods via trophic interactions (Barton et al., 2018; Senzaki, Kadoya & Francis, 2020), which can collectively change arthropod abundances (Bunkley et al., 2017). Intermediate arthropod predators, such as spiders, are both predators of insects and prey of many taxa themselves, thus offer the potential to explore how the acoustic environment shapes food webs via both top-down (Riechert & Lockley, 1984; Nyffeler & Birkhofer, 2017) and bottom-up (Guinan & Sealy, 1987; Baxter, Fausch & Carl Saunders, 2005; Pagani–Núñez et al., 2011) processes.

Here we describe a 3-year, large-scale natural noise playback experiment in the Pioneer Mountains of Idaho, in which we continuously broadcast whitewater river noise across 15 sites in a riparian landscape. We monitored orb-weaving spider (Araneidae and Tetragnathidae) abundance, web-building behavior, prey capture rates, and body condition across 15 independent sites, 7 km apart on average, to test our hypothesis that the natural acoustic environment is an important ecological niche axis.

Methods

Site setup

We collected data during the months of May-July in 2017, 2018, and 2019 along the riparian areas of Fish Creek (43.467060, -113.635988), Cottonwood Creek (43.467060, -113.635988), and Copper Creek (43.440288, -113.714253) on Lava Lake Ranch in the Pioneer Mountains of Idaho. We sampled spider abundance and behavior within 78 'locations,' which were nested within 15 acoustically-independent 'sites' (average of 5 locations per site), with the closest pair of sites being 825 m apart (mean site-site distance: 7.3 km). Most locations were only sampled once during the three-year experiment (range: 1 – 5), while each site was sampled on average 8 times (range: 2 – 25). The differences in site/location sampling effort were due to logistical and practical reasons. That is, some sites had more suitable vegetation with which spiders could build their webs (see below for transect selection), while some specific locations became flooded or destroyed by avalanches in subsequent years.

Each site was exposed to the same treatment for all three years of the experiment, and treatments were pseudo-randomly spread across the landscape, and designed to be matched for elevation and habitat. Five of our sites had unaltered acoustic environments (controls), which contained a natural range of sound pressure levels (mean ± SD: 60.6 ± 7.7 dBF; range: 39.5 – 76.4 dBF). During the entire data collection period, we experimentally altered the remaining ten sites by playing continuous noise from arrays of speakers (see *'Noise playback'* below). We designed five of our experimental sites to have the sound pressure levels and frequency spectra of whitewater rivers (mean ± SD: 68.7 ± 4.9 dBF; range: 55.4 – 76.7 dBF). We created these 'phantom rivers' by broadcasting sound files, which were recorded from nearby whitewater rapids. At the remaining five sites, we broadcast the same files that were 'shifted' upwards in frequency and had similar sound pressure levels (mean ± SD: 70.2 ± 7.1 dBF; range: 60.7 – 84.4 dBF) and amplitude modulation profiles. Our shifted river treatment allowed us to test whether the patterns we observed were specific to river spectra, or general to noisy environments more broadly.

Noise playback

We suspended speakers from tripods constructed of 4.5 m long metal conduit (height: ~3m) to improve noise propagation. We broadcast river noise (avg. median frequency ± SD: 2.1 ± 1.3 kHz; Figure 3.1) at each phantom river site (see above) with two Octasound SP820A speakers (KDM Electronics Incorporated, Ajax, ON, Canada). Whereas, we broadcast shifted noise (4.8 ± 1.3 kHz) at each shifted site via three Octasound SP800A speakers (KDM Electronics Incorporated), to expose a similar amount of area to noise as in our river noise treatment due to reduced attenuation of the higher frequencies in our shifted noise treatment.

Speakers were powered by an amplifier (AD1200.1, PRV audio) connected to two 12 V deep cycle RV/marine batteries (DURDC12-100P; Duracell), which were charged by solar panels (Suniva OPT285-60-4-100; MidNite Solar Inc., WA, USA) via solar controllers (The Kid 30A MPPT; MidNite Solar Inc., WA, USA). This allowed us to continuously playback noise, 24 hours a day for months.

Data collection

We walked along streams (average above-ground width: 1.67 m; range: < 0.01 – 3.66 m) until we found an orb-weaving spider (either Araneidae or Tetragnathidae) that was occupying a web within riparian space. Once we located one adult female orb-weaver, we assumed that the habitat was suitable for web-building (as the habitat was occupied), and a transect survey begun. Transects were 4 m long, along the stream, whereby we identified and counted how many orb-weaving spiders were ‘actively foraging’ directly over the stream. An orb-weaver was considered actively foraging, and thus counted in our survey, if we verified the animal was sitting on or directly touching the hub or radii of a web - since these animals do not forage without a web. Additionally, only adult female spiders were counted and measured. When spiders were unassociated with a web, or when webs lacked spiders, we did not count them. When spider webs were freshly made, or undamaged (not missing significant portions of adhesive strands or radii), we measured web dimensions with a tape measure, and collected spiders for confirmation of identification and body condition data. Once we collected spiders from a sampling location, we did not return to that location for the remainder of the year. During only 2019, we visually identified captured insects (to the Order level) within a subset of webs as a metric of insect availability, not *prey* capture, since prey are likely consumed and not counted.

Spider identification and measurement

We identified spiders to genus by hand under a dissection microscope with a dichotomous key (Ubick, Paquin & Cushing, 2017), and then to species with references therein, and with the World Spider Catalog (Platnick, 2012). All spiders identified in the field were confirmed as adult females of one of two species: *Larinioides patagiatus* (Family Araneidae) and *Tetragnatha versicolor* (Family Tetragnathidae). Spider wet weight and front right femur lengths were measured with a digital scale and calipers, respectively. Body condition was calculated with the residual index by regressing femur length against body weight and using the residuals as values of body condition (Jakob, Marshall & Uetz, 1996).

Web analysis

We used a tape measure to quantify vertical web diameter (D_v), horizontal web diameter (D_h), free-zone diameter (D_{fz}), and upper radius (R_u; following Tew & Hesselberg, 2017; Gomes, 2020a), which allowed us to calculate web capture area with the Ellipse-Hub equation (Herberstein & Tso, 2000):

$$\text{Web area} = \pi\left(\frac{Dv}{2}\right)\left(\frac{Dh}{2}\right) - \pi\left(\frac{Dfz}{2}\right)^2$$

Environmental variables

We measured sound levels with a 3-minute Leq (SPL dBF re 20 mPa) using a Larson Davis (model 824; Depew, NY, USA) sound level meter. To measure temperature and wind speed, we used a portable weather meter (Kestrel 3000; Boothwyn, PA, USA) and a 1-minute integration. Each of these variables was measured once per 4 m transect (as opposed to at each web) due to trivial variation in measurements within each transect.

Statistics

We fit all data with (generalized) linear mixed effects models in R (R Core Team, 2017), with the Bayesian package `rstanarm` (Gabry & Goodrich, 2016). We fit spider transect data and prey capture data (overdispersed counts) with negative binomial distributions (log link), web capture area (positive and right-skewed) with a log-normal distribution (log-transformed response and Gaussian distribution), and body condition residuals with Gaussian distributions (identity link). There were no divergent transitions, all chains mixed well, we visually checked model fits and residuals, and examined each model for collinearity.

We included sound pressure level (dBF; hereafter dB), noise treatment (*i.e.* control, phantom river, and shifted river), time after sunset, ordinal date, year, elevation, temperature, and wind speed as explanatory variables in our models (except as noted below in exceptions). To make direct comparisons between variables that were both continuous and factors, we centered all fixed effects by the mean, and scaled by 2 standard deviations (Gelman, 2008). In all models, we fit site as a random effect (intercept). We fit year as a fixed effect rather than a random effect as it included less than 5 levels (Harrison et al., 2018). Model table (Table 3.1) was created with the help of the R package `sjstats` (Lüdecke, 2020).

Covariate exceptions

As we defined our transects as linear along the stream (4 m long), we included stream width as a covariate in transect models, which accounted for differences in transect area, while allowing us to make inferences about stream width. We collected prey capture data in 2019 only, thus we did not include year in these models. Body condition is a response that is affected by longer-term trends, thus we did not include daily temperature, wind speed, and time after sunset in these models, as we could not see a clear biological interpretation of such short-term variables.

Results

Our analyses of 117 spider transects revealed that both species of orb-weaving spiders markedly increased in abundance with an increase in sound level (Figure 3.2). *T. versicolor* increased by a factor of 1.8 (90% CI: 1.4 – 2.3) for every 12 dB increase in background sound level, whereas *L. patagiatus* increased by a factor of 2.1 (90% CI: 1.6 – 2.8) over the same increase in sound level. For both spiders, sound pressure level had the strongest effect (over the standardized range of variable values) of any other variable measured (time after sunset, ordinal day, year, stream width, temperature, or wind speed; Table 3.1**;** Figure 3.3A).

Web capture area was analyzed for 190 individual webs (93 *T. versicolor* and 97 *L. patagiatus*). Sound pressure level was the only variable with a substantial effect for *L. patagiatus*, which decreased web capture area by 32.8% (90% CI: 19.2 – 43.4%) every 12 dB increase in sound pressure level (Figure 3.4). *T. versicolor*, on the other hand, did not change web size with sound level, but did increase web size at lower elevations, higher temperatures, and later in the year (Figure 3.3B**;** Table 3.1). Ordinal date was the strongest predictor for *T. versicolor* web size (Figure 3.3B): web capture area is estimated to increase 43.9% (25.8 – 65.0%) every 5 days.

Of the 947 prey counted in 72 webs (33 *T. versicolor* and 39 *L. patagiatus*), 795 (84%) of them were flies (Order Diptera), visually identified as the Family Chironomidae (although this identification was not confirmed with a dichotomous key for logistical reasons), and 143 (15%) were mayflies (Order Ephemeroptera). Capture of Dipteran prey increased for *T. versicolor* by a factor of 4.5 (90% CI: 1.3 – 16.2; Figure 3.3C) every 12 dB increase in sound pressure level, but decreased for *L. patagiatus* by a factor of 0.37 (90% CI: 0.14 – 0.95). The capture of Ephemeropteran prey, on the other hand, did not change for either species of orb-weaving spider (Table 3.1).

Body condition was analyzed for 234 spiders (104 *T. versicolor* and 130 *L. patagiatus*), which did not differ greatly with sound pressure levels, or any other environmental variables (although year did have an effect; Figure 3.3D). However, body condition for *L. patagiatus* did have a positive-trending response to sound pressure levels (80% credible intervals do not overlap 0).

Discussion

In a natural noise playback experiment, high sound levels, yet not noise spectra (i.e., treatment), had an overall positive effect on orb-weaving spider abundance. This may be due to indirect effects via predator-prey interactions. Bird and bat predators, for example, are known to decline in abundance and activity with increasing sound pressure levels of anthropogenic noise (Bunkley et al., 2015; Cinto Mejia, McClure & Barber, 2019). While we do not yet know how strong any links between these predators and orb-weaving spiders are, spiders (including *L. patagiatus* studied here) have been found in the diets of many songbird and bat species, including those found within our system (Clare et al., 2011; Carlisle et al., 2012; Jedlicka, Sharma & Almeida, 2013; Gordon et al., 2019a).

Alternatively, it may be that these spiders can detect the amplitude of vibrations, but not differentiate between frequencies.

For *Tetragnatha versicolor,* prey capture success increased with increasing sound levels, despite no changes to web capture area, which seems likely to have contributed to the increased abundance we quantified. However *Larinioides patagiatus* exhibited decreasing capture rates in noise, which clearly cannot contribute to the increase in abundance we measured. Surprisingly, this species also built smaller webs in noise, which generally occurs when spiders are more satiated, not food deprived (Sherman, 1994; Adams, 2000; Herberstein, Craig & Elgar, 2000). However, in this case, it might be that smaller webs capture fewer prey (rather than food deprived spiders build smaller webs). That is, *L. patagiatus* might build smaller webs near noisy rivers because those places are more likely to have turbulent waters that might cause more web damage. In this case, it might be less energetically costly to build, and repair or lose, smaller webs (Tew, Adamson & Hesselberg, 2015).

Despite the increase in prey capture success for *T. versicolor*, this species showed no changes in body condition. *L. patagiatus* appeared to have marginally higher body condition with increasing sound levels, which may reflect energetic savings from building smaller webs, since they are energetically costly (Opell, 1998). *L. patagiatus* also caught fewer prey with increasing sound levels, which is not to be expected from a spider with higher body condition. However, it is possible that our metric of prey capture is not an accurate representation of prey intake, since growth should be dependent on food availability (Kleinteich & Schneider, 2011). We measured the number of uneaten prey in webs – a proxy for *prey availability* rather than *prey intake,* since prey are likely consumed by spiders before we observed the webs. It is possible that we are measuring a change in insect behavior or web-building frequency with the number of insects in webs. Furthermore, many have argued that rare large prey, or total prey biomass, rather than the number of prey, are more important for fitness (Venner & Casas, 2005; Eberhard, 2013; Harmer et al., 2015), which might be why web capture rates do not appear to be correlated with body condition.

While indirect effects seem likely to be involved in orb-weaver responses, it is also possible that these spiders are responding directly to noise. Lycosids respond to birdsong that is transduced as substrate-borne vibration (Lohrey et al., 2009), and Salticids can respond to far field sounds in the laboratory (Shamble et al., 2016). Recent work suggests that air-borne sounds can be transduced into orb-weaver silk vibrations (Zhou & Miles, 2017), which may allow orb-weavers to use their webs as large acoustic sensors (Mortimer et al., 2015, 2016). It is unclear if orb-weaving spiders are directly attracted to river sounds, but it is possible that they serve as habitat selection cues (Zhao et al., 2017; Kacem et al., 2020). Regardless, it does appear that natural acoustic environments play a role in shaping orb-weaving spider abundance and behavior.

This work demonstrates that intermediate predators, such as orb-weaving spiders may benefit from high sound level acoustic environments via either a decrease in predator abundance, an increase in prey capture, direct effects (*e.g.* habitat selection), or a combination of these drivers. This suggests that natural noise may have far-reaching consequences via top-down or bottom-up interactions. An emphasis on understanding the importance of natural acoustic environments will likely reveal critical links connecting organisms and further clarify the role of an underappreciated niche axis. Basic knowledge of how the natural acoustic environment affects arthropod communities will shed light on conservation as we continue to alter acoustic environments (Buxton et al., 2017). Especially while we witness likely worldwide declines in arthropods (Montgomery et al., 2020; van Klink et al., 2020), in which the underlying mechanisms remain unclear.

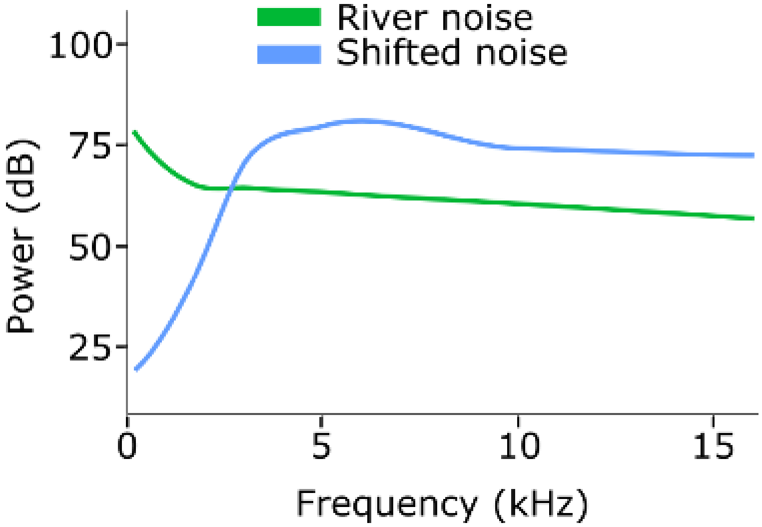


Figure 3.1 Power spectra of river noise and shifted river noise broadcast experimentally.

The average median frequency of river noise was 2.1 ± 1.3 kHz (SD) while shifted noise was 4.8 ± 1.3 kHz.

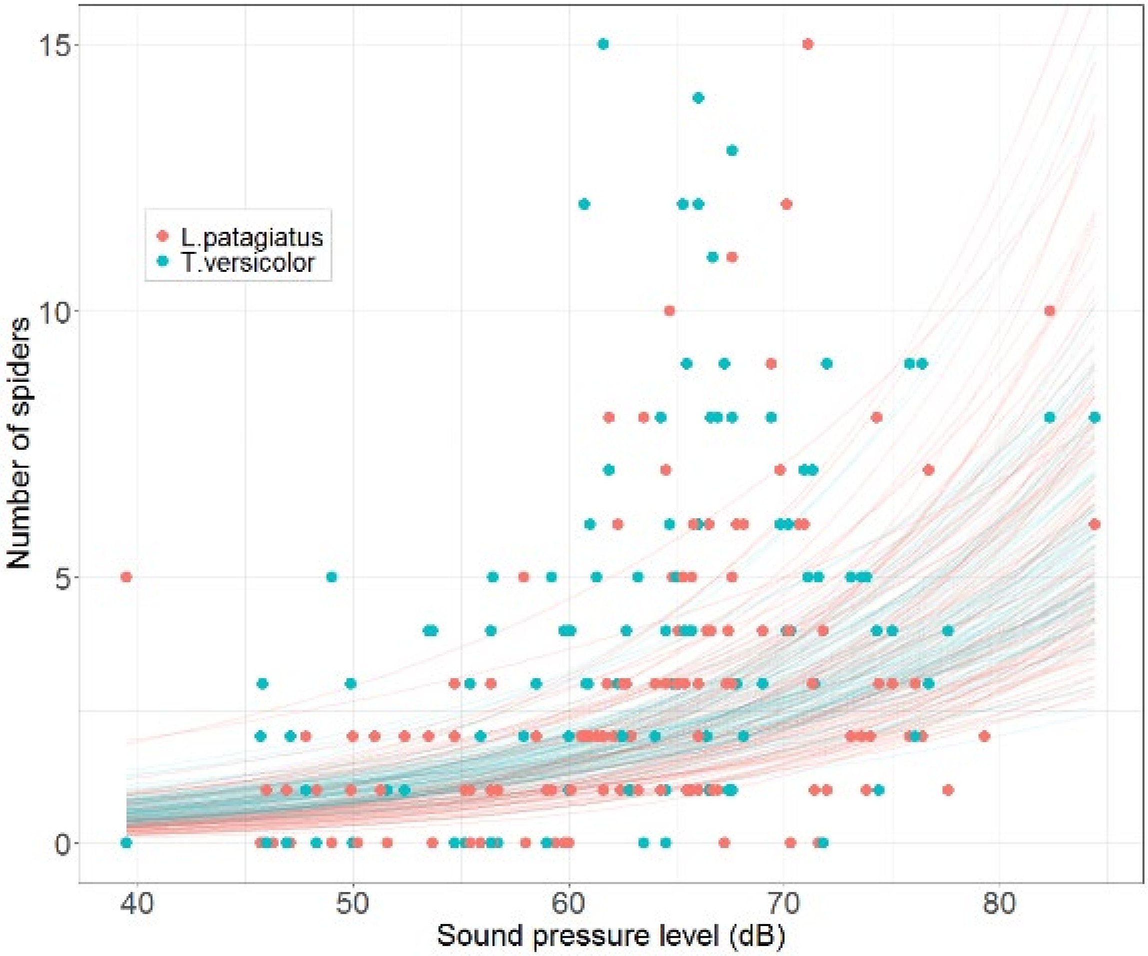


Figure 3.2 Spider abundance increases as sound pressure level increases.

Points represent raw data, while lines represent 100 posterior draws from Bayesian models for *L. patagiatus* (red) and *T. versicolor* (blue).

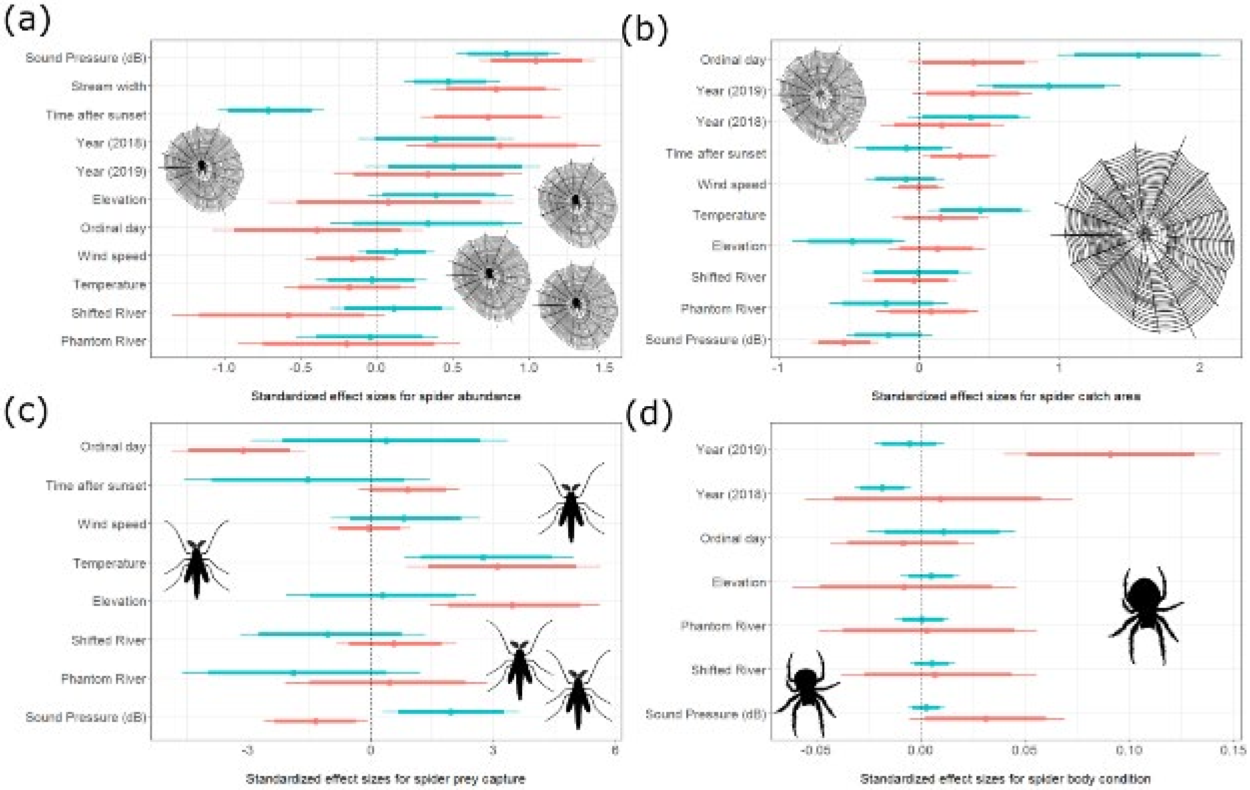


Figure 3.3 Model estimates for L. patagiatus and T. versicolor.

L. patagiatus (red) and *T. versicolor* (blue) model estimates where thick and thin lines indicate 80% and 90% credible intervals, respectively. Panel A: estimates of spider abundance; panel B: estimates of spider web capture area; panel C: estimates of dipteran prey capture; panel D estimates of body condition.

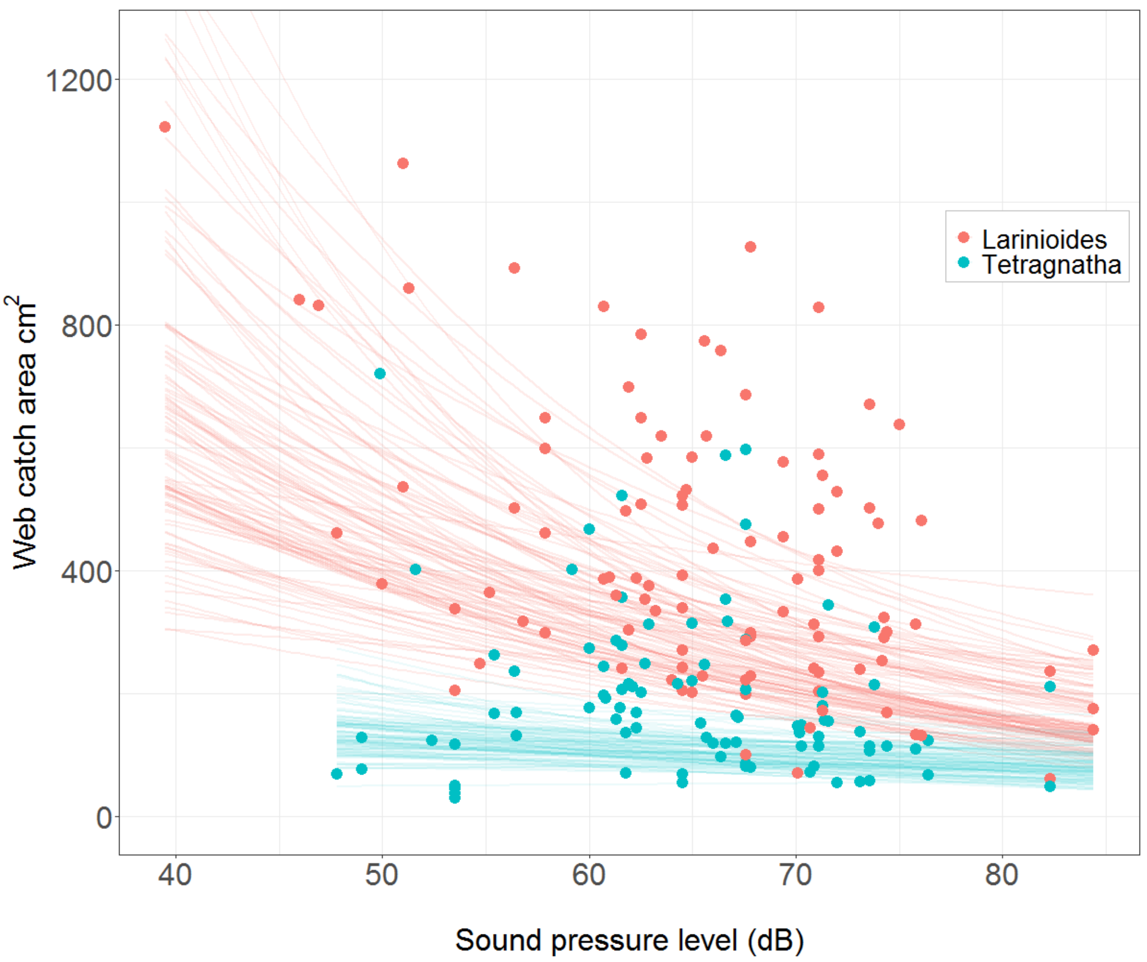


Figure 3.4 Web capture area declines with increasing sound pressure level for Larinioides patagiatus, but not for Tetragnatha versicolor.

Points represent raw data, while lines represent 100 posterior draws from Bayesian models for *L. patagiatus* (red) and *T. versicolor* (blue).

Table 3.1 Output from web capture area, prey capture, body condition, and abundance models.

Est = Estimate; SE = standard error; Probability of Direction (PD) is an index for the probability that the effect is non-zero; ESS = effective sample size; $\hat{r}$ (or Rhat) statistics above 1 indicates that chain has not converged yet; MCSE = Monte Carlo standard error, defined as the standard deviation of the chains divided by their effective sample size (see Lüdecke D. 2020).

Response	*species*	Parameter	Est	SE	80% CI	90% CI	PD	ESS	$\hat{r}$	MCSE
Capture area	*L. patagiatus*	Sound pressure level	-0.54	0.14	[-0.72, -0.35]	[-0.77, -0.29]	1.00	3043	1.00	0.00
Capture area	*L. patagiatus*	River playback	0.08	0.22	[-0.19, 0.36]	[-0.27, 0.45]	0.64	2305	1.00	0.00
Capture area	*L. patagiatus*	Shifted River playback	-0.04	0.21	[-0.31, 0.22]	[-0.43, 0.27]	0.59	2536	1.00	0.00
Capture area	*L. patagiatus*	Year: 2018	0.18	0.27	[-0.19, 0.52]	[-0.29, 0.62]	0.75	3081	1.00	0.00
Capture area	*L. patagiatus*	Year: 2019	0.41	0.28	[0.04, 0.73]	[-0.05, 0.84]	0.93	2989	1.00	0.00
Capture area	*L. patagiatus*	Time after sunset	0.29	0.16	[0.08, 0.48]	[0.03, 0.57]	0.96	3305	1.00	0.00
Capture area	*L. patagiatus*	Ordinal day	0.39	0.28	[0.01, 0.72]	[-0.06, 0.85]	0.93	2849	1.00	0.01
Capture area	*L. patagiatus*	Temperature	0.15	0.21	[-0.11, 0.41]	[-0.19, 0.48]	0.77	3122	1.00	0.00
Capture area	*L. patagiatus*	Wind speed	0.00	0.11	[-0.14, 0.14]	[-0.21, 0.17]	0.51	4680	1.00	0.00

Capture area	*L. patagiatus*	Elevation	0.12	0.21	[-0.13, 0.41]	[-0.20, 0.50]	0.73	2555	1.00	0.00
Capture area	*T. versicolor*	Sound pressure level	-0.54	0.14	[-0.72, -0.35]	[-0.77, -0.29]	1.00	3043	1.00	0.00
Capture area	*T. versicolor*	River playback	0.08	0.22	[-0.19, 0.36]	[-0.27, 0.45]	0.64	2305	1.00	0.00
Capture area	*T. versicolor*	Shifted River playback	-0.04	0.21	[-0.31, 0.22]	[-0.43, 0.27]	0.59	2536	1.00	0.00
Capture area	*T. versicolor*	Year: 2018	0.18	0.27	[-0.19, 0.52]	[-0.29, 0.62]	0.75	3081	1.00	0.00
Capture area	*T. versicolor*	Year: 2019	0.41	0.28	[0.04, 0.73]	[-0.05, 0.84]	0.93	2989	1.00	0.00
Capture area	*T. versicolor*	Time after sunset	0.29	0.16	[0.08, 0.48]	[0.03, 0.57]	0.96	3305	1.00	0.00
Capture area	*T. versicolor*	Ordinal day	0.39	0.28	[0.01, 0.72]	[-0.06, 0.85]	0.93	2849	1.00	0.01
Capture area	*T. versicolor*	Temperature	0.15	0.21	[-0.11, 0.41]	[-0.19, 0.48]	0.77	3122	1.00	0.00
Capture area	*T. versicolor*	Wind speed	0.00	0.11	[-0.14, 0.14]	[-0.21, 0.17]	0.51	4680	1.00	0.00
Capture area	*T. versicolor*	Elevation	0.12	0.21	[-0.13, 0.41]	[-0.20, 0.50]	0.73	2555	1.00	0.00
Prey (Diptera)	*L. patagiatus*	Sound pressure level	-1.38	0.79	[-2.38, -0.36]	[-2.69, -0.08]	0.95	2006	1.00	0.02
Prey (Diptera)	*L. patagiatus*	River playback	0.71	1.85	[-1.74, 3.09]	[-2.45, 3.86]	0.65	1959	1.00	0.04
Prey (Diptera)	*L. patagiatus*	Shifted River playback	0.57	0.93	[-0.65, 1.77]	[-0.94, 2.19]	0.73	1722	1.00	0.02
Prey (Diptera)	*L. patagiatus*	Time after sunset	0.90	0.73	[-0.12, 1.78]	[-0.39, 2.10]	0.88	2634	1.00	0.01

Prey (Diptera)	*L. patagiatus*	Ordinal day	-3.20	0.97	[-4.39, -1.94]	[-4.77, -1.63]	1.00	2214	1.00	0.02
Prey (Diptera)	*L. patagiatus*	Temperature	3.06	1.46	[1.16, 4.98]	[0.61, 5.60]	0.98	2798	1.00	0.03
Prey (Diptera)	*L. patagiatus*	Wind speed	-0.05	0.60	[-0.84, 0.69]	[-1.08, 0.93]	0.53	2310	1.00	0.01
Prey (Diptera)	*L. patagiatus*	Elevation	3.61	1.23	[2.05, 5.31]	[1.50, 5.77]	1.00	1427	1.00	0.03
Prey (Diptera)	*T. versicolor*	Sound pressure level	2.15	0.99	[0.87, 3.40]	[0.55, 3.89]	0.98	3598	1.00	0.02
Prey (Diptera)	*T. versicolor*	River playback	-2.91	2.02	[-5.42, 0.00]	[-6.30, 0.86]	0.91	2046	1.00	0.05
Prey (Diptera)	*T. versicolor*	Shifted River playback	-1.48	1.59	[-3.58, 0.52]	[-4.25, 1.15]	0.81	2327	1.00	0.04
Prey (Diptera)	*T. versicolor*	Time after sunset	-1.58	1.92	[-3.92, 0.85]	[-4.64, 1.60]	0.79	1111	1.00	0.06
Prey (Diptera)	*T. versicolor*	Ordinal day	0.67	1.98	[-2.09, 3.09]	[-2.53, 4.16]	0.64	1590	1.00	0.05
Prey (Diptera)	*T. versicolor*	Temperature	2.95	1.27	[1.41, 4.60]	[0.79, 5.02]	0.99	3065	1.00	0.02
Prey (Diptera)	*T. versicolor*	Wind speed	0.84	1.07	[-0.46, 2.32]	[-1.03, 2.62]	0.78	1630	1.00	0.03
Prey (Diptera)	*T. versicolor*	Elevation	-0.10	1.45	[-2.15, 1.63]	[-2.59, 2.35]	0.53	2210	1.00	0.03
Prey (Eph.)	*L. patagiatus*	Sound pressure level	-0.40	2.20	[-3.55, 2.37]	[-4.16, 3.69]	0.57	3120	1.00	0.04
Prey (Eph.)	*L. patagiatus*	River playback	-1.10	3.40	[-5.41, 3.64]	[-6.87, 5.19]	0.62	2567	1.00	0.07
Prey (Eph.)	*L. patagiatus*	Shifted River playback	-6.74	3.23	[-10.64, -2.24]	[-12.66, -1.62]	0.99	2885	1.00	0.06

Prey (Eph.)	*L. patagiatus*	Time after sunset	0.47	1.46	[-1.48, 2.30]	[-2.11, 2.97]	0.62	2426	1.00	0.03
Prey (Eph.)	*L. patagiatus*	Ordinal day	-2.08	1.92	[-4.73, 0.43]	[-5.58, 1.22]	0.86	2675	1.00	0.04
Prey (Eph.)	*L. patagiatus*	Temperature	2.98	2.95	[-0.88, 6.94]	[-2.31, 7.89]	0.84	2524	1.00	0.06
Prey (Eph.)	*L. patagiatus*	Wind speed	0.80	1.42	[-1.09, 2.56]	[-1.53, 3.43]	0.73	2494	1.00	0.03
Prey (Eph.)	*L. patagiatus*	Elevation	2.55	2.32	[-0.68, 5.32]	[-1.52, 6.54]	0.87	2522	1.00	0.05
Prey (Eph.)	*T. versicolor*	Sound pressure level	1.45	2.40	[-1.92, 4.92]	[-4.36, 5.23]	0.69	505	1.01	0.14
Prey (Eph.)	*T. versicolor*	River playback	-0.54	3.40	[-4.87, 3.89]	[-5.87, 5.79]	0.56	2774	1.00	0.07
Prey (Eph.)	*T. versicolor*	Shifted River playback	-8.67	8.10	[-20.23, 1.87]	[-27.61, 3.45]	0.89	2530	1.00	0.19
Prey (Eph.)	*T. versicolor*	Time after sunset	-2.87	2.78	[-6.61, 0.67]	[-7.84, 1.78]	0.85	2986	1.00	0.05
Prey (Eph.)	*T. versicolor*	Ordinal day	3.53	4.51	[-2.44, 9.09]	[-4.19, 10.81]	0.78	450	1.01	0.22
Prey (Eph.)	*T. versicolor*	Temperature	0.90	3.09	[-3.25, 5.06]	[-4.84, 6.01]	0.62	513	1.01	0.15
Prey (Eph.)	*T. versicolor*	Wind speed	-2.46	5.45	[-9.83, 4.29]	[-12.05, 6.40]	0.68	3209	1.00	0.10
Prey (Eph.)	*T. versicolor*	Elevation	-1.29	2.88	[-4.90, 2.56]	[-5.66, 4.25]	0.67	1524	1.00	0.08
Body condition	*L. patagiatus*	Sound pressure level	0.03	0.02	[-0.00, 0.06]	[-0.01, 0.07]	0.92	3650	1.00	0.00
Body condition	*L. patagiatus*	River playback	0.01	0.03	[-0.03, 0.04]	[-0.04, 0.06]	0.60	2925	1.00	0.00

Body condition	*L. patagiatus*	Shifted River playback	0.00	0.03	[-0.04, 0.04]	[-0.05, 0.06]	0.54	3076	1.00	0.00
Body condition	*L. patagiatus*	Ordinal day	-0.01	0.02	[-0.03, 0.02]	[-0.04, 0.03]	0.65	3053	1.00	0.00
Body condition	*L. patagiatus*	Elevation	-0.01	0.03	[-0.05, 0.03]	[-0.06, 0.04]	0.62	2775	1.00	0.00
Body condition	*L. patagiatus*	Year: 2018	0.01	0.04	[-0.04, 0.06]	[-0.05, 0.08]	0.61	2513	1.00	0.00
Body condition	*L. patagiatus*	Year: 2019	0.09	0.03	[0.06, 0.14]	[0.04, 0.14]	1.00	3268	1.00	0.00
Body condition	*T. versicolor*	Sound pressure level	0.00	0.01	[-0.00, 0.01]	[-0.01, 0.01]	0.69	4048	1.00	0.00
Body condition	*T. versicolor*	River playback	0.01	0.01	[-0.00, 0.01]	[-0.01, 0.02]	0.80	3270	1.00	0.00
Body condition	*T. versicolor*	Shifted River playback	0.00	0.01	[-0.01, 0.01]	[-0.01, 0.01]	0.54	3306	1.00	0.00
Body condition	*T. versicolor*	Ordinal day	0.01	0.02	[-0.02, 0.03]	[-0.02, 0.05]	0.66	2993	1.00	0.00
Body condition	*T. versicolor*	Elevation	0.01	0.01	[-0.01, 0.02]	[-0.01, 0.02]	0.74	2042	1.00	0.00
Body condition	*T. versicolor*	Year: 2018	-0.02	0.01	[-0.03, -0.01]	[-0.03, -0.01]	0.99	2473	1.00	0.00
Body condition	*T. versicolor*	Year: 2019	-0.01	0.01	[-0.02, 0.01]	[-0.02, 0.01]	0.72	2532	1.00	0.00
Abundance	*L. patagiatus*	Sound pressure level	1.06	0.23	[0.76, 1.36]	[0.65, 1.42]	1.00	4176	1.00	0.00
Abundance	*L. patagiatus*	River playback	-0.21	0.43	[-0.79, 0.33]	[-0.91, 0.55]	0.69	2157	1.00	0.01
Abundance	*L. patagiatus*	Shifted River playback	-0.60	0.43	[-1.18, -0.07]	[-1.31, 0.11]	0.93	1908	1.00	0.01

Abundance	*L. patagiatus*	Time after sunset	0.72	0.27	[0.36, 1.07]	[0.28, 1.21]	1.00	2869	1.00	0.01
Abundance	*L. patagiatus*	Ordinal day	-0.37	0.41	[-0.88, 0.18]	[-1.06, 0.31]	0.82	3373	1.00	0.01
Abundance	*L. patagiatus*	Stream width	0.77	0.25	[0.46, 1.11]	[0.38, 1.22]	1.00	3326	1.00	0.00
Abundance	*L. patagiatus*	Elevation	0.03	0.44	[-0.56, 0.57]	[-0.72, 0.81]	0.53	2315	1.00	0.01
Abundance	*L. patagiatus*	Temperature	-0.18	0.27	[-0.52, 0.14]	[-0.58, 0.26]	0.75	4128	1.00	0.00
Abundance	*L. patagiatus*	Wind speed	-0.16	0.19	[-0.39, 0.08]	[-0.47, 0.14]	0.82	5271	1.00	0.00
Abundance	*L. patagiatus*	Year: 2018	0.84	0.38	[0.33, 1.34]	[0.24, 1.52]	0.98	2885	1.00	0.01
Abundance	*L. patagiatus*	Year: 2019	0.36	0.38	[-0.15, 0.85]	[-0.26, 0.99]	0.82	3206	1.00	0.01
Abundance	*T. versicolor*	Sound pressure level	0.86	0.21	[0.60, 1.12]	[0.50, 1.18]	1.00	3236	1.00	0.00
Abundance	*T. versicolor*	River playback	-0.04	0.27	[-0.40, 0.30]	[-0.51, 0.41]	0.56	2712	1.00	0.01
Abundance	*T. versicolor*	Shifted River playback	0.11	0.24	[-0.21, 0.43]	[-0.29, 0.52]	0.68	3382	1.00	0.00
Abundance	*T. versicolor*	Time after sunset	-0.72	0.22	[-0.99, -0.43]	[-1.08, -0.37]	1.00	3187	1.00	0.00
Abundance	*T. versicolor*	Ordinal day	0.36	0.40	[-0.12, 0.92]	[-0.33, 0.99]	0.80	2379	1.00	0.01
Abundance	*T. versicolor*	Stream width	0.47	0.18	[0.22, 0.68]	[0.18, 0.79]	1.00	2933	1.00	0.00
Abundance	*T. versicolor*	Elevation	0.38	0.29	[0.02, 0.77]	[-0.07, 0.90]	0.91	2077	1.00	0.01

Abundance	*T. versicolor*	Temperature	-0.03	0.22	[-0.30, 0.28]	[-0.38, 0.34]	0.56	3611	1.00	0.00
Abundance	*T. versicolor*	Wind speed	0.13	0.16	[-0.07, 0.34]	[-0.13, 0.39]	0.80	3966	1.00	0.00
Abundance	*T. versicolor*	Year: 2018	0.41	0.31	[0.04, 0.85]	[-0.15, 0.92]	0.90	3202	1.00	0.01
Abundance	*T. versicolor*	Year: 2019	0.53	0.35	[0.07, 0.98]	[-0.07, 1.09]	0.93	2639	1.00	0.01

CHAPTER FOUR: EXPERIMENTAL RIVER NOISE ALTERS ARTHROPOD ABUNDANCE

Abstract

While anthropogenic noise has received considerable attention, we know comparatively little about the role that sources of natural noise have on wildlife abundance and distributions. Rivers and streams represent an evolutionarily ancient source of natural noise that is widespread and covers much of Earth.

For two summers, we continuously broadcasted whitewater river noise and spectrally-altered river noise (shifted upwards in frequency, but maintaining the same temporal profile) to experimentally tease apart the effects of two characteristics of noise - sound levels and background frequency – on arthropod abundances. We used five types of trapping methods, placed across 20 sites within the Pioneer Mountains of Idaho, USA, to collect and identify 151,992 specimens to the order level. We built Bayesian generalized linear mixed-effects models with noise characteristics and other habitat variables such as riparian vegetation, elevation, temperature, and moonlight.

Of the 42 models we built (one for each order-trap type combination), 26 (62%) indicated a substantial response to at least one noise variable - sound pressure level, background frequency, or an interaction between the two. Fourteen of seventeen (82%) arthropod orders responded to noise in some capacity: Araneae, Coleoptera, Collembola, Dermaptera, Hemiptera, Hymenoptera, Lepidoptera, Neuroptera, Opiliones, Orthoptera,

Plecoptera, Raphidioptera, Thysanoptera, and Trichoptera, while the only three groups that appear to be unaffected were Acari, Archaeognatha, and Diptera.

These results suggest that the natural acoustic environment can shape arthropod abundances both directly and indirectly (via predator-prey relationships). Future work should further examine the role that the indirect effects of noise play in food webs. Natural noise should be considered an important ecological niche axis, especially as we continue to alter natural acoustic environments and replace them with anthropogenic ones.

Introduction

Riparian areas are well-known biodiversity hotspots (Naiman, Decamps & Pollock, 1993; Hauer et al., 2016) that have the ability to shape communities (Malanson, 1993; Naiman & Decamps, 1997). However, it is not always clear what components of the riparian zone contribute to community structure. Streamflow, for example, can influence animal community structure (Bain, Finn & Booke, 1988; Mitchell & Cunjak, 2007; McIntosh et al., 2008), yet this variable is inextricably linked to another that we know little about – noise (Kacem et al., 2020).

While our understanding of the effects of anthropogenic noise on wildlife is ever accumulating (Nowacek et al., 2007; Wright et al., 2007; Barber, Crooks & Fristrup, 2010; Kight & Swaddle, 2011; Ellison et al., 2012; Francis & Barber, 2013; Williams et al., 2015; Shannon et al., 2016; Jerem & Mathews, 2020), we are in the early stages in understanding how natural sources of abiotic noise might constrain and structure animal behavior, populations, and communities (Le et al., 2019; Gomes, Hesselberg & Barber, 2020; Gomes, Francis & Barber, 2021). Recent work with orb-weaving spiders, for example, suggests that actively foraging spiders are more abundant and build smaller webs with increasing intensity of river noise (Gomes, Hesselberg & Barber, 2020).

Arthropods belong to the most species-rich group of organisms on the planet, yet they are greatly understudied in anthropogenic noise research (Shannon et al., 2016; Jerem & Mathews, 2020). Further, arthropods are one of the least studied groups in conservation research in general (Clark & May, 2002; Donaldson et al., 2016; Troudet et al., 2017), despite being indicators of disturbance and restoration success (Williams, 1993; Willett, 2001; Longcore, 2003) and essential to ecosystem services and functions (Yang & Gratton, 2014; Noriega et al., 2018; Elizalde et al., 2020).

While habitat preferences and essential niche parameters remain unknown for many groups of arthropods, at least some are affected by noise (Morley, Jones & Radford, 2014; Bunkley et al., 2017; Phillips et al., 2019; Raboin & Elias, 2019; Gomes, Hesselberg & Barber, 2020). Hearing has evolved at least 24 times in insects (Hoy & Robert, 1996; Greenfield, 2016), and arthropods are known to produce sounds for a number of reasons including aggression, species recognition, mate attraction, predator avoidance, and prey detection (reviewed in Morley et al., 2014 and Raboin & Elias, 2019). Thus, arthropod communication and perception can be directly affected by noise via airborne sound or substrate-borne vibrations (Lampe et al., 2012; Raboin & Elias, 2019). Indirect effects are also possible, since noise can disrupt predator-prey interactions (Purser & Radford, 2011; Gomes et al., 2016; Mason, McClure & Barber, 2016; Barton et al., 2018; Senzaki, Kadoya & Francis, 2020), and drives away many arthropod predators, such as birds and bats (Gomes et al., accepted; Schaub, Ostwald & Siemers, 2008; Francis, Ortega & Cruz, 2011; McClure et al., 2013; Bunkley & Barber, 2015).

Here we used a noise-playback experiment and a large-scale arthropod monitoring scheme to explore how river noise and other habitat variables influence arthropod abundance. For three months, in each of two years, we broadcast whitewater river noise and spectrally altered river noise, containing the same temporal profile, across the Pioneer Mountains of Idaho, USA. We used this experimental manipulation along with variation in the intensity and frequency of natural stream noise to create continuous gradients of sound level and frequency across the landscape. After collecting and identifying 152,262 invertebrate specimens, we used continuous noise predictors to understand how the acoustic environment altered arthropod abundance with Bayesian generalized linear mixed effects models. We predicted that the majority of arthropods would be affected by noise through either: 1) direct responses to noise, since many taxa are likely able to detect river noise (Morley, Jones & Radford, 2014; Greenfield, 2016), 2) indirect effects via noise avoidance of bird and bat predators, which largely avoid whitewater river noise at our sites (Gomes et al., accepted), or 3) some combination of the above. For arthropods that use sound for communication or predator detection and avoidance, we expected declines in abundance due to noise, since those taxa can move away from the noise source or have decreased survival due to not hearing predator or prey sounds. We expected those that are prey to birds and bats to increase in abundance in noise via top-down effects (*e.g.* through predator shielding effects). However, some taxa will likely fit into both categories and may elicit more complex patterns.

Methods

Site setup

We conducted this study in riparian areas of the Pioneer Mountains of Idaho, USA, which are dominated by willow (*Salix* sp), cottonwood (*Populus trichocarpa / angustifolia*), and aspen trees (*Populus tremuloides*). Riparian areas were sparsely surrounded by conifers on north-facing slopes, but otherwise surrounded by sagebrush steppe. Twenty sites were selected and matched for elevation and riparian habitat [spanning five drainages: Copper Creek (43.440288, -113.714253), Cottonwood Creek (43.467060, -113.635988), and Fish Creek (43.467060, -113.635988) on Lava Lake Ranch, and Trail Creek (43.755391, -114.287517) and Hyndman Creek (43.696034, -114.190139) near Sun Valley; see Figure 2.1A, Gomes et al. *in review*]. These 20 sites consisted of 10 noise-playback sites and 10 control sites (Figure 2.1A). Sites were an average of 1,377 m (median: 1,310 m; range: 650 – 3,526 m) away from their nearest neighboring site, as measured along the riparian area (both noise and invertebrates travel through the riparian valley easier than over the tops of mountain ridges), ensuring all sites were acoustically and biologically independent.

Sites

Control sites ranged from slow-moving streams to whitewater torrents, and represented unaltered acoustic environments that contained a natural range of sound pressure levels (mean ± SD: 51.6 ± 9.1 dBA; range: 35.1 – 69.8 dBA) and median frequencies (mean ± SD: 3.4 ± 2.0 kHz; range: 1.2 – 10.3 kHz; *see Acoustic environment quantification* for more information on acoustic measurements). Noise-playback sites, on the other hand, were relatively slow-moving stream sites pre-noise exposure (i.e. low sound level) where we broadcast high sound level whitewater river recordings via speaker arrays. We designed five of these experimental sites to have natural sound pressure levels and frequency spectra of whitewater rivers – termed “river noise” sites (mean SPL ± SD: 66.1 ± 4.9 dBA; SPL range: 48.4 – 73.2 dBA; mean frequency ± SD: 2.1 ± 1.6 kHz; frequency range: 0.6 – 8.5 kHz). At the remaining five “shifted river” sites, we broadcast the same audio files at similar sound pressure levels (mean SPL ± SD: 69.9 ± 5.6 dBA; SPL range: 50.6 – 78.9 dBA) and amplitude modulation profiles as our other playback sites, but that were shifted upwards in frequency (mean frequency ± SD: 5.1 ± 1.1 kHz; frequency range: 3.0 – 7.4 kHz). Our shifted-river treatment allowed us to test whether the patterns we observed were specific to river spectra, or general to intense acoustic environments more broadly.

Noise playback

We suspended noise-playback speakers from tripods (height: ~3 m) constructed of 4.5 m metal conduit. We broadcasted river noise at each river-noise site (see above) with two Octasound SP820A speakers (KDM Electronics Incorporated, Ajax, ON, Canada) placed 100 m apart. We broadcasted shifted-river noise at each shifted site via three Octasound SP800A speakers (KDM Electronics Incorporated) placed 50 m from each other in a line parallel to the stream (Figure B.15). This disparity in equipment was to ensure similar noise exposure between treatments, as the higher frequencies in our shifted-noise treatment experienced greater attenuation with distance from the speakers (see Gomes et al., in review and Figure B.3 for more details). At control sites we placed speaker horns on three dummy towers (each 50 m apart) made of 4.5 m long PVC (Figure B.3) and particle board spray-painted black to mimic the infrastructure at experimental sites. Because the river-noise sites only had two speakers 100 m apart, we likewise placed a dummy tower at their center such that all sites within our experimental paradigm consisted of three towers spaced at 50 m increments (Figure B.3).

Speakers were powered by an amplifier (AD1200.1, PRV audio) connected to two 12 V deep cycle RV/marine batteries (DURDC12-100P; Duracell), which were charged by solar panels (Suniva OPT285-60-4-100; MidNite Solar Inc., WA, USA) via solar controllers (The Kid 30A MPPT; MidNite Solar Inc., WA, USA). This allowed us to continuously playback noise, 24 hours a day for three continuous months in 2017 and 2018.

Data collection

We collected arthropods during the months of May-July in 2017 and 2018 along the riparian areas of our 20 sites (Figure 2.1A). We sampled each site (n = 20) twice per year with the exception of two Trail Creek sites, which were only sampled once during 2017 due to limited access to these locations (*i.e.* 38 site sampling visits). We used six types of trapping methods to collect arthropods near the center of each site: beat-netting, pitfall traps, blue and yellow fly (vane) traps, Malaise traps, and ultraviolet light bucket traps. We deployed all traps (excluding beat-netting) in the morning (0800 – 1000 hours), left in the field for two nights, and then collected traps in the afternoon (1200 – 1400) of the third day.

Beat-netting

We located a willow tree (*Salix* sp.) adjacent to the stream at each site (Figure B.15). We beat-netted this willow with the following protocol: we placed an insect sweep net (42 cm diameter) underneath a South-facing willow branch and beat the branch four times with a metal rod. We then collected the arthropods that had fallen into the net and placed them into a vial containing 95% ethanol and repeated this sampling procedure for the other three cardinal directions around the tree. All specimens were placed in the same vial of ethanol for all four branches and treated as a single sample.

Pitfall traps

We buried five round clear plastic containers (opening diameter: 9 cm) in the ground such that the tops (opening) of the containers were flush with the ground surface. Bird netting (1 cm x 1 cm mesh size) covered these containers to keep vertebrates out of the containers. We placed these five pitfall traps 5 m from the stream and 5 cm apart from each other in a straight line parallel to the stream (Figure B.15). Each pitfall trap contained propylene glycol that was poured to a depth of 1 cm to act as a killing and preserving agent. During trap and sample collection, we combined the five pitfall traps and they together were treated as one sample.

Fly (vane) traps

We placed two vane traps (one yellow, and another blue) at each site during each sampling effort. Vane traps were fixed to 1 m sections of bent rebar that were driven approximately 25 cm into the ground, just adjacent to the pitfall traps (Figure B.15). Thus, the top of the vane traps hung about 0.5 m off the ground. The bottom of each vane trap was attached to a collection container that held a 4 cm^2 piece of insect pest poison strips (HG-96554, Hot Shot, Spectrum Brands, Inc.) that rapidly killed any insects that entered the container. We counted the contents of each colored vane trap separately (Table 4.1), but we aggregate them for statistical analysis (Table 4.2) since they both attract flower visitors.

Malaise traps

We set up Malaise intercept traps (#2869; BioQuip Products, Inc.) 10 m from the stream (Figure B.15), and staked down on all four corners to withstand wind. We placed a 4 cm^2 piece of insect pest poison strips (HG-96554, Hot Shot, Spectrum Brands, Inc.) into the collection vials of the Malaise traps (see above).

Ultraviolet (UV) light traps

We placed ultraviolet bucket traps (#2851A; BioQuip Products, Inc.) next to Malaise traps (approximately 0.5 m apart) such that the UV bucket and Malaise trap were in a line, parallel with the stream (Figure B.15). We powered ultraviolet bulbs (12 watt; FUL12T6/BL; #2807W; BioQuip Products, Inc.) with 12 V batteries (35Ah AGM; DURA12-35C, Duracell), which we automated to turn on after sunset, and turn off after sunrise, with a photo sensor (LCA612D; Precision Multiple Controls, Inc.) that acts as a power switch. The UV bucket traps contained a depth of approximately 3 cm with propylene glycol to act as a killing and preserving agent.

Arthropod identification

We identified all arthropods to order with the aid of a dissection microscope and dichotomous key (Johnson & Triplehorn, 2005) using an updated taxonomy (Misof et al., 2014), except when arthropods were too damaged to identify (Table 4.1; 0.18% of specimens). We chose to identify samples to the order level, as it can offer similar inferences to species-level identification in ecological studies (Bolger et al., 2000; Biaggini et al., 2007). Our decision to avoid finer taxonomic resolution was also driven by an increase in time, financial costs, and erroneous identifications (Duelli & Obrist, 1998; Jones, 2008).

Environmental variables

Acoustic environment quantification

There was variation in noise propagation and attenuation through the landscape and natural variation in background acoustic environments across our sites. Thus, we ultimately created continua of treatments – or realized treatments. Instead of trying to arbitrarily categorize these realized treatments, we chose to quantify the acoustic environment and ask specifically what components of noise (i.e. sound levels and frequency; Francis & Barber, 2013; Gomes et al., 2021) drive arthropod abundance. We argue that a categorical analysis of a gradient is almost always going to be a cruder approach than a continuous analysis since categories unnecessarily collapse information that can be useful in estimating effects of predictor variables.

We quantified the acoustic environment with long-term recordings from Roland R05 recorders (hereafter referred to as an ARU: acoustic recording unit; ARU settings: 44.1 kHz sampling rate, 128 kbps MP3 recording mode, input gain was set to 55, mic gain = 'H', limiter = 'off', and low cut = 'off'). We converted 106,769 hours of long-term ARU recordings into daily averaged median sound pressure levels (L50; measured as dBA rel. 20 µPa) using custom software 'AUDIO2NVSPL' and 'Acoustic Monitoring Toolbox' (Damon Joyce, Natural Sounds and Night Skies Division, National Park Service).

For background frequency, we used custom software (Gomes, 2020b) in the programming language R (R Core Team, 2017) and the package 'FFmpeg' (FFmpeg Developers, 2018) in command prompt to convert the above long-term recordings into 71,282 individual 3-minute files starting each hour of the day. Thus 24, 3-minute files were created per acoustic recording location per day (one for every hour). We then used the packages `tuneR` (Ligges, 2013) and `seewave` (Sueur, Aubin & Simonis, 2008) to read in and measure the median frequency of sound files, respectively. These hourly median frequencies were then averaged by date to create a daily metric of average median background noise frequency.

Percent riparian vegetation

We quantified the proportion of riparian vegetation surrounding sampling locations as a location-specific parameter in our models. We used high spatial resolution land-cover data to manually create polygon vertices surrounding all patches of riparian vegetation (defined as non-coniferous trees and non-*Artemisia* ground cover) within a 100 m radius of each sampling location. Following riparian vegetation classification, we calculated the proportion of land-cover within a 100 m radius of each sampling location that was riparian vegetation using ‘Tabulate Intersection’ in ArcMap 10.2 (Esri, CA, USA).

Moon illuminance and temperature

Moonlight is known to alter insect activity and abundance measured in traps (Williams, 1936; Bowden & Church, 1973; McGeachie, 1989; Yela & Holyoak, 1997). Thus, we calculated moon illuminance using custom windows command line code, *sunmoon* program (Jeff Conrad *unpublished software*), which calculates illuminance based on the latitude and longitude of our sites, and the position of the earth, sun, and moon. The methods are similar to those of Janiczek and DeYoung (1987). Sun and Moon positions are determined using the more accurate formulas of Van Flandern and Pulkkinen (1979). In these calculations we ignored cloud cover because our sites are within an arid, desert environment that rarely experienced clouds during our experiment and sampling scheme. We used logging weather meters placed across the drainages to measure temperature over the course of the experiment (Kestrel 4000; Boothwyn, PA, USA).

Statistics

We explored data following the protocol of Zuur, Ieno & Elphick (2010). We built a generalized linear (mixed) effects model within a Bayesian framework with MCMC in Stan within the R programming language (R Core Team, 2017), with the package `rstanarm` (Gabry & Goodrich, 2016). MCMC is essentially a simulation technique to obtain the distribution of each parameter in a model (Zuur & Ieno, 2016). Most model settings were `stan_glmer.nb` defaults (see Gabry & Goodrich, 2016). For example, priors were weakly informed normal distributions ($\mu = 0$, $\sigma = 2.5$). Each model ran for 4000 iterations (2000 sample iterations after 2000 “burn-in” iterations) in each of 4 chains. There were no divergent transitions in simulated parameter trajectories, suggesting the posterior was well-explored, all chains mixed well (Gelman-Rubin coefficients near 1), we visually checked model fits and residuals (Zuur & Ieno, 2016), and examined each model for collinearity by using Variance Inflation Factors (VIF) with the package `performace` (Lüdecke et al., 2019). We did not thin chains, as it is not recommended in most cases (Link & Eaton, 2012).

We fit arthropod abundance data as a response variable (overdispersed counts) with negative binomial distributions (log link). We built individual models for each arthropod order and trap type combination because different taxa were found within each trap, and more importantly, each trap often caught species from different foraging guilds.

For example, Hymenoptera in pitfall traps are almost always ground-dwelling ants, which are quite different from Hymenoptera in UV bucket traps, which were mostly parasitic wasps. Thus, while financial, logistical, and time constraints did not allow us to identify our 150,000+ specimens below the order level, we analyze them separately by trap so that we can make distinct inferences (as to not potentially obfuscate meaningful results) and compare our work to others that use only one trap type (Montgomery et al., 2021). However, we decided *a priori* to only build models for order-trap type combinations that seemed biologically-relevant (indicated in Table 4.1). For example, we did not analyze Lepidoptera in pitfall traps because Lepidoptera are not cursorial, ground-dwelling insects, and thus we would be unsure how to interpret those data.

In all models, we included sound pressure level (dB), median frequency (kHz), the interaction between the two, ordinal date, riparian vegetation (%), elevation (m), moon illuminance (lux), temperature (°C), year (2017 or 2018) as explanatory variables (fixed effects). Additionally, in all models we fit site as a random effect (intercept). We fit year as a fixed effect rather than a random effect as it included fewer than 5 levels necessary for estimation (Harrison et al., 2018; Silk, Harrison & Hodgson, 2020). To make direct comparisons between variables that were continuous and those that are factors, we centered all continuous variables by their mean, and scaled by 2 standard deviations (Gelman, 2008). We combined all models into a table (Table B.14), which we created with help from the R packages \`bayestestR\` and \`sjstats\` (Makowski, Ben-Shachar & Lüdecke, 2019; Lüdecke, 2020), and we plotted figures with R packages \`bayesplot\`, \`sjPlot\`, and \`ggplot2\` (Wickham, 2011; Gabry & Mahr, 2017; Lüdecke, 2018). Supplemental data and code on Zenodo (Gomes & Barber, 2021)

Results

We collected 152,262 invertebrates and identified 151,992 of them to one of 27 orders (99.8% identified to order, with 270 (0.02%) treated as unidentifiable due to damage; Table 4.1). Orders with the greatest abundance were Lepidoptera (42.6%), Diptera (28.5%), Hymenoptera (8.6%), Collembola (6.7%), Hemiptera (3.6%), Trichoptera (3.6%), Coleoptera (3.1%), and Araneae (1.0%) with the remaining 19 orders making up the remaining 2.4% (Table 4.1).

Based on 80% credible intervals, eight order-trap combinations (including six different arthropod orders: Araneae, Coleoptera, Collembola, Dermaptera, Hemiptera, and Opiliones) increased in abundance with increasing sound pressure levels (Figure 4.1a; Table B.14), while two order-trap combinations decreased in abundance with increasing sound pressure levels (Araneae in Malaise traps and Thysanoptera in vane traps). For three order-trap combinations, sound pressure level was the strongest predictor in the model; Coleoptera in pitfalls and Araneae in UV traps responded positively to sound levels while Thysanoptera in vane traps responded negatively (see supplement for individual model estimates).

Two order-trap combinations demonstrated increased abundance with increasing median frequency of the background acoustic environment (Neuroptera in UV traps and Opiliones in pitfall traps), while twelve order-trap combinations decreased in abundance with increasing background frequency (Figure 4.1b).

Seven order-trap combinations have negative estimates (80% CI does not overlap 0) for sound level by median frequency interactions (Figure 4.2a), indicating that the effect of sound level decreases, or becomes more negative, as median frequency increases (see representative examples in Figure 4.2b, c). Six order-trap combinations have positive estimates (80% CI does not overlap 0) for sound level by median frequency interactions, suggesting that the effect of sound level increases as median frequency increases (see Figure 4.2d, e). For eight order-trap combinations, the sound level by frequency interaction was the strongest predictor of abundance in the model; Plecoptera and Trichoptera in Malaise traps (Figure 4.3), Lepidoptera larvae from beat-netting, and Hemiptera in vane traps had negative estimates (see above for interpretation), while Hemiptera and Araneae in Malaise traps and Hemiptera and Hymenoptera from beat-netting had positive estimates.

Of the 42 models we built (one for each order-trap type combination), 26 (62%) indicate a substantial response (not overlapping at 80% CI) to sound pressure level, background frequency, or an interaction between the two (see Figures 4.1, 4.2; Table B.14). Fourteen of seventeen arthropod orders responded to noise in some capacity: Araneae, Coleoptera, Collembola, Dermaptera, Hemiptera, Hymenoptera, Lepidoptera, Neuroptera, Opiliones, Orthoptera, Plecoptera, Raphidioptera, Thysanoptera, and Trichoptera, while the only three groups that appear to be unaffected are Acari, Archaeognatha, and Diptera.

Twelve order-trap combinations increased in abundance with increased moon illumination (Figure 4.4: Archaeognatha, Dermaptera, and Orthoptera in pitfall traps; Coleoptera in vane traps; Diptera in vane, Malaise, and UV traps; Hemiptera in Malaise and pitfall traps; Hymenoptera in Malaise traps; and Trichoptera in Malaise and UV traps), while three order-trap combinations decreased in abundance with increasing moon illuminance (Araneae, Lepidoptera, and Neuroptera in UV traps).

Discussion

Our data indicate that whitewater river noise alters the abundances of some arthropods at the order level. Sound pressure level, background frequency, and their interaction had demonstrable effects on many arthropod order-trap combinations, indicating that the acoustic environment is an important force that shapes the local abundance of these animals. It is possible that some of the taxa studied here are using stream noise as an indicator of habitat quality (reviewed in Gomes et al., 2021; Kacem et al., 2020; Zhao et al., 2017). Obligate aquatic insects, such as Plecoptera and Trichoptera were more abundant in intense low-frequency noise, but less abundant in intense high-frequency noise (Figure 4.3). This might suggest that low frequencies are indicative of higher quality stream habitat for these taxa.

Some patterns found here conflict with those found in a previous study that examined the impact of anthropogenic noise (Bunkley et al., 2017). Spiders (Araneae) in pitfall traps here were more abundant with higher sound levels, whereas those in natural gas fields were either not affected by sound levels (family: Salticidae and Gnaphosidae) or showed negative relationships (family: Lycosidae; Bunkley et al., 2017). However, the number of salticid and lycosid specimens collected in this previous study was relatively small, and thus the effects reported might be influenced by stochastic noise in the data-generating process. Bunkley et al. (2017) also found no effect of sound levels on beetles (Coleoptera) in pitfalls, while here we show demonstrably strong positive effects. These differences in patterns for both spiders and beetles might exist for several reasons. Firstly, the characteristics of the noise exposure differed [whitewater river noise appears much more broadband (Gomes, Francis & Barber, 2021) than compressor stations (Cinto Mejia, McClure & Barber, 2019)]. Additionally, the studies were in two different locations with likely different abiotic habitat conditions and arthropod communities. While habitat differences limits the comparison, Bunkley et al. (2017) is the only other, to our knowledge, experimental study of noise on arthropod abundance.

Other patterns are consistent with previous work. Hymenoptera and Orthoptera in our pitfall traps were dominated by ants (Formicidae) and grasshoppers (Acrididae) respectively, which did not appear to respond to sound levels of river noise in this study or of compressor noise in Bunkley et al. (2017). This is a bit surprising as grasshoppers can hear and communicate with airborne sound (Hoy & Robert, 1996; Greenfield, 2016). If exposed to road-traffic noise during development, bow-winged grasshoppers (*Chorthippus biguttulus*) call at higher frequencies, presumably to maintain communication in noise (Lampe et al., 2012; Lampe, Reinhold & Schmoll, 2014). It seems likely that communicating orthopterans at our sites are coping with noise via myriad mechanisms (Gerhardt & Huber, 2002; Schmidt & Römer, 2011; Römer, 2013; Gomes, Francis & Barber, 2021)

Cicadellidae, the dominant family of Hemiptera in Bunkley et al. (2017), were more abundant in pitfall traps located in high sound level environments during that study. Here, Hemiptera in pitfalls trend in the same direction with an 88.1% probability of a positive response. However, we do not know the family composition of Hemiptera within this current study, which limits this comparison. Acoustic communication plays an essential role across several families of the Hemiptera (Liao & Yang, 2015; Greenfield, 2016; Hegde, 2019). Thus, their affinity for high sound level environments is somewhat surprising and might suggest that they are able to communicate effectively in these types of noise exposure (Schmidt & Römer, 2011; Römer, 2013), but this is speculative.

Noise can directly affect arthropods if it can be perceived via sensory systems. Noise consists of particle motion, which occurs mostly near a source (within 1 wavelength from the source), and pressure waves, which can travel much further (reviewed in Raboin & Elias, 2019). Particle motion detection, or near-field hearing, occurs in many arthropods via Johnston's organs or filiform hairs, while the ability to hear far-field sounds, or pressure waves, is less common among arthropods, but has received far more attention (reviewed in Raboin & Elias, 2019). Of the six orders in the present study that are known to use far-field sound (Coleoptera, Diptera, Hemiptera, Lepidoptera, Neuroptera, and Orthoptera; Greenfield, 2016), Diptera is the only one that did not seem to be affected by any characterization of the acoustic environment. It is possible that some members of the order are attracted to river noise because it represents favorable breeding environments, whereas others might be averse to it because it may interfere with courtship signals (Kirchner, 1997), resulting in no change at the order level. In other words, the family, genus, or species-level resolution might show different, and possibly opposing, patterns that are lost at the order level. This may be especially true for Diptera because the order is comprised of an especially high diversity of ecologies and highly tuned sensory systems (Wiegmann et al., 2011; Strauß & Lakes-Harlan, 2014; Su et al., 2018).

Some of the patterns presented here are suspected to be at least somewhat influenced by indirect effects since many insectivorous bird and bat predators avoid high sound levels within this system (Gomes et al., accepted). Araneae, Coleoptera, Collembola, Dermaptera, Hemiptera, and Opiliones in some (but not all) trap types all increased in abundance with increasing sound pressure levels. Araneae, Coleoptera, and Hemiptera are commonly found within the diets of the noise-averse predators within this system (*Corynorhinus townsendii, Myotis californicus, Myotis ciliolabrum, Myotis lucifigus, Myotis yumanensis, Empidonax oberholseri, Melospiza melodia, Piranga ludoviciana*; Table 4.2) (Clare et al., 2011; Carlisle et al., 2012; Girard et al., 2012; Gordon et al., 2019a). Collembola DNA sequences were found in two bat species' diets (*Corynorhinus townsendii* and *Myotis yumanensis*), although collembolans may have been consumed by something that these bats ate, rather than directly consumed by the bats themselves. We cannot say as much about Dermaptera and Opiliones in vertebrate diets, since many of these studies (e.g. Elizabeth L. Clare, Symondson, Broders, et al., 2014; Elizabeth L. Clare, Symondson, & Fenton, 2014; Gordon et al., 2019) used primer sets that are unable to amplify these orders (Jusino et al., 2019). Future research should seek to elucidate these indirect links more clearly, as these suggested patterns are possible, but largely speculative.

Many orders increased in abundance with increasing moon illumination (Archaeognatha, Dermaptera, Diptera, Hemiptera, Hymenoptera, Orthoptera, and Trichoptera). Possible underlying reasons include both direct (e.g. success with increased visual access to foraging patches or oviposition sites) and indirect (e.g. arthropod predators might avoid moonlight) causes (Saldaña-Vázquez & Munguía-Rosas, 2013; Prugh & Golden, 2014). Indirect effects are likely as nearly all bat predators in our system decline with increased moon illuminance (Gomes et al., accepted), and many of these species are known to consume the above orders (excluding Archaeognatha and

Dermaptera) (Johnson, Lacki & Baker, 2007; Clare et al., 2011, 2014; Clare, Symondson & Fenton, 2014; Gordon et al., 2019a; Maucieri & Barclay, 2020).

Other orders decreased in abundance with increased moon illumination (Araneae, Lepidoptera, and Neuroptera). However, this result may not reflect changes in abundance, but rather is likely an artifact of the sampling method, as the decrease occurred only with ultraviolet light trap samples. Indeed, other studies have shown a decrease in light trapping capture success on well-lit nights (Williams, 1936; Williams & Singh, 1951; Bowden & Church, 1973; Persson, 1976; McGeachie, 1989; Yela & Holyoak, 1997).

This research highlights the importance of natural noise as an ecological niche axis for arthropods, which may shape their abundance via both direct (e.g. communication) and indirect (e.g. predator-prey) mechanisms. Finer taxonomic resolution and diet studies are necessary to further elucidate these patterns. Arthropods are declining rapidly across the world (Wagner et al., 2021), and additional emphasis on understanding links between sensory systems and sensory environments is much needed (Gomes, Francis & Barber, 2021). As we continue to alter natural acoustic environments and replace them with anthropogenic ones (Buxton et al., 2017) there will likely be drastic changes to community composition and food web dynamics, which are ripe for future exploration.

Table 4.1 Identified arthropod counts by trap type and order.

Counts are summed across all sites. Shaded cells indicate that Bayesian generalized linear mixed-effects models were built (see Table 4.2; Figures 4.1, 4. 2, 4.4). ϕ Acari consist of the orders Parasitiformes and Acariformes. ʔ Lepidoptera larvae are not their own order, but are kept separate from Lepidoptera to keep inferences about the different life stages separate. ʒ "Damaged" are not an order, but are the number of specimens too damaged to be able to identify to the order level. † Haplotaxida are not arthropods.

		Vane (fly) traps:						
Order	UV bucket	Yellow vane	Blue vane	Pitfall	Malaise	Beat-net	Sum	% of total
Lepidoptera	57015	365	48	120	7012	11	64571	42.41
Diptera	26749	688	858	1882	12981	232	43390	28.5
Hymenoptera	2751	686	199	7407	1884	233	13160	8.64
Collembola	2307	16	3	6226	1632	13	10197	6.7
Hemiptera	592	303	75	851	3176	497	5494	3.61
Trichoptera	4793	18	8	47	571	13	5450	3.58
Coleoptera	1103	1063	414	1037	975	138	4730	3.11
Araneae	136	25	14	1230	38	100	1543	1.01
Acari ϕ	89	9	7	681	59	3	848	0.56
Raphidioptera	45	39	12	0	437	2	535	0.35
Plecoptera	50	46	5	14	309	24	448	0.29
Thysanoptera	13	128	105	61	41	15	363	0.24
Opiliones	19	4	0	254	1	1	279	0.18
Lepidoptera larvae ʔ	29	20	21	54	36	113	273	0.18
Damaged ʒ	100	26	19	44	56	25	270	0.18
Dermaptera	86	7	10	106	35	2	246	0.16
Archaeognatha	3	0	0	151	0	0	154	0.1
Orthoptera	21	2	0	80	9	0	112	0.07
Neuroptera	81	0	0	2	23	4	110	0.07
Diplopoda	2	0	0	24	0	0	26	0.02
Ephemeroptera	2	2	1	1	9	3	18	0.01
Pseudoscorpiones	1	2	0	5	0	0	8	0.01
Haplotaxida †	0	0	0	7	0	0	7	0
Chilopoda	0	0	0	7	0	0	7	0
Blattodea	1	0	0	5	1	0	7	0
Psocoptera	1	0	0	3	2	0	6	0
Zygentoma	0	1	0	4	0	0	5	0
Odonata	0	0	1	0	2	1	4	0
Siphonaptera	0	0	0	1	0	0	1	0
Total	95989	3450	1800	20304	29289	1430	152262	100

Table 4.2 **Possible patterns of indirect relationships.**

Each column consists of bat and bird predators that decreased in the system in response to higher sound levels (Gomes et al., accepted), while each row consists of arthropod orders that increased under the same conditions in the current study. Citations within the table are linking those orders to those predator taxa via diet analysis studies. * = Collembola are likely from a lower trophic level (see main text). ? = primers used in Gordon et al. 2019 and Clare et al. 2011 do not amplify Dermaptera or Opiliones DNA (Jusino et al. 2019). Blank cells represent that we did not find any studies linking the predator and prey.

Insectivorous predators that **decreased** in high sound level environments

Insect orders that **increased** in high sound level	Bats				
	Townsend's big-eared bat *Corynorhinus townsendii*	California myotis *Myotis californicus*	Western small-footed bat *Myotis ciliolabrum*	Little brown bat *Myotis lucifigus*	Yuma myotis *Myotis yumanensis*
Araneae	Gordon et al. 2019	Gordon et al. 2019	Gordon et al. 2019	Clare et al. 2011	Gordon et al. 2019
Coleoptera	Gordon et al. 2019	Gordon et al. 2019	Gordon et al. 2019	Clare et al. 2011	Gordon et al. 2019
Collembola	Gordon et al. 2019*				Gordon et al. 2019*
Dermaptera	?	?	?	?	?
Hemiptera	Gordon et al. 2019	Gordon et al. 2019	Gordon et al. 2019	Clare et al. 2011	Gordon et al. 2019
Opiliones	?	?	?	?	?

Insect orders that **increased** in high sound level	Birds		
	Dusky Flycatcher *Empidonax oberholseri*	Song sparrow *Melospiza melodia*	Western Tanager *Piranga ludoviciana*
Araneae	Carlisle et al. 2012	Girard et al. 2012	Carlisle et al. 2012
Coleoptera	Carlisle et al. 2012	Girard et al. 2012	Carlisle et al. 2012
Collembola			
Dermaptera			
Hemiptera	Carlisle et al. 2012	Girard et al. 2012	Carlisle et al. 2012
Opiliones			

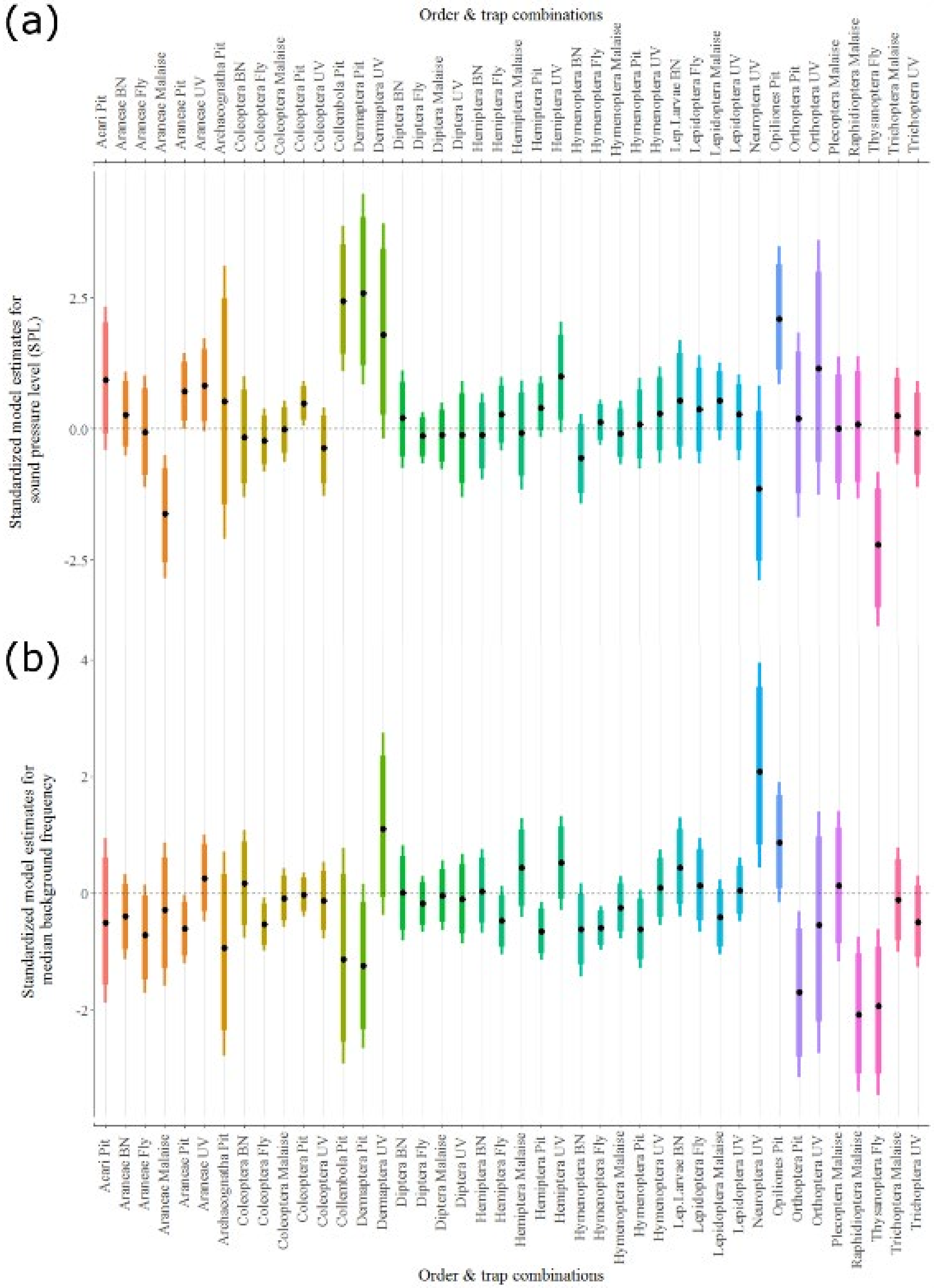


Figure 4.1 **Estimates of the effects of sound pressure level and median background frequency on arthropod abundance.**

Black dots represent point estimates for standardized effect sizes (y axis) for each order-trap combination (x axis). Thin vertical bars around estimates represent 90% credible intervals and thick vertical bars represent 80% credible intervals. Colors of bars differ at the order level. Dashed line at 0 indicates no effect on arthropod abundance.

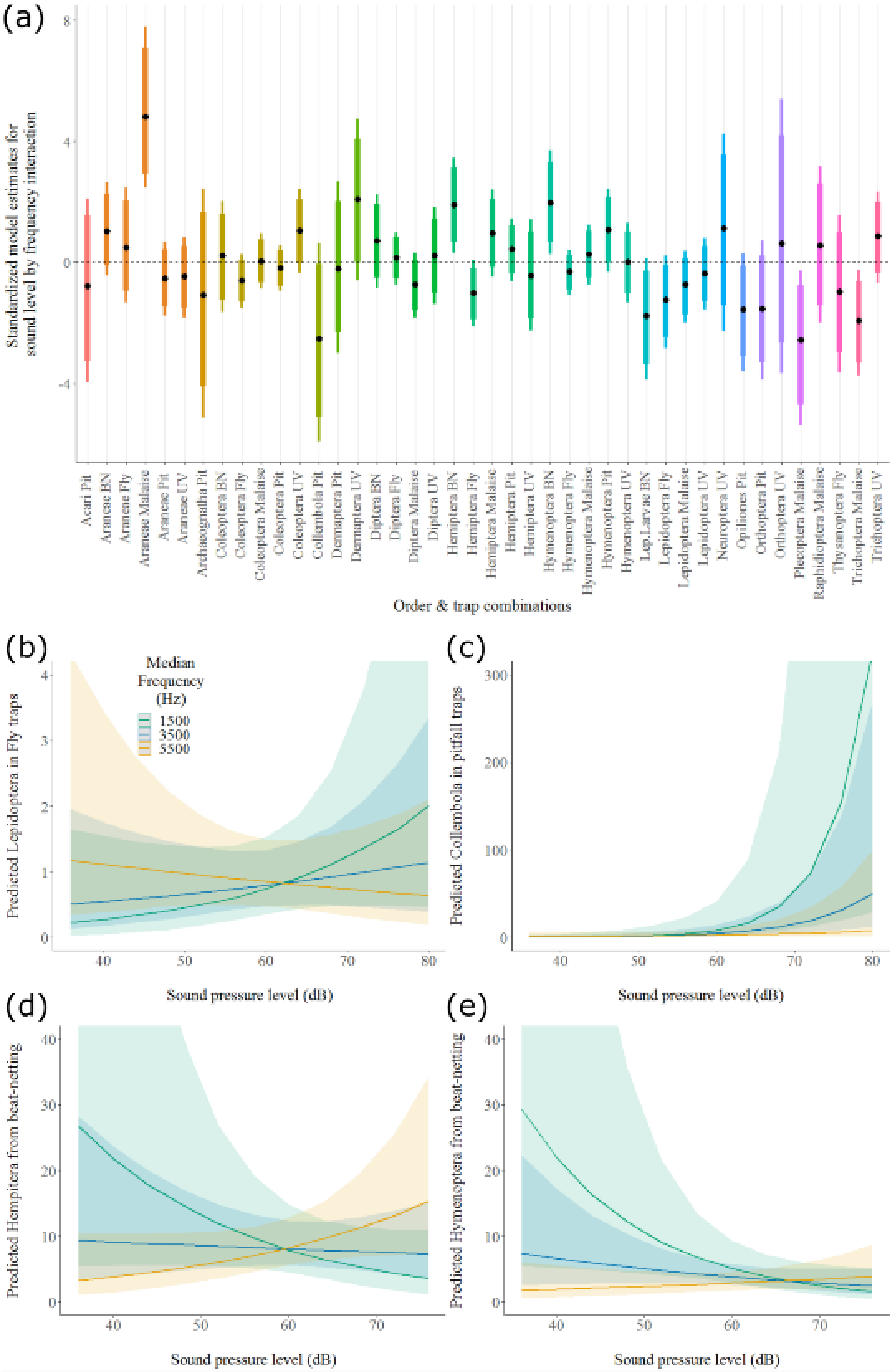


Figure 4.2 Estimates of the interaction effects of sound pressure level by median background frequency on arthropod abundance.

Black dots represent point estimates for standardized effect sizes (y axis) for each order-trap combination (x axis). Thin vertical bars around estimates represent 90% credible intervals (CI) and thick vertical bars represent 80% CI. Colors of bars differ at the order level. Dashed line at 0 indicates no effect on arthropod abundance. Interaction effects for four representative order-trap combinations are plotted to demonstrate negative interactions (b, c) and positive interactions (d, e). Lines indicate model predictions and shaded areas are 90% CI.

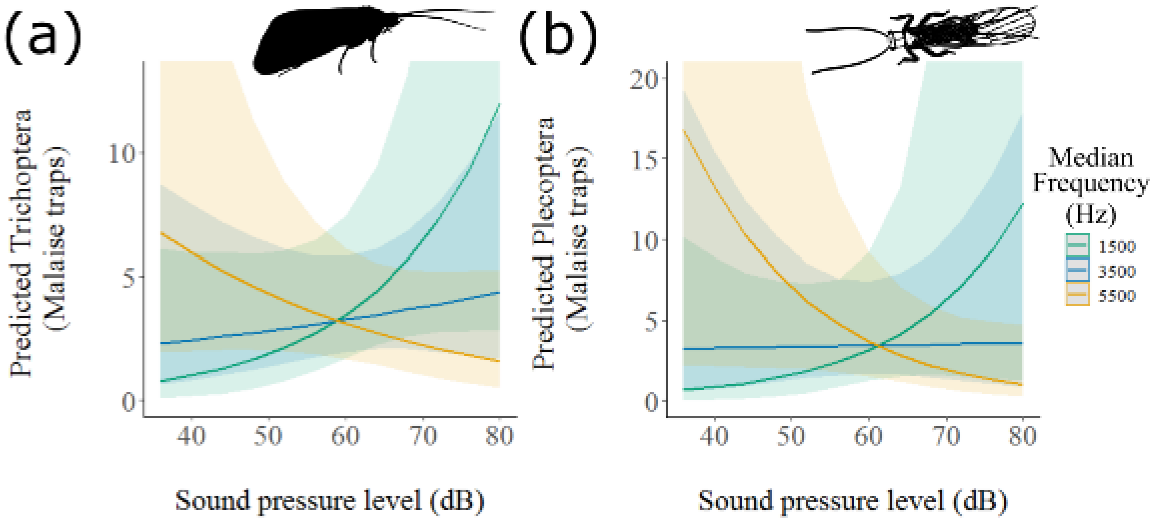


Figure 4.3 Interaction effects for two orders of aquatic insects are plotted to demonstrate negative interactions.

At relatively low frequencies, insect abundance increases along the sound pressure level gradient, while the abundance decreases along the same gradient at relatively high frequencies. Lines indicate model predictions and shaded areas are 90% credible intervals.

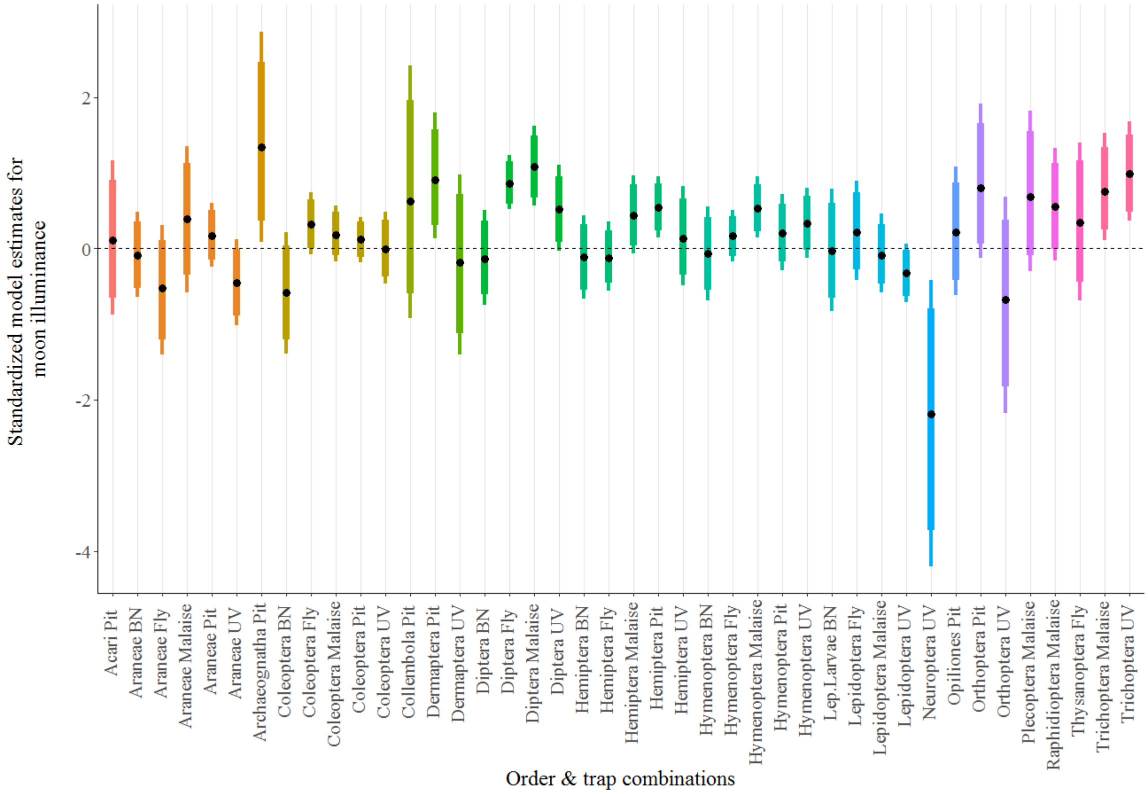


Figure 4.4 Estimates of the effects of moon illuminance on arthropod abundance.

Black dots represent point estimates for standardized effect sizes (y axis) for each order-trap combination (x axis). Thin vertical bars around estimates represent 90% credible intervals and thick vertical bars represent 80% credible intervals. Colors of bars differ at the order level. Dashed line at 0 indicates no effect on arthropod abundance.

CONCLUSION

The world is an increasingly noisy place, but animals have evolved in a natural din of noise since the evolution of hearing organs (Chapter 1). While researchers continue to highlight the negative effects that anthropogenic noise has on wildlife, we know relatively little about how animals respond to natural sources of noise. To build a knowledge base around this question, we reproduced whitewater river noise and spectrally-altered whitewater river noise continuously across a landscape for three summers. We then monitored arthropod, bat, and bird abundance and activity and assessed various predator-prey relationships with the aim of understanding how the system changed with noise exposure.

Animals respond in diverse ways to noise (highlighted in Chapters 2 – 4). Overall, it appears that bird and bat insectivores largely avoid high sound level noise (Chapter 2), which matches previous work with anthropogenic noise (Schaub, Ostwald & Siemers, 2008; McClure et al., 2013; Cinto Mejia, McClure & Barber, 2019; Finch, Schofield & Mathews, 2020). At low to moderate sound levels, birds seem to avoid noise that overlaps with their song vocalization, suggesting that communication is disrupted (Chapter 2). This appears to be stronger for low frequency singers, which signifies that those birds experience substantial masking of their vocalizations. At high sound levels, the background frequency does not matter as much, suggesting general surveillance for predators and prey might be more important. For bats, higher frequency echolocators are more likely to avoid high sound level noise. We suggest two potential explanations. First, these bats might rely on smaller prey (which are more available to high frequency echolocation) and these smaller prey avoid high sound level areas (and the bats follow). Second, high frequency echolocators tend to hear higher frequencies better than lower frequencies. Since high frequencies attenuate more quickly, these bats might have smaller listening areas – which are perhaps exacerbated by noise exposure. We do not have much data to address these two hypotheses specifically, but on the speculative side, none of our models show a change in Diptera (which are the only consistently small bat prey) in relation to the acoustic environment (Chapter 4), suggesting the first hypothesis might be less likely.

Most arthropods respond in some way to noise characteristics, yet direction of effects are not consistent across taxa (Chapter 4). Some arthropods, which are likely prey to birds and bats, increase in abundance in high sound level areas – perhaps in response to the absence of bird and bat predators (Chapters 2, 4). Indeed, it does appear that visually foraging birds and passive listening (gleaning) bats decreased foraging effort more than expected due to the decrease in abundance and activity (Chapter 2), which may allow some arthropod prey to persist with higher abundances.

Intermediate predators, such as orb-weaving spiders, appeared to increase dramatically in high sound level areas (Chapter 3). This could be due to the indirect effects of having a release from predation (as above), or it could at least partially be due to an increase in prey capture in high sound levels (which was the case for one species of orb-weaver but not the other). These prey that were more likely to be caught in webs of *Tetragnatha versicolor* (Chapter 3) were within the Order Diptera, which did not appear to be more abundant in high sound level areas (Chapter 4). It is possible that our Order-level analysis was too course of a resolution to demonstrate changes at the Family (Chironomidae) or Genus level. Alternatively, it is possible that changes in Chironomid behavior led to a difference in capture success by *T. versicolor*.

Overall, we demonstrate large changes to many vertebrate and invertebrate taxa following whitewater river noise playback. We are able to parse out the effects of sound pressure level and background frequency on these individual taxa as well as predator-prey behaviors. It is clear that this source of natural noise can alter animal abundances and behavior in a way that likely reverberates through entire communities and food webs. Future work should focus on strengthening the relationships between these potential predators and prey and highlight how the structure of the system changes under such noise treatments.

Ultimately, understanding how natural noise shapes animal decision making will give us evolutionary insight into how animals might deal with novel sources of anthropogenic noise. As one example, Brewer's sparrows were more abundant in acoustic environments with high sound level river noise (Chapter 2), even though the same species avoided human-made energy-extraction noise in another experimental study (Cinto Mejia, McClure & Barber, 2019). Together, these results lead to many possibilities that can be explored further. Perhaps characteristics of each noise type differ enough to lead to different responses in the same species (Chapter 1). Comparing power spectra and spectrograms from Chapter 1 and Cinto Mejia, McClure & Barber (2019), we can see that the temporal envelopes of the two noise types do not appear to differ much while river noise is much more broadband than compressor noise. Thus, we might infer that noise at lower frequencies are disruptive to Brewer's sparrow songs (indicated by avoidance of compressor noise), while higher frequencies are somehow beneficial to Brewer's sparrows – and enough so to outweigh the costs of low frequencies (indicated by positive relationship to river noise sound levels). One possible explanation is that high frequency noise acts as a shield from predation, as birds that stay in noisy areas can experience reduced nest predation (Francis et al., 2012b). However, instead of noise characteristics driving this pattern, differences in habitat types might explain the discrepancy. In non-riparian sagebrush steppe there might not be many nest predators. Thus, in these habitats there are only costs to persisting in noise. In riparian habitats, where nest predation is generally high (Vander Haegen & Degraaf, 1996; Tewksbury et al., 2006), persistence in noise might be 'worth it' because of the added predator shield. Only by comparing noise types (from anthropogenic to natural sources) in the same environmental context can we understand how animals are affected by characteristics of noise, and thus how we might mitigate these effects by changing the noise that we produce.

Here we use experimental whitewater river noise playbacks to study many diverse taxa spanning multiple trophic levels simultaneously. This gives us the ability to explain the mechanisms at play during noise disturbance, and gives us the opportunity to study an entire system of connected species. It is our aim that this large-scale and integrated effort serves as a strong foundation for future noise research to build upon.

REFERENCES

Acoustics W. 2018. Wildlife Acoustics—Bioacoustics Monitoring Systems for bats, birds, frogs, whales, dolphins and many other species.

Adams MR. 2000. Choosing hunting sites: web site preferences of the orb weaver spider, Neoscona crucifera, relative to light cues. Journal of insect behavior 13:299–305.

Alcamo J, Flörke M, Märker M. 2007. Future long-term changes in global water resources driven by socio-economic and climatic changes. Hydrological Sciences Journal 52:247–275.

Appel G, López-Baucells A, Magnusson WE, Bobrowiec PED. 2017. Aerial insectivorous bat activity in relation to moonlight intensity. Mammalian Biology 85:37–46.

Appel G, López-Baucells A, Magnusson WE, Bobrowiec PED. 2019. Temperature, rainfall, and moonlight intensity effects on activity of tropical insectivorous bats. Journal of Mammalogy 100:1889–1900.

Arrowsmith SJ, Hedlin MA. 2005. Observations of infrasound from surf in southern California. Geophysical Research Letters 32.

Aubin T, Jouventin P. 1998. Cocktail–party effect in king penguin colonies. Proceedings of the Royal Society of London. Series B: Biological Sciences 265:1665–1673.

Bacon SP, Grantham DW. 1989. Modulation masking: Effects of modulation frequency, depth, and phase. The Journal of the Acoustical Society of America 85:2575–2580. DOI: 10.1121/1.397751.

Bailey WJ, Gwynne DT. 1988. Mating system, mate choice and ultrasonic calling in a zaprochiline katydid (Orthoptera: Tettigoniidae). Behaviour 105:202–223.

Bain MB, Finn JT, Booke HE. 1988. Streamflow regulation and fish community structure. Ecology 69:382–392.

Barber JR, Crooks KR, Fristrup KM. 2010. The costs of chronic noise exposure for terrestrial organisms. Trends in ecology & evolution 25:180–189.

Barclay RM. 1985. Long-versus short-range foraging strategies of hoary (Lasiurus cinereus) and silver-haired (Lasionycteris noctivagans) bats and the consequences for prey selection. Canadian Journal of Zoology 63:2507–2515.

Barclay RM. 1991. Population structure of temperate zone insectivorous bats in relation to foraging behaviour and energy demand. The Journal of Animal Ecology:165–178.

Barton BT, Hodge ME, Speights CJ, Autrey AM, Lashley MA, Klink VP. 2018. Testing the AC/DC hypothesis: rock and roll is noise pollution and weakens a trophic cascade. Ecology and Evolution 8:7649–7656.

Bates DM. 2010. lme4: Mixed-effects modeling with R. Berlin.

Bates D, Maechler M, Bolker B, Walker S, Christensen RHB, Singmann H, Dai B, Grothendieck G, Eigen C, Rcpp L. 2015. Package ‘lme4.’ Convergence 12.

Bates ME, Stamper SA, Simmons JA. 2008. Jamming avoidance response of big brown bats in target detection. Journal of Experimental Biology 211:106–113.

Baxter CV, Fausch KD, Carl Saunders W. 2005. Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. Freshwater biology 50:201–220.

Bee MA. 2007. Sound source segregation in grey treefrogs: spatial release from masking by the sound of a chorus. Animal Behaviour 74:549–558.

Bee MA, Micheyl C. 2008. The cocktail party problem: what is it? How can it be solved? And why should animal behaviorists study it? Journal of comparative psychology 122:235.

Bee MA, Vélez A. 2018. Masking release in temporally fluctuating noise depends on comodulation and overall level in Cope’s gray treefrog. The Journal of the Acoustical Society of America 144:2354–2362. DOI: 10.1121/1.5064362.

Benítez-López A, Alkemade R, Verweij PA. 2010. The impacts of roads and other infrastructure on mammal and bird populations: a meta-analysis. Biological conservation 143:1307–1316.

Biaggini M, Consorti R, Dapporto L, Dellacasa M, Paggetti E, Corti C. 2007. The taxonomic level order as a possible tool for rapid assessment of Arthropod diversity in agricultural landscapes. Agriculture, Ecosystems & Environment 122:183–191.

Blickley JL, Blackwood D, Patricelli GL. 2012. Experimental evidence for the effects of chronic anthropogenic noise on abundance of greater sage-grouse at leks. Conservation Biology 26:461–471.

Bolger DT, Suarez AV, Crooks KR, Morrison SA, Case TJ. 2000. Arthropods in urban habitat fragments in southern California: area, age, and edge effects. Ecological Applications 10:1230–1248.

Both C, Grant T. 2012. Biological invasions and the acoustic niche: the effect of bullfrog calls on the acoustic signals of white-banded tree frogs. Biology letters 8:714–716.

Bowden J, Church BM. 1973. The influence of moonlight on catches of insects in light-traps in Africa. Part II. The effect of moon phase on light-trap catches. Bulletin of entomological research 63:129–142.

Bradbury JW, Vehrencamp SL. 1998. Principles of animal communication.

Brattstrom BH, Bondello MC. 1983. Effects of off-road vehicle noise on desert vertebrates. In: Environmental effects of off-road vehicles. Springer, 167–206.

Brumm H. 2004. The impact of environmental noise on song amplitude in a territorial bird. Journal of animal ecology 73:434–440.

Brumm H. 2006. Signalling through acoustic windows: nightingales avoid interspecific competition by short-term adjustment of song timing. Journal of Comparative Physiology A 192:1279–1285.

Brumm H. 2013. Animal communication and noise. Springer.

Brumm H, Naguib M. 2009. Environmental acoustics and the evolution of bird song. Advances in the Study of Behavior 40:1–33.

Brumm H, Slabbekoorn H. 2005. Acoustic communication in noise. Advances in the Study of Behavior 35:151–209.

Brumm H, Slater PJ. 2006. Ambient noise, motor fatigue, and serial redundancy in chaffinch song. Behavioral Ecology and Sociobiology 60:475–481.

Brumm H, Zollinger SA. 2011. The evolution of the Lombard effect: 100 years of psychoacoustic research. Behaviour:1173–1198.

Brumm H, Zollinger SA. 2013. Avian vocal production in noise. In: Animal communication and noise. Springer, 187–227.

Brumm H, Zollinger SA. 2017. Vocal plasticity in a reptile. Proceedings of the Royal Society B: Biological Sciences 284:20170451.

Brumm H, Zollinger SA, Niemelä PT, Sprau P. 2017. Measurement artefacts lead to false positives in the study of birdsong in noise. Methods in Ecology and Evolution 8:1617–1625.

Buchler ER. 1976. The use of echolocation by the wandering shrew (Sorex vagrans). Animal Behaviour 24:858–873.

Bunkley JP, Barber JR. 2015. Noise reduces foraging efficiency in pallid bats (Antrozous pallidus). Ethology 121:1116–1121.

Bunkley JP, McClure CJW, Kawahara AY, Francis CD, Barber JR. 2017. Anthropogenic noise changes arthropod abundances. Ecology and evolution 7:2977–2985.

Bunkley JP, McClure CJW, Kleist NJ, Francis CD, Barber JR. 2015. Anthropogenic noise alters bat activity levels and echolocation calls. Global Ecology and Conservation 3:62–71.

Burnham KP, Anderson DR. 2004. Multimodel inference: understanding AIC and BIC in model selection. Sociological methods & research 33:261–304.

Buxton RT, McKenna MF, Mennitt D, Fristrup K, Crooks K, Angeloni L, Wittemyer G. 2017. Noise pollution is pervasive in US protected areas. Science 356:531–533.

Buxton VL, Ward MP, Sperry JH. 2015. Use of chorus sounds for location of breeding habitat in 2 species of anuran amphibians. Behavioral Ecology 26:1111–1118.

Campo JL, Gil MG, Davila SG. 2005. Effects of specific noise and music stimuli on stress and fear levels of laying hens of several breeds. Applied Animal Behaviour Science 91:75–84.

Cardoso GC. 2014. Nesting and acoustic ecology, but not phylogeny, influence passerine urban tolerance. Global change biology 20:803–810.

Cardoso GC, Hu Y, Francis CD. 2018. The comparative evidence for urban species sorting by anthropogenic noise. Royal Society open science 5:172059.

Cardoso GC, Klingbeil BT, La Sorte FA, Lepczyk CA, Fink D, Flather CH. 2020. Exposure to noise pollution across North American passerines supports the noise filter hypothesis. Global Ecology and Biogeography 00:1–5.

Carlisle JD, Olmstead KL, Richart CH, Swanson DL. 2012. Food availability, foraging behavior, and diet of autumn migrant landbirds in the Boise foothills of southwestern Idaho. The Condor 114:449–461.

Chan AAY-H, Giraldo-Perez P, Smith S, Blumstein DT. 2010. Anthropogenic noise affects risk assessment and attention: the distracted prey hypothesis. Biology Letters 6:458–461.

Christy JH. 1995. Mimicry, mate choice, and the sensory trap hypothesis. The American Naturalist 146:171–181.

Cinto Mejia E, McClure CJ, Barber JR. 2019. Large-scale manipulation of the acoustic environment can alter the abundance of breeding birds: Evidence from a phantom natural gas field. Journal of Applied Ecology 56:2091–2101.

Clare EL, Barber BR, Sweeney BW, Hebert PDN, Fenton MB. 2011. Eating local: influences of habitat on the diet of little brown bats (Myotis lucifugus). Molecular Ecology 20:1772–1780.

Clare EL, Symondson WO, Broders H, Fabianek F, Fraser EE, MacKenzie A, Boughen A, Hamilton R, Willis CK, Martinez-Nuñez F. 2014. The diet of M yotis lucifugus across C anada: assessing foraging quality and diet variability. Molecular Ecology 23:3618–3632.

Clare EL, Symondson WO, Fenton MB. 2014. An inordinate fondness for beetles? Variation in seasonal dietary preferences of night-roosting big brown bats (Eptesicus fuscus). Molecular Ecology 23:3633–3647.

Clark JA, May RM. 2002. Taxonomic bias in conservation research. Science 297:191–193.

Clarke D, Whitney H, Sutton G, Robert D. 2013. Detection and learning of floral electric fields by bumblebees. Science 340:66–69.

Cody ML, Brown JH. 1969. Song asynchrony in neighbouring bird species. Nature 222:778–780.

Connelly F, Johnsson RD, Aulsebrook AE, Mulder RA, Hall ML, Vyssotski AL, Lesku JA. 2020. Urban noise restricts, fragments, and lightens sleep in Australian magpies. Environmental Pollution:115484.

Corcoran AJ, Moss CF. 2017. Sensing in a noisy world: lessons from auditory specialists, echolocating bats. Journal of Experimental Biology 220:4554–4566.

Cushman RM. 1985. Review of ecological effects of rapidly varying flows downstream from hydroelectric facilities. North American journal of fisheries Management 5:330–339.

Cvikel N, Levin E, Hurme E, Borissov I, Boonman A, Amichai E, Yovel Y. 2015. On-board recordings reveal no jamming avoidance in wild bats. Proceedings of the Royal Society B: Biological Sciences 282:20142274.

Davidson BM, Antonova G, Dlott H, Barber JR, Francis CD. 2017. Natural and anthropogenic sounds reduce song performance: insights from two emberizid species. Behavioral Ecology 28:974–982.

Debusschere E, Hostens K, Adriaens D, Ampe B, Botteldooren D, De Boeck G, De Muynck A, Sinha AK, Vandendriessche S, Van Hoorebeke L. 2016. Acoustic stress responses in juvenile sea bass Dicentrarchus labrax induced by offshore pile driving. Environmental pollution 208:747–757.

Dent ML, Larsen ON, Dooling RJ. 1997. Free-field binaural unmasking in budgerigars (Melopsittacus undulatus). Behavioral neuroscience 111:590.

Denzinger A, Tschapka M, Schnitzler H-U. 2018. The role of echolocation strategies for niche differentiation in bats. Canadian Journal of Zoology 96:171–181.

Derryberry EP, Phillips JN, Derryberry GE, Blum MJ, Luther D. 2020. Singing in a silent spring: Birds respond to a half-century soundscape reversion during the COVID-19 shutdown. Science.

Dominoni DM, Halfwerk W, Baird E, Buxton RT, Fernández-Juricic E, Fristrup KM, McKenna MF, Mennitt DJ, Perkin EK, Seymoure BM. 2020. Why conservation biology can benefit from sensory ecology. Nature Ecology & Evolution:1–10.

Donaldson MR, Burnett NJ, Braun DC, Suski CD, Hinch SG, Cooke SJ, Kerr JT. 2016. Taxonomic bias and international biodiversity conservation research. Canadian Science Publishing 65 Auriga Drive, Suite 203, Ottawa, ON K2E 7W6.

Dooling R. 2002. Avian hearing and the avoidance of wind turbines. National Renewable Energy Lab., Golden, CO.(US).

Dooling RJ, Popper AN. 2007. The effects of highway noise on birds. Sacramento, CA: The California Department of Transportation Division of Environmental Analysis 74.

Douglas HD, Conner WE. 1999. Is there a sound reception window in coastal environments? Evidence from shorebird communication systems. Naturwissenschaften 86:228–230.

Dudley R. 2002. The biomechanics of insect flight: form, function, evolution. Princeton University Press.

Duelli P, Obrist MK. 1998. In search of the best correlates for local organismal biodiversity in cultivated areas. Biodiversity & Conservation 7:297–309.

Dunlop RA, Cato DH, Noad MJ. 2010. Your attention please: increasing ambient noise levels elicits a change in communication behaviour in humpback whales (Megaptera novaeangliae). Proceedings of the Royal Society B: Biological Sciences 277:2521–2529.

Eberhard WG. 2013. The rare large prey hypothesis for orb web evolution: a critique. The Journal of Arachnology 41:76–80.

Elizalde L, Arbetman M, Arnan X, Eggleton P, Leal IR, Lescano MN, Saez A, Werenkraut V, Pirk GI. 2020. The ecosystem services provided by social insects: traits, management tools and knowledge gaps. Biological Reviews 95:1418–1441.

Ellison WT, Southall BL, Clark CW, Frankel AS. 2012. A new context-based approach to assess marine mammal behavioral responses to anthropogenic sounds. Conservation Biology 26:21–28.

Evans WE. 1973. Echolocation by marine delphinids and one species of fresh-water dolphin. The Journal of the Acoustical Society of America 54:191–199.

Faure PA, Barclay RMR. 1994. Substrate-gleaning versus aerial-hawking: plasticity in the foraging and echolocation behaviour of the long-eared bat, Myotis evotis. Journal of Comparative Physiology A 174:651–660.

Feng AS, Narins PM, Xu C-H, Lin W-Y, Yu Z-L, Qiu Q, Xu Z-M, Shen J-X. 2006. Ultrasonic communication in frogs. Nature 440:333.

FFmpeg Developers. 2018. FFmpeg.

Ficken RW, Ficken MS, Hailman JP. 1974. Temporal pattern shifts to avoid acoustic interference in singing birds. Science 183:762–763.

Finch D, Schofield H, Mathews F. 2020. Traffic noise playback reduces the activity and feeding behaviour of free-living bats. Environmental Pollution 263:114405.

Foote AD, Osborne RW, Hoelzel AR. 2004. Whale-call response to masking boat noise. Nature 428:910–910.

Francis CD. 2015. Vocal traits and diet explain avian sensitivities to anthropogenic noise. Global change biology 21:1809–1820.

Francis CD, Barber JR. 2013. A framework for understanding noise impacts on wildlife: an urgent conservation priority. Frontiers in Ecology and the Environment 11:305–313.

Francis CD, Kleist NJ, Ortega CP, Cruz A. 2012a. Noise pollution alters ecological services: enhanced pollination and disrupted seed dispersal. Proceedings of the Royal Society B: Biological Sciences 279:2727–2735.

Francis CD, Ortega CP, Cruz A. 2009. Noise pollution changes avian communities and species interactions. Current biology 19:1415–1419.

Francis CD, Ortega CP, Cruz A. 2011. Noise pollution filters bird communities based on vocal frequency. PLoS one 6:e27052.

Francis CD, Ortega CP, Kennedy RI, Nylander PJ. 2012b. Chapter 9: Are nest predators absent from noisy areas or unable to locate nests? Ornithological Monographs 74:101–110.

Froidevaux JS, Fialas PC, Jones G. 2018. Catching insects while recording bats: impacts of light trapping on acoustic sampling. Remote Sensing in Ecology and Conservation 4:240–247.

Fuller RA, Warren PH, Gaston KJ. 2007. Daytime noise predicts nocturnal singing in urban robins. Biology letters 3:368–370.

Fuzessery ZM, Buttenhoff P, Andrews B, Kennedy JM. 1993. Passive sound localization of prey by the pallid bat (Antrozous p. pallidus). Journal of Comparative Physiology A 171:767–777.

Gabry J, Goodrich B. 2016. rstanarm: Bayesian applied regression modeling via Stan. R package version 2.10. 0.

Gabry J, Mahr T. 2017. bayesplot: Plotting for Bayesian models. R package version 1.

Garamszegi LZ. 2014. Uncertainties due to within-species variation in comparative studies: measurement errors and statistical weights. In: Modern phylogenetic comparative methods and their application in evolutionary biology. Springer, 157–199.

Garstang M. 2004. Long-distance, low-frequency elephant communication. Journal of Comparative Physiology A 190:791–805.

Geipel I, Smeekes MJ, Halfwerk W, Page RA. 2019. Noise as an informational cue for decision-making: the sound of rain delays bat emergence. Journal of Experimental Biology:jeb-192005.

Gelman A. 2008. Scaling regression inputs by dividing by two standard deviations. Statistics in medicine 27:2865–2873.

Gerhardt HC, Huber F. 2002. Acoustic communication in insects and anurans: common problems and diverse solutions. University of Chicago Press.

Gil D, Honarmand M, Pascual J, Pérez-Mena E, Macías Garcia C. 2014. Birds living near airports advance their dawn chorus and reduce overlap with aircraft noise. Behavioral Ecology 26:435–443.

Gill SA, Job JR, Myers K, Naghshineh K, Vonhof MJ. 2015. Toward a broader characterization of anthropogenic noise and its effects on wildlife. Behavioral Ecology 26:328–333.

Gillam EH, Ulanovsky N, McCracken GF. 2007. Rapid jamming avoidance in biosonar. Proceedings of the Royal Society B: Biological Sciences 274:651–660.

Girard J, Baril A, Mineau P, Fahrig L. 2012. Foraging habitat and diet of Song Sparrows (Melospiza melodia) nesting in farmland: a stable isotope approach. Canadian journal of zoology 90:1339–1350.

Giurfa M, Nunez J, Chittka L, Menzel R. 1995. Colour preferences of flower-naive honeybees. Journal of Comparative Physiology A 177:247–259.

Glass DC, Singer JE. 1972. Behavioral Aftereffects of Unpredictable and Uncontrollable Aversive Events: Although subjects were able to adapt to loud noise and other stressors in laboratory experiments, they clearly demonstrated adverse aftereffects. American Scientist 60:457–465.

Goerlitz HR, Greif S, Siemers BM. 2008. Cues for acoustic detection of prey: insect rustling sounds and the influence of walking substrate. Journal of Experimental Biology 211:2799–2806.

Gomes DGE. 2020a. Orb-weaving spiders are fewer but larger and catch more prey in lit bridge panels from a natural artificial light experiment. PeerJ 8:e8808.

Gomes DGE. 2020b. A guide to analyzing spectral information from large sound files (with R and ffmpeg). Zenodo.

Gomes DG, Appel G, Barber JR. 2020. Time of night and moonlight structure vertical space use by insectivorous bats in a Neotropical rainforest: an acoustic monitoring study. PeerJ 8:e10591.

Gomes DGE, Barber JR. 2021. Dataset for: Experimental river noise alters arthropod abundances.

Gomes DGE, Francis CD, Barber JR. 2021. Using Past to Understand Present: Coping with Natural and Anthropogenic Noise. BioScience biaa161:1–12.

Gomes DGE, Halfwerk W, Taylor RC, Ryan MJ, Page RA. 2017. Multimodal weighting differences by bats and their prey: probing natural selection pressures on sexually selected traits. Animal Behaviour 134:99–102.

Gomes DGE, Hesselberg T, Barber JR. 2020. Phantom river noise alters orb-weaving spider abundance, web size, and prey capture. Functional Ecology.

Gomes DGE, Page RA, Geipel I, Taylor RC, Ryan MJ, Halfwerk W. 2016. Bats perceptually weight prey cues across sensory systems when hunting in noise. Science 353:1277–1280.

Gomes DGE, Toth CA, Cole HJ, Francis CD, Barber JR. accepted. Phantom rivers filter birds and bats by acoustic niche. Nature Communications.

Gomes DGE, Toth CA, Cole HJ, Francis CD, Barber JR. 2020. Data for: Phantom rivers filter birds and bats by acoustic niche.

Gordon R, Ivens S, Ammerman LK, Fenton MB, Littlefair JE, Ratcliffe JM, Clare EL. 2019a. Molecular diet analysis finds an insectivorous desert bat community dominated by resource sharing despite diverse echolocation and foraging strategies. Ecology and Evolution 9:3117–3129.

Gordon TA, Radford AN, Davidson IK, Barnes K, McCloskey K, Nedelec SL, Meekan MG, McCormick MI, Simpson SD. 2019b. Acoustic enrichment can enhance fish community development on degraded coral reef habitat. Nature Communications 10:1–7.

Götze S, Koblitz JC, Denzinger A, Schnitzler H-U. 2016. No evidence for spectral jamming avoidance in echolocation behavior of foraging pipistrelle bats. Scientific reports 6:1–13.

Goutte S, Dubois A, Legendre F. 2013. The importance of ambient sound level to characterise anuran habitat. Plos one 8.

Greenfield MD. 1988. Interspecific acoustic interactions among katydids Neoconocephalus: inhibition-induced shifts in diel periodicity. Animal Behaviour 36:684–695.

Greenfield MD. 2016. Evolution of acoustic communication in insects. In: Insect hearing. Springer, 17–47.

Griffin DR, Webster FA, Michael CR. 1960. The echolocation of flying insects by bats. Animal behaviour 8:141–154.

Grindal SD, Morissette JL, Brigham RM. 1999. Concentration of bat activity in riparian habitats over an elevational gradient. Canadian Journal of Zoology 77:972–977.

Guinan DM, Sealy SG. 1987. Diet of house wrens (Troglodytes aedon) and the abundance of the invertebrate prey in the dune-ridge forest, Delta Marsh, Manitoba. Canadian Journal of Zoology 65:1587–1596.

Haff TM, Magrath RD. 2010. Vulnerable but not helpless: nestlings are fine-tuned to cues of approaching danger. Animal behaviour 79:487–496.

Hage SR, Jiang T, Berquist SW, Feng J, Metzner W. 2013. Ambient noise induces independent shifts in call frequency and amplitude within the Lombard effect in echolocating bats. Proceedings of the National Academy of Sciences 110:4063–4068.

Hagstrum JT. 2000. Infrasound and the avian navigational map. Journal of Experimental Biology 203:1103–1111.

Halfwerk W, Blaas M, Kramer L, Hijner N, Trillo PA, Bernal XE, Page RA, Goutte S, Ryan MJ, Ellers J. 2019. Adaptive changes in sexual signalling in response to urbanization. Nature ecology & evolution 3:374.

Halfwerk W, Holleman LJ, Slabbekoorn H. 2011. Negative impact of traffic noise on avian reproductive success. Journal of applied Ecology 48:210–219.

Halfwerk W, Slabbekoorn H. 2015. Pollution going multimodal: the complex impact of the human-altered sensory environment on animal perception and performance. Biology letters 11:20141051.

Harmer AM, Clausen PD, Wroe S, Madin JS. 2015. Large orb-webs adapted to maximise total biomass not rare, large prey. Scientific reports 5:14121.

Harrison XA, Donaldson L, Correa-Cano ME, Evans J, Fisher DN, Goodwin CE, Robinson BS, Hodgson DJ, Inger R. 2018. A brief introduction to mixed effects modelling and multi-model inference in ecology. PeerJ 6:e4794.

Hartig F. 2019. DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models. R package.

Hauer FR, Locke H, Dreitz VJ, Hebblewhite M, Lowe WH, Muhlfeld CC, Nelson CR, Proctor MF, Rood SB. 2016. Gravel-bed river floodplains are the ecological nexus of glaciated mountain landscapes. Science Advances 2:e1600026.

Heffner HE, Heffner RS. 2008. High-frequency hearing. Handbook of the senses: Audition 55:60.

Hegde SS. 2019. Acoustic Communication in Orthopteran and Hemipteran Insects. International Journal of Bioinformatics and Biological Sciences 7:7–13.

Hennigar B, Ethier JP, Wilson DR. 2019. Experimental traffic noise attracts birds during the breeding season. Behavioral Ecology.

Herberstein ME, Craig CL, Elgar MA. 2000. Foraging strategies and feeding regimes: web and decoration investment in Argiope keyserlingi Karsch (Araneae: Araneidae). Evolutionary Ecology Research 2:41–67.

Herberstein ME, Tso I-M. 2000. Evaluation of formulae to estimate the capture area and mesh height of orb webs (Araneoidea, Araneae). Journal of Arachnology 28:180–184.

Herrick SZ, Wells KD, Farkas TE, Schultz ET. 2018. Noisy Neighbors: Acoustic Interference and Vocal Interactions between Two Syntopic Species of Ranid Frogs, Rana clamitans and Rana catesbeiana. Journal of Herpetology 52:176–184.

Hildebrand JA. 2009. Anthropogenic and natural sources of ambient noise in the ocean. Marine Ecology Progress Series 395:5–20.

Hine JE, Martin RL, Moore DR. 1994. Free-field binaural unmasking in ferrets. Behavioral neuroscience 108:196.

Holt MM, Noren DP, Dunkin RC, Williams TM. 2015. Vocal performance affects metabolic rate in dolphins: implications for animals communicating in noisy environments. Journal of Experimental Biology 218:1647–1654.

Houston RD, Boonman AM, Jones G. 2004. Do echolocation signal parameters restrict bats' choice of prey. Echolocation in bats and dolphins 339:345.

Hoy RR, Robert D. 1996. Tympanal hearing in insects. Annual review of entomology 41:433–450.

Hu Y, Cardoso GC. 2009. Are bird species that vocalize at higher frequencies preadapted to inhabit noisy urban areas? Behavioral Ecology 20:1268–1273.

Hutto RL. 2016. Should scientists be required to use a model-based solution to adjust for possible distance-based detectability bias? Ecological Applications 26:1287–1294.

IEC. 2013. 1: Specifications, International Standard IEC 61672-1: 2013. Tech. Rep.

IPCC CC. 2007. The physical science basis. Contribution of Working Group I to the fourth assessment report of the Intergovernmental Panel on Climate Change 996.

Ives AR, Midford PE, Garland Jr T. 2007. Within-species variation and measurement error in phylogenetic comparative methods. Systematic biology 56:252–270.

Jakob EM, Marshall SD, Uetz GW. 1996. Estimating fitness: a comparison of body condition indices. Oikos:61–67.

Jang Y, Greenfield MD. 1996. Ultrasonic communication and sexual selection in wax moths: female choice based on energy and asynchrony of male signals. Animal Behaviour 51:1095–1106.

Janiczek PM, DeYoung JA. 1987. Computer programs for sun and moon illuminance: with contingent tables and diagrams. US Naval Observatory.

Jedlicka JA, Sharma AM, Almeida RP. 2013. Molecular tools reveal diets of insectivorous birds from predator fecal matter. Conservation Genetics Resources 5:879–885.

Jerem P, Mathews F. 2020. Trends and knowledge gaps in field research investigating effects of anthropogenic noise. Conservation Biology.

Jetz W, Thomas GH, Joy JB, Hartmann K, Mooers AO. 2012. The global diversity of birds in space and time. Nature 491:444–448.

Johnson JS, Lacki MJ, Baker MD. 2007. Foraging ecology of long-legged myotis (Myotis volans) in north-central Idaho. Journal of Mammalogy 88:1261–1270.

Johnson JB, Ripepe M. 2011. Volcano infrasound: A review. Journal of Volcanology and Geothermal Research 206:61–69.

Johnson NF, Triplehorn CA. 2005. Borror and DeLong’s Introduction to the Study of Insects. Thompson Brooks/Cole Belmont, CA.

Jones G. 2005. Echolocation. Current Biology 15:R484–R488.

Jones FC. 2008. Taxonomic sufficiency: the influence of taxonomic resolution on freshwater bioassessments using benthic macroinvertebrates. Environmental Reviews 16:45–69.

Jung K, Kalko EK. 2010. Where forest meets urbanization: foraging plasticity of aerial insectivorous bats in an anthropogenically altered environment. Journal of Mammalogy 91:144–153.

Jusino MA, Banik MT, Palmer JM, Wray AK, Xiao L, Pelton E, Barber JR, Kawahara AY, Gratton C, Peery MZ. 2019. An improved method for utilizing high-throughput amplicon sequencing to determine the diets of insectivorous animals. Molecular ecology resources 19:176–190.

Kacem Z, Rodríguez MA, Roca IT, Proulx R. 2020. The riverscape meets the soundscape: Acoustic cues and habitat use by brook trout in a small stream. Canadian Journal of Fisheries and Aquatic Sciences:1–9.

Kämper G, Dambach M. 1979. Communication by infrasound in a non-stridulating cricket. Naturwissenschaften 66:530–530.

Kawahara AY, Plotkin D, Espeland M, Meusemann K, Toussaint EF, Donath A, Gimnich F, Frandsen PB, Zwick A, dos Reis M. 2019. Phylogenomics reveals the evolutionary timing and pattern of butterflies and moths. Proceedings of the National Academy of Sciences 116:22657–22663.

Kern JD, Characklis GW, Doyle MW, Blumsack S, Whisnant RB. 2011. Influence of deregulated electricity markets on hydropower generation and downstream flow regime. Journal of Water Resources Planning and Management 138:342–355.

Kight CR, Swaddle JP. 2011. How and why environmental noise impacts animals: an integrative, mechanistic review. Ecology letters 14:1052–1061.

Kirchner WH. 1997. Acoustical communication in social insects. In: Orientation and communication in arthropods. Springer, 273–300.

Kjellberg A, LandstrÖM ULF, Tesarz M, Söderberg L, Akerlund E. 1996. The effects of nonphysical noise characteristics, ongoing task and noise sensitivity on annoyance and distraction due to noise at work. Journal of Environmental Psychology 16:123–136.

Kleinteich A, Schneider JM. 2011. Developmental strategies in an invasive spider: constraints and plasticity. Ecological Entomology 36:82–93.

Kleist NJ, Guralnick RP, Cruz A, Lowry CA, Francis CD. 2018. Chronic anthropogenic noise disrupts glucocorticoid signaling and has multiple effects on fitness in an avian community. Proceedings of the national academy of sciences 115:E648–E657.

van Klink R, Bowler DE, Gongalsky KB, Swengel AB, Gentile A, Chase JM. 2020. Meta-analysis reveals declines in terrestrial but increases in freshwater insect abundances. Science 368:417–420.

Klump GM, Larsen ON. 1992. Azimuthal sound localization in the European starling (Sturnus vulgaris). Journal of Comparative Physiology A 170:243–251.

Koay G, Heffner HE, Heffner RS. 1997. Audiogram of the big brown bat (Eptesicus fuscus). Hearing research 105:202–210.

Kreithen ML, Quine DB. 1979. Infrasound detection by the homing pigeon: a behavioral audiogram. Journal of Comparative Physiology 129:1–4.

Kunz TH. 1982. Lasionycteris noctivagans. Mammalian Species:1–5.

Kwon BJ, Turner CW. 2001. Consonant identification under maskers with sinusoidal modulation: Masking release or modulation interference? The Journal of the Acoustical Society of America 110:1130–1140. DOI: 10.1121/1.1384909.

Lampe U, Reinhold K, Schmoll T. 2014. How grasshoppers respond to road noise: developmental plasticity and population differentiation in acoustic signalling. Functional Ecology 28:660–668.

Lampe U, Schmoll T, Franzke A, Reinhold K. 2012. Staying tuned: grasshoppers from noisy roadside habitats produce courtship signals with elevated frequency components. Functional Ecology 26:1348–1354.

Lazure L, Fenton MB. 2011. High duty cycle echolocation and prey detection by bats. Journal of Experimental Biology 214:1131–1137.

Le M-LT, Garvin CM, Barber JR, Francis CD. 2019. Natural sounds alter California ground squirrel, Otospermophilus beecheyi, foraging, vigilance and movement behaviours. Animal Behaviour 157:51–60.

Lee N, Ward JL, Vélez A, Micheyl C, Bee MA. 2017. Frogs exploit statistical regularities in noisy acoustic scenes to solve cocktail-party-like problems. Current Biology 27:743–750.

Lengagne T, Aubin T, Lauga J, Jouventin P. 1999. How do king penguins (Aptenodytes patagonicus apply the mathematical theory of information to communicate in windy conditions? Proceedings of the Royal Society of London. Series B: Biological Sciences 266:1623–1628.

Levenhagen MJ, Miller ZD, Petrelli AR, Ferguson LA, Shr Y-H, Gomes DG, Taff BD, White C, Fristrup K, Monz C. 2020. Ecosystem services enhanced through soundscape management link people and wildlife. People and Nature.

Liao Y-C, Yang M-M. 2015. Acoustic communication of three closely related psyllid species: a case study in clarifying allied species using substrate-borne signals (Hemiptera: Psyllidae: Cacopsylla). Annals of the Entomological Society of America 108:902–911.

Ligges U. 2013. tuneR–analysis of music.

Link WA, Eaton MJ. 2012. On thinning of chains in MCMC. Methods in ecology and evolution 3:112–115.

Lohr B, Wright TF, Dooling RJ. 2003. Detection and discrimination of natural calls in masking noise by birds: estimating the active space of a signal. Animal Behaviour 65:763–777.

Lohrey AK, Clark DL, Gordon SD, Uetz GW. 2009. Antipredator responses of wolf spiders (Araneae: Lycosidae) to sensory cues representing an avian predator. Animal Behaviour 77:813–821.

Lombard E. 1911. Le signe de l’elevation de la voix. Ann. Mal. de L’Oreille et du Larynx:101–119.

Longcore T. 2003. Terrestrial arthropods as indicators of ecological restoration success in coastal sage scrub (California, USA). Restoration Ecology 11:397–409.

Losey JE, Vaughan M. 2006. The economic value of ecological services provided by insects. Bioscience 56:311–323.

Love EK, Bee MA. 2010. An experimental test of noise-dependent voice amplitude regulation in Cope’s grey treefrog, Hyla chrysoscelis. Animal Behaviour 80:509–515.

Lüdecke D. 2018. sjPlot: Data visualization for statistics in social science. R package version 2.4. 1. The Comprehensive R Archive Network. https://CRAN. R-project. org/package= sjPlot.

Lüdecke D. 2020. sjstats: statistical functions for regression models (version 0.17. 9).

Lüdecke D, Makowski D, Waggoner P, Patil I. 2019. performance: assessment of regression models performance. R package version 0.4. 0.

Luo J, Goerlitz HR, Brumm H, Wiegrebe L. 2015. Linking the sender to the receiver: vocal adjustments by bats to maintain signal detection in noise. Scientific reports 5:18556.

Luo J, Hage SR, Moss CF. 2018. The Lombard effect: From acoustics to neural mechanisms. Trends in neurosciences 41:938–949.

Luther DA. 2008. Signaller: receiver coordination and the timing of communication in Amazonian birds. Biology letters 4:651–654.

Luther D, Baptista L. 2009. Urban noise and the cultural evolution of bird songs. Proceedings of the Royal Society B: Biological Sciences 277:469–473.

Luther D, Magnotti J. 2014. Can animals detect differences in vocalizations adjusted for anthropogenic noise? Animal behaviour 92:111–116.

Luther DA, Phillips J, Derryberry EP. 2016. Not so sexy in the city: urban birds adjust songs to noise but compromise vocal performance. Behavioral Ecology 27:332–340.

Magnusson A, Skaug H, Nielsen A, Berg C, Kristensen K, Maechler M, van Bentham K, Bolker B, Brooks M, Brooks MM. 2017. Package 'glmmTMB.' R Package Version 0.2. 0.

Makowski D, Ben-Shachar MS, Lüdecke D. 2019. bayestestR: Describing effects and their uncertainty, existence and significance within the Bayesian framework. Journal of Open Source Software 4:1541.

Malanson GP. 1993. Riparian landscapes. Cambridge University Press.

Manley GA. 2012. Evolutionary paths to mammalian cochleae. Journal of the Association for Research in Otolaryngology 13:733–743.

Mason JT, McClure CJ, Barber JR. 2016. Anthropogenic noise impairs owl hunting behavior. Biological Conservation 199:29–32.

Matthews KA, Scheier MF, Brunson BI, Carducci B. 1980. Attention, unpredictability, and reports of physical symptoms: Eliminating the benefits of predictability. Journal of Personality and Social Psychology 38:525.

Maucieri D, Barclay RM. 2020. Consumption of spiders by the little brown bat (Myotis lucifugus) and the long-eared bat (Myotis evotis) in the Rocky Mountains of Alberta. Canadian Journal of Zoology.

Mazar O, Yovel Y. 2020. A sensorimotor model shows why a spectral jamming avoidance response does not help bats deal with jamming. Elife 9:e55539.

McClure CJ, Ware HE, Carlisle J, Kaltenecker G, Barber JR. 2013. An experimental investigation into the effects of traffic noise on distributions of birds: avoiding the phantom road. Proceedings of the Royal Society of London B: Biological Sciences 280:20132290.

McGeachie WJ. 1989. The effects of moonlight illuminance, temperature and wind speed on light-trap catches of moths. Bulletin of Entomological Research 79:185–192.

McIntosh MD, Schmitz JA, Benbow ME, Burky AJ. 2008. Structural and functional changes of tropical riffle macroinvertebrate communities associated with stream flow withdrawal. River Research and Applications 24:1045–1055.

Medeiros CI, Both C, Grant T, Hartz SM. 2017. Invasion of the acoustic niche: variable responses by native species to invasive American bullfrog calls. Biological invasions 19:675–690.

Medina I, Francis CD. 2012. Environmental variability and acoustic signals: a multi-level approach in songbirds. Biology Letters 8(6): 928-931.

Mennitt DJ, Fristrup KM. 2012. Obtaining calibrated sound pressure levels from consumer digital audio recorders. Applied Acoustics 73:1138–1145.

Merchant ND, Fristrup KM, Johnson MP, Tyack PL, Witt MJ, Blondel P, Parks SE. 2015. Measuring acoustic habitats. Methods in Ecology and Evolution 6:257–265.

Misof B, Liu S, Meusemann K, Peters RS, Donath A, Mayer C, Frandsen PB, Ware J, Flouri T, Beutel RG. 2014. Phylogenomics resolves the timing and pattern of insect evolution. Science 346:763–767.

Mitchell SC, Cunjak RA. 2007. Stream flow, salmon and beaver dams: roles in the structuring of stream fish communities within an anadromous salmon dominated stream. Journal of Animal Ecology 76:1062–1074.

Montgomery GA, Belitz MW, Guralnick RP, Tingley MW. 2021. Standards and best practices for monitoring and benchmarking insects. Frontiers in Ecology and Evolution 8:513.

Montgomery GA, Dunn RR, Fox R, Jongejans E, Leather SR, Saunders ME, Shortall CR, Tingley MW, Wagner DL. 2020. Is the insect apocalypse upon us? How to find out. Biological Conservation 241:108327.

Mooney TA, Samson JE, Schlunk AD, Zacarias S. 2016. Loudness-dependent behavioral responses and habituation to sound by the longfin squid (Doryteuthis pealeii). Journal of Comparative Physiology A 202:489–501.

Morley EL, Jones G, Radford AN. 2014. The importance of invertebrates when considering the impacts of anthropogenic noise. Proc. R. Soc. B 281:20132683.

Morris GK, Mason AC, Wall P, Belwood JJ. 1994. High ultrasonic and tremulation signals in neotropical katydids (Orthoptera: Tettigoniidae). Journal of Zoology 233:129–163.

Morris-Drake A, Bracken AM, Kern JM, Radford AN. 2017. Anthropogenic noise alters dwarf mongoose responses to heterospecific alarm calls. Environmental pollution 223:476–483.

Morris-Drake A, Kern JM, Radford AN. 2016. Cross-modal impacts of anthropogenic noise on information use. Current Biology 26:R911–R912.

Mortimer B, Holland C, Windmill JF, Vollrath F. 2015. Unpicking the signal thread of the sector web spider Zygiella x-notata. Journal of The Royal Society Interface 12:20150633.

Mortimer B, Soler A, Siviour CR, Zaera R, Vollrath F. 2016. Tuning the instrument: sonic properties in the spider’s web. Journal of The Royal Society Interface 13:20160341.

Moseley DL, Derryberry GE, Phillips JN, Danner JE, Danner RM, Luther DA, Derryberry EP. 2018. Acoustic adaptation to city noise through vocal learning by a songbird. :9.

Naiman RJ, Decamps H. 1997. The ecology of interfaces: riparian zones. Annual review of Ecology and Systematics 28:621–658.

Naiman RJ, Decamps H, Pollock M. 1993. The role of riparian corridors in maintaining regional biodiversity. Ecological applications 3:209–212.

Nakano R, Skals N, Takanashi T, Surlykke A, Koike T, Yoshida K, Maruyama H, Tatsuki S, Ishikawa Y. 2008. Moths produce extremely quiet ultrasonic courtship songs by rubbing specialized scales. Proceedings of the National Academy of Sciences 105:11812–11817.

Narins PM, Feng AS, Lin W, Schnitzler H-U, Denzinger A, Suthers RA, Xu C. 2004. Old World frog and bird vocalizations contain prominent ultrasonic harmonics. The Journal of the Acoustical Society of America 115:910–913.

Nelson DA, Marler P. 1990. The perception of birdsong and an ecological concept of signal space.

Nemeth E, Brumm H. 2010. Birds and anthropogenic noise: are urban songs adaptive? The American Naturalist 176:465–475.

Nemeth E, Pieretti N, Zollinger SA, Geberzahn N, Partecke J, Miranda AC, Brumm H. 2013. Bird song and anthropogenic noise: vocal constraints may explain why birds sing higher-frequency songs in cities. Proceedings of the Royal Society B: Biological Sciences 280:20122798.

Neo YY, Seitz J, Kastelein RA, Winter HV, Ten Cate C, Slabbekoorn H. 2014. Temporal structure of sound affects behavioural recovery from noise impact in European seabass. Biological Conservation 178:65–73.

Nocera JJ, Forbes GJ, Giraldeau L-A. 2005. Inadvertent social information in breeding site selection of natal dispersing birds. Proceedings of the Royal Society B: Biological Sciences 273:349–355.

Nordt A, Klenke R. 2013. Sleepless in town–drivers of the temporal shift in dawn song in urban European blackbirds. PloS one 8:e71476.

Noriega JA, Hortal J, Azcárate FM, Berg MP, Bonada N, Briones MJ, Del Toro I, Goulson D, Ibanez S, Landis DA. 2018. Research trends in ecosystem services provided by insects. Basic and Applied Ecology 26:8–23.

Norris KS, Prescott JH, Asa-Dorian PV, Perkins P. 1961. An experimental demonstration of echolocation behavior in the porpoise, Tursiops truncatus (Montagu). The Biological Bulletin 120:163–176.

Nowacek DP, Thorne LH, Johnston DW, Tyack PL. 2007. Responses of cetaceans to anthropogenic noise. Mammal Review 37:81–115.

Nyby J, Whitney G. 1978. Ultrasonic communication of adult myomorph rodents. Neuroscience & Biobehavioral Reviews 2:1–14.

Nyffeler M, Birkhofer K. 2017. An estimated 400–800 million tons of prey are annually killed by the global spider community. The Science of Nature 104:30.

Oberweger K, Goller F. 2001. The metabolic cost of birdsong production. Journal of Experimental Biology 204:3379–3388.

Ogawa K, Sato H. 1993. Relationship between male acoustic response and female wingbeat frequency in a chironomid midge, Chironomus yoshimatsui (Diptera: Chironomidae). Medical entomology and zoology 44:355–360.

Opell BD. 1998. Economics of spider orb-webs: the benefits of producing adhesive capture thread and of recycling silk. Functional Ecology 12:613–624.

Orci KM, Petróczki K, Barta Z. 2016. Instantaneous song modification in response to fluctuating traffic noise in the tree cricket Oecanthus pellucens. Animal Behaviour 112:187–194.

Ortega CP, Francis CD. 2012. Chapter 7: Effects of gas-well-compressor noise on the ability to detect birds during surveys in northwest New Mexico. Ornithological Monographs 74:78–90.

Pacifici K, Simons TR, Pollock KH. 2008. Effects of vegetation and background noise on the detection process in auditory avian point-count surveys. The Auk 125:600–607.

Pagani–Núñez E, Ruiz Í, Quesada J, Negro JJ, Senar JC. 2011. The diet of Great Tit Parus major nestlings in a Mediterranean Iberian forest: the important role of spiders. Animal Biodiversity and Conservation 34:355–361.

Parks SE, Johnson M, Nowacek D, Tyack PL. 2011. Individual right whales call louder in increased environmental noise. Biology letters 7:33–35.

Parris KM, McCarthy MA. 2013. Predicting the effect of urban noise on the active space of avian vocal signals. The American Naturalist 182:452–464.

Partan SR. 2017. Multimodal shifts in noise: switching channels to communicate through rapid environmental change. Animal Behaviour 124:325–337.

Partan SR, Fulmer AG, Gounard MA, Redmond JE. 2010. Multimodal alarm behavior in urban and rural gray squirrels studied by means of observation and a mechanical robot. Current Zoology 56.

Pater LL, Grubb TG, Delaney DK. 2009. Recommendations for improved assessment of noise impacts on wildlife. The Journal of Wildlife Management 73:788–795.

Patricelli GL, Blickley JL. 2006. Avian communication in urban noise: causes and consequences of vocal adjustment. The Auk 123:639–649.

Persson B. 1976. Influence of weather and nocturnal illumination on the activity and abundance of populations of Noctuids (Lepidoptera) in south coastal Queensland. Bulletin of Entomological Research 66:33–63.

Phillips JN, Ruef SK, Garvin CM, Le M-LT, Francis CD. 2019. Background noise disrupts host–parasitoid interactions. Royal Society open science 6:190867.

Pijanowski BC, Villanueva-Rivera LJ, Dumyahn SL, Farina A, Krause BL, Napoletano BM, Gage SH, Pieretti N. 2011. Soundscape ecology: the science of sound in the landscape. BioScience 61:203–216.

Pinheiro J, Bates D, DebRoy S, Sarkar D, Team RC. 2013. nlme: Linear and nonlinear mixed effects models. R package version 3:111.

Platnick NI. 2012. The world spider catalog, version 13.0. American Museum of Natural History, online at http://research. amnh. org/iz/spiders/catalog. DOI 10.

Popper AN, Platt C, Edds PL. 1992. Evolution of the vertebrate inner ear: an overview of ideas. In: The evolutionary biology of hearing. Springer, 49–57.

Prugh LR, Golden CD. 2014. Does moonlight increase predation risk? Meta-analysis reveals divergent responses of nocturnal mammals to lunar cycles. Journal of Animal Ecology 83:504–514.

Purser J, Radford AN. 2011. Acoustic noise induces attention shifts and reduces foraging performance in three-spined sticklebacks (Gasterosteus aculeatus). PLOS one 6:e17478.

Quine DB. 1982. Infrasounds: a potential navigational cue for homing pigeons. In: Avian navigation. Springer, 373–376.

R Core Team. 2017. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing; 2016.

Rabin LA, Greene CM. 2002. Changes to acoustic communication systems in human-altered environments. Journal of Comparative Psychology 116:137.

Raboin M, Elias DO. 2019. Anthropogenic noise and the bioacoustics of terrestrial invertebrates. Journal of Experimental Biology 222:jeb178749.

Ratcliffe JM, Dawson JW. 2003. Behavioural flexibility: the little brown bat, Myotis lucifugus, and the northern long-eared bat, M. septentrionalis, both glean and hawk prey. Animal Behaviour 66:847–856.

Ratcliffe JM, Fenton MB, Shettleworth SJ. 2006. Behavioral flexibility positively correlated with relative brain volume in predatory bats. Brain, behavior and evolution 67:165–176.

Read J, Jones G, Radford AN. 2014. Fitness costs as well as benefits are important when considering responses to anthropogenic noise. Behavioral Ecology 25:4–7.

Reijnen R, Foppen R, Meeuwsen H. 1996. The effects of traffic on the density of breeding birds in Dutch agricultural grasslands. Biological conservation 75:255–260.

Revell LJ. 2010. Phylogenetic signal and linear regression on species data. Methods in Ecology and Evolution 1:319–329.

Rhebergen F, Taylor RC, Ryan MJ, Page RA, Halfwerk W. 2015. Multimodal cues improve prey localization under complex environmental conditions. Proceedings of the Royal Society B: Biological Sciences 282:20151403.

Rheindt FE. 2003. The impact of roads on birds: does song frequency play a role in determining susceptibility to noise pollution? Journal für Ornithologie 144:295–306.

Riechert SE, Lockley T. 1984. Spiders as biological control agents. Annual review of Entomology 29:299–320.

Roca IT, Desrochers L, Giacomazzo M, Bertolo A, Bolduc P, Deschesnes R, Martin CA, Rainville V, Rheault G, Proulx R. 2016. Shifting song frequencies in response to anthropogenic noise: a meta-analysis on birds and anurans. Behavioral Ecology 27:1269–1274.

Römer H. 2013. Masking by noise in acoustic insects: problems and solutions. In: Animal communication and noise. Springer, 33–63.

Ronacher B, Hoffmann C. 2003. Influence of amplitude modulated noise on the recognition of communication signals in the grasshopper Chorthippus biguttulus. Journal of Comparative Physiology A 189:419–425.

Rosenberg KV, Dokter AM, Blancher PJ, Sauer JR, Smith AC, Smith PA, Stanton JC, Panjabi A, Helft L, Parr M. 2019. Decline of the North American avifauna. Science 366:120–124.

Roslin T, Hardwick B, Novotny V, Petry WK, Andrew NR, Asmus A, Barrio IC, Basset Y, Boesing AL, Bonebrake TC. 2017. Higher predation risk for insect prey at low latitudes and elevations. Science 356:742–744.

Saldaña-Vázquez RA, Munguía-Rosas MA. 2013. Lunar phobia in bats and its ecological correlates: a meta-analysis. Mammalian Biology 78:216–219.

Sales G. 2012. Ultrasonic communication by animals. Springer Science & Business Media.

Sanders TA, Edge WD. 1998. Breeding bird community composition in relation to riparian vegetation structure in the western United States. The Journal of wildlife management:461–473.

Schaub A, Ostwald J, Siemers BM. 2008. Foraging bats avoid noise. Journal of Experimental Biology 211:3174–3180.

Schmidt AK, Riede K, Römer H. 2011. High background noise shapes selective auditory filters in a tropical cricket. Journal of Experimental Biology 214:1754–1762.

Schmidt AK, Römer H. 2011. Solutions to the cocktail party problem in insects: selective filters, spatial release from masking and gain control in tropical crickets. PLoS One 6:e28593.

Schneider C, Laizé CLR, Acreman MC, Flörke M. 2013. How will climate change modify river flow regimes in Europe? Hydrology and Earth System Sciences 17:325–339.

Schwartz JJ, Bee MA. 2013. Anuran acoustic signal production in noisy environments. In: Animal communication and noise. Springer, 91–132.

Schwartz JJ, Gerhardt HC. 1989. Spatially mediated release from auditory masking in an anuran amphibian. Journal of Comparative Physiology A 166:37–41.

Senzaki M, Kadoya T, Francis CD. 2020. Direct and indirect effects of noise pollution alter biological communities in and near noise-exposed environments. Proceedings of the Royal Society B 287:20200176.

Sewell GD. 1970. Ultrasonic communication in rodents. Nature 227:410–410.

Shamble PS, Menda G, Golden JR, Nitzany EI, Walden K, Beatus T, Elias DO, Cohen I, Miles RN, Hoy RR. 2016. Airborne acoustic perception by a jumping spider. Current Biology 26:2913–2920.

Shannon G, Angeloni LM, Wittemyer G, Fristrup KM, Crooks KR. 2014. Road traffic noise modifies behaviour of a keystone species. Animal Behaviour 94:135–141.

Shannon G, McKenna MF, Angeloni LM, Crooks KR, Fristrup KM, Brown E, Warner KA, Nelson MD, White C, Briggs J. 2016. A synthesis of two decades of research documenting the effects of noise on wildlife. Biological Reviews 91:982–1005.

Sherman PM. 1994. The orb-web: an energetic and behavioural estimator of a spider's dynamic foraging and reproductive strategies.

Siemers BM, Schaub A. 2011. Hunting at the highway: traffic noise reduces foraging efficiency in acoustic predators. Proceedings of the Royal Society of London B: Biological Sciences 278:1646–1652.

Silk MJ, Harrison XA, Hodgson DJ. 2020. Perils and pitfalls of mixed-effects regression models in biology. PeerJ 8:e9522.

Sills JM, Southall BL, Reichmuth C. 2017. The influence of temporally varying noise from seismic air guns on the detection of underwater sounds by seals. The Journal of the Acoustical Society of America 141:996–1008.

Simpson SD, Radford AN, Nedelec SL, Ferrari MC, Chivers DP, McCormick MI, Meekan MG. 2016. Anthropogenic noise increases fish mortality by predation. Nature communications 7:10544.

Slabbekoorn H, Peet M. 2003. Birds sing at a higher pitch in urban noise. Nature 424 (6946): 267-267.

Sólymos P, Matsuoka SM, Bayne EM, Lele SR, Fontaine P, Cumming SG, Stralberg D, Schmiegelow FK, Song SJ. 2013. Calibrating indices of avian density from non-standardized survey data: making the most of a messy situation. Methods in Ecology and Evolution 4:1047–1058.

Sólymos P, Matsuoka SM, Cumming SG, Stralberg D, Fontaine P, Schmiegelow FK, Song SJ, Bayne EM. 2018. Evaluating time-removal models for estimating availability of boreal birds during point count surveys: Sample size requirements and model complexity. The Condor: Ornithological Applications 120:765–786.

Sólymos P, Moreno M, Lele SR. 2014. detect: Analyzing wildlife data with detection error. R package version 0.3-2.

Song H, Béthoux O, Shin S, Donath A, Letsch H, Liu S, McKenna DD, Meng G, Misof B, Podsiadlowski L. 2020. Phylogenomic analysis sheds light on the evolutionary pathways towards acoustic communication in Orthoptera. Nature Communications 11:1–16.

Spangler HG, Greenfield MD, Takessian A. 1984. Ultrasonic mate calling in the lesser wax moth. Physiological Entomology 9:87–95.

Strauß J, Lakes-Harlan R. 2014. Evolutionary and phylogenetic origins of tympanal hearing organs in insects. Insect hearing and acoustic communication:5–26.

Su MP, Andrés M, Boyd-Gibbins N, Somers J, Albert JT. 2018. Sex and species specific hearing mechanisms in mosquito flagellar ears. Nature communications 9:1–16.

Sueur J, Aubin T, Simonis C. 2008. Seewave, a free modular tool for sound analysis and synthesis. Bioacoustics 18:213–226.

Sueur J, Krause B, Farina A. 2019. Climate Change Is Breaking Earth's Beat. Trends in ecology & evolution.

Sun JW, Narins PM. 2005. Anthropogenic sounds differentially affect amphibian call rate. Biological conservation 121:419–427.

Surlykke A, Kalko EK. 2008. Echolocating bats cry out loud to detect their prey. PLoS one 3.

Swaddle JP, Francis CD, Barber JR, Cooper CB, Kyba CC, Dominoni DM, Shannon G, Aschehoug E, Goodwin SE, Kawahara AY. 2015. A framework to assess evolutionary responses to anthropogenic light and sound. Trends in ecology & evolution 30:550–560.

Tennessen JB, Parks SE, Tennessen TP, Langkilde T. 2016. Raising a racket: invasive species compete acoustically with native treefrogs. Animal Behaviour 114:53–61.

Tew ER, Adamson A, Hesselberg T. 2015. The web repair behaviour of an orb spider. Animal Behaviour 103:137–146.

Tew N, Hesselberg T. 2017. The Effect of Wind Exposure on the Web Characteristics of a Tetragnathid Orb Spider. Journal of insect behavior 30:273–286.

Tewksbury JJ, Garner L, Garner S, Lloyd JD, Saab V, Martin TE. 2006. Tests of landscape influence: nest predation and brood parasitism in fragmented ecosystems. Ecology 87:759–768.

Thode AM, Blackwell SB, Conrad AS, Kim KH, Marques T, Thomas L, Oedekoven CS, Harris D, Bröker K. 2020. Roaring and repetition: How bowhead whales adjust their call density and source level (Lombard effect) in the presence of natural and seismic airgun survey noise. The Journal of the Acoustical Society of America 147:2061–2080.

Tomasi TE. 1979. Echolocation by the short-tailed shrew Blarina brevicauda. Journal of Mammalogy 60:751–759.

Tressler J, Smotherman MS. 2009. Context-dependent effects of noise on echolocation pulse characteristics in free-tailed bats. Journal of Comparative Physiology A 195:923–934.

Troudet J, Grandcolas P, Blin A, Vignes-Lebbe R, Legendre F. 2017. Taxonomic bias in biodiversity data and societal preferences. Scientific reports 7:1–14.

Turnbull SD. 1994. Changes in masked thresholds of a harbour seal (Phoca vitulina) associated with angular separation of signal and noise sources. Canadian Journal of Zoology 72:1863–1866.

Tuttle MD, Ryan MJ. 1982. The role of synchronized calling, ambient light, and ambient noise, in anti-bat-predator behavior of a treefrog. Behavioral Ecology and Sociobiology 11:125–131.

Ubick D, Paquin P, Cushing PE. 2017. Spiders of North America: an identification manual. American Arachnological Society.

von Uexküll J. 1909. Umwelt und innenwelt der tiere. Berlin: Springer.

Ulanovsky N, Fenton MB, Tsoar A, Korine C. 2004. Dynamics of jamming avoidance in echolocating bats. Proceedings of the Royal Society of London. Series B: Biological Sciences 271:1467–1475.

Upham NS, Esselstyn JA, Jetz W. 2019. Inferring the mammal tree: Species-level sets of phylogenies for questions in ecology, evolution, and conservation. PLoS Biology 17.

USDOT USD of T. 2011. Highway Traffic Noise Analyses and Abatement Guidance.

Van Dyck H. 2012. Changing organisms in rapidly changing anthropogenic landscapes: the significance of the 'Umwelt'-concept and functional habitat for animal conservation. Evolutionary Applications 5:144–153.

Van Flandern TC, Pulkkinen KF. 1979. Low-precision formulae for planetary positions. The Astrophysical Journal Supplement Series 41:391–411.

Vander Haegen WM, Degraaf RM. 1996. Predation on artificial nests in forested riparian buffer strips. The Journal of wildlife management: 542–550.

Vargas-Salinas F, Amézquita A. 2013. Traffic noise correlates with calling time but not spatial distribution in the threatened poison frog Andinobates bombetes. Behaviour 150:569–584.

Vargas-Salinas F, Amézquita A. 2014. Abiotic noise, call frequency and stream-breeding anuran assemblages. Evolutionary ecology 28:341–359.

Vélez A, Bee MA. 2011. Dip listening and the cocktail party problem in grey treefrogs: signal recognition in temporally fluctuating noise. Animal Behaviour 82:1319–1327.

Vélez A, Höbel G, Gordon NM, Bee MA. 2012. Dip listening or modulation masking? Call recognition by green treefrogs (Hyla cinerea) in temporally fluctuating noise. Journal of Comparative Physiology A 198:891–904.

Venner S, Casas J. 2005. Spider webs designed for rare but life-saving catches. Proceedings of the Royal Society B: Biological Sciences 272:1587–1592.

Verzano K, Menzel L. 2009. Snow conditions in mountains and climate change–a global view. Hydrology in Mountain Regions: Observations, Processes and Dynamics, IAHS-Publication, Wallingford, Oxfordshire, UK 326:147–154.

Wagner DL, Grames EM, Forister ML, Berenbaum MR, Stopak D. 2021. Insect decline in the Anthropocene: Death by a thousand cuts. Proceedings of the National Academy of Sciences 118.

Wale MA, Simpson SD, Radford AN. 2013a. Noise negatively affects foraging and antipredator behaviour in shore crabs. Animal Behaviour 86:111–118.

Wale MA, Simpson SD, Radford AN. 2013b. Size-dependent physiological responses of shore crabs to single and repeated playback of ship noise. Biology letters 9:20121194.

Ward MP, Schlossberg S. 2004. Conspecific attraction and the conservation of territorial songbirds. Conservation biology 18:519–525.

Ware HE, McClure CJ, Carlisle JD, Barber JR. 2015. A phantom road experiment reveals traffic noise is an invisible source of habitat degradation. Proceedings of the National Academy of Sciences 112:12105–12109.

West-Eberhard MJ. 1984. Sexual selection, competitive communication and species specific signals in insects. In: Insect Communication (Proceedings of the 12th Symposium of the Royal Entomological Society of London. Acedemic Press,.

Wickham H. 2011. ggplot2. Wiley Interdisciplinary Reviews: Computational Statistics 3:180–185.

Wiegmann BM, Trautwein MD, Winkler IS, Barr NB, Kim J-W, Lambkin C, Bertone MA, Cassel BK, Bayless KM, Heimberg AM. 2011. Episodic radiations in the fly tree of life. Proceedings of the National Academy of Sciences 108:5690–5695.

Wiley RH. 2015. Noise matters: the evolution of communication. Harvard University Press.

Willett TR. 2001. Spiders and other arthropods as indicators in old-growth versus logged redwood stands. Restoration Ecology 9:410–420.

Williams CB. 1936. IX-The influence of moonlight on the activity of certain nocturnal insects, particularly of the family Noctuidae, as indicated by a light trap. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences 226:357–389.

Williams KS. 1993. Use of terrestrial arthropods to evaluate restored riparian woodlands. Restoration Ecology 1:107–116.

Williams CB, Singh BP. 1951. Effect of moonlight on insect activity. Nature 167:853–853.

Williams R, Wright AJ, Ashe E, Blight LK, Bruintjes R, Canessa R, Clark CW, Cullis-Suzuki S, Dakin DT, Erbe C. 2015. Impacts of anthropogenic noise on marine life: Publication patterns, new discoveries, and future directions in research and management. Ocean & Coastal Management 115:17–24.

Wilson DR, Hare JF. 2004. Ground squirrel uses ultrasonic alarms. Nature 430:523–523.

Wood WE, Yezerinac SM. 2006. Song sparrow (Melospiza melodia) song varies with urban noise. The Auk 123:650–659.

Wright AJ, Soto NA, Baldwin AL, Bateson M, Beale CM, Clark C, Deak T, Edwards EF, Fernández A, Godinho A. 2007. Do marine mammals experience stress related to anthropogenic noise? International Journal of Comparative Psychology 20.

Yang LH, Gratton C. 2014. Insects as drivers of ecosystem processes. Current Opinion in Insect Science 2:26–32.

Yela JL, Holyoak M. 1997. Effects of moonlight and meteorological factors on light and bait trap catches of noctuid moths (Lepidoptera: Noctuidae). Environmental Entomology 26:1283–1290.

Zelick RD, Narins PM. 1982. Analysis of acoustically evoked call suppression behaviour in a neotropical treefrog. Animal behaviour 30:728–733.

Zelick RD, Narins PM. 1983. Intensity discrimination and the precision of call timing in two species of neotropical treefrogs. Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology 153:403–412.

Zeng R, Cai X. 2014. Analyzing streamflow changes: Irrigation-enhanced interaction between aquifer and streamflow in the Republican River Basin. Hydrology and Earth System Sciences 18:493–502.

Zhao L, Zhu B, Wang J, Brauth SE, Tang Y, Cui J. 2017. Sometimes noise is beneficial: stream noise informs vocal communication in the little torrent frog Amolops torrentis. Journal of Ethology 35:259–267. DOI: 10.1007/s10164-017-0515-y.

Zhou J, Miles RN. 2017. Sensing fluctuating airflow with spider silk. Proceedings of the National Academy of Sciences:201710559.

Zollinger SA, Brumm H. 2011. The lombard effect. Current Biology 21:R614–R615.

Zollinger SA, Goller F, Brumm H. 2011. Metabolic and respiratory costs of increasing song amplitude in zebra finches. PLoS One 6:e23198.

Zollinger SA, Podos J, Nemeth E, Goller F, Brumm H. 2012. On the relationship between, and measurement of, amplitude and frequency in birdsong. Animal Behaviour 84:e1–e9.

Zollinger SA, Slater PJ, Nemeth E, Brumm H. 2017. Higher songs of city birds may not be an individual response to noise. Proceedings of the Royal Society B: Biological Sciences 284:20170602.

Zuur AF, Ieno EN. 2016. A protocol for conducting and presenting results of regression-type analyses. Methods in Ecology and Evolution 7:636–645.

Zuur AF, Ieno EN, Elphick CS. 2010. A protocol for data exploration to avoid common statistical problems. Methods in ecology and evolution 1:3–14.

APPENDIX A

Quantifying noise

Quantifying noise is important for dissecting the effects of noise on wildlife populations (Pater, Grubb & Delaney, 2009; Gill et al., 2015). Yet, in practice it is almost never done, especially beyond measuring sound pressure levels (Shannon et al., 2016). Here we offer an introduction to quantifying acoustic environments.

I) Frequency:

Sound frequency is the number of oscillations that a sound pressure wave completes in 1 second, and is thus measured in hertz (Hz), or often kilohertz (kHz). Spectra of acoustic environments can be complicated to quantify as they are likely to change throughout the day due to shifts in biotic activity, weather patterns, and temperature – the latter of which affects frequency-specific attenuation properties of sound (Bradbury and Vehrencamp 1998). Thus, short-term measurements may not capture important characteristics of chronic background noise frequencies. However, long-term measurements may integrate over time periods of largely unimportant activity. If one is interested in whether or not a female frog can hear a calling male at night, for example, then daytime frequencies are likely uninformative at best. At worst their inclusion in quantifying the acoustic environment could mask any relationship between nighttime conditions and measurements of female listening behavior. In contrast, if one is interested in how noise might act as a chronic stressor to animals (Campo, Gil & Davila, 2005), integrating over the duration of an entire 24-hour period may be more relevant.

Deciding on an appropriate metric to characterize the frequency content of acoustic environments can also prove difficult. Peak frequency, median frequency, and bandwidth are all characteristics that can be easily measured from a sound recording, yet they may not shed light on the question at hand. Peak frequency may be important if animals are responding mostly to the loudest perceived sound, but given that each animal is sensitive to a different range of frequencies, a measured peak frequency may not be what is perceived by that animal as the loudest sound in the environment. It may be more useful to measure the sound energy (see Amplitude below) within the frequency band to which the focal animal uses for vocal signals (Halfwerk, Holleman & Slabbekoorn, 2011) or that reflects its best hearing sensitivity.

II) Amplitude:

Amplitude is a measure of the magnitude of pressure a sound produces. This is generally measured in sound pressure level (SPL) and reported in decibels (dB), which is used to express the ratio of a measured pressure to a reference level. This reference level is 20 µPa in terrestrial environments, and 1 µPa in marine environments by convention, which is equal to 0 dB, or the threshold for human hearing. Some researchers will report the reference level they used (e.g. 55 dB rel. 20 µPa), but it is often omitted and measurements are assumed to be relative to the conventional level. SPL measurements that are reported relative to two different reference levels (i.e. in terrestrial and marine environments) are not directly comparable. Similarly, as sound attenuates with distance from a source, the recorded SPL will vary depending on the relative location between the microphone and source. Thus, the distance between the two should be reported along with reference levels (e.g. 55 dB rel. 20 µPa at 1 m), because SPL measurements without reference levels or distances are meaningless. For acoustic environment quantification, background SPLs can be integrated and averaged over long periods of time, such as days or weeks (Mennitt & Fristrup, 2012; Merchant et al., 2015; see Levenhagen et al., 2020 for an example). It is important to note, however, that special care must be taken when integrating sound pressure levels; they cannot be directly averaged since they are on a logarithmic scale.

While anthropogenic sources are often considered to produce noise of higher SPLs than natural sources (Brattstrom & Bondello, 1983), this is not always the case. There are many natural sources, such as flowing streams (78.8 dBA rel. 20 µPa at 10 m, 3-min Leq, Pioneer Mountains of Idaho) and pounding surf (68.7 dBA rel. 20 µPa at 60 m, 3-min Leq, Central California Coast) which can be as loud or louder than some traffic noise (70 dBA, 1,000 vehicles per hour at 55 mph, USDOT 2011; 76 dBA rel. 20 µPa at 10 m, 3-min Leq, Bunkley and Barber, 2015). Amplitude has been the most well-reported measure of noise, yet some researchers still fail to measure or report this metric at the source or the received level (Shannon et al. 2016), the latter of which is most important for understanding biological responses.

III) Frequency and amplitude:

Since, we have historically used sound pressure meters to measure noise relevant to humans, these devices are often sensitive within the human hearing range (10 Hz and 20 kHz), and are weighted relative to human hearing. Due to international standards, all sound amplitude measuring devices come with an “A-weighting” option (often denoted dBA as above, IEC 2013). The resulting sound pressure level is ‘weighted’ roughly based on perceptual equal-loudness of pure tones by the human ear. That is, frequencies that are more readily transduced by the human ear, will bear more weight in the dBA measurement than frequencies that do not. When considering non-human animals, it is important to note that frequencies that are not audible by humans are filtered out from this dBA measurement. This can be problematic given that many taxa can hear outside the range of human hearing.

Z-weighting standards (also sometimes called flat-weighting or unweighted) consist of a “flat” response between 10 Hz and 20 kHz – that is, all frequencies within this range contribute equally to the measure of sound pressure level (denoted dBZ, IEC 2013). It is possible to have a ‘flat’ or ‘unweighted’ response for a microphone that records ultrasonic frequencies (> 20 kHz), yet this technically is not considered Z-weighting, which ends at 20 kHz (IEC, 2013).

Z-weighting (or even ‘flat’ weighting for microphones outside of human hearing) is only unweighted across the sensitive frequency range of the microphone or recording unit. Thus, the frequency-response curve of the microphone – that is the relative sensitivity of the microphone to various frequencies – must be reported. Most microphones are not perfectly “flat” in their frequency response, and appropriate compensations must be performed to know the true spectrum of the acoustic environment. Additionally, microphones that are considered “flat” (pick up all frequencies more or less equally), are only flat to an upper and lower limit. These limits more often than not correspond with human hearing, since most microphone applications are human-centric. This problem is especially exaggerated with respect to infrasonic and ultrasonic frequencies.

IV) Temporal patterns:

Temporal patterns of noise are often overlooked, yet they may help elucidate differences in seemingly similar noise backgrounds (Figure 1.2). Time adds a degree of complexity to amplitude and frequency measurements. The integration time of sound level measurements, for example, can drastically change the outcome. Integrating dB over longer time periods will lessen the importance of sudden bursts of noise or continuous sounds restricted to a particular time of day on the SPL measurement.

Background noise may vary in how quickly and to what magnitude amplitude or frequency is modulated, how often a sound is repeated within a given period of time (e.g. call rate), or how long a noise source continues producing a sound (duration). Noise may be present only during certain times of the day (e.g. dawn bird chorus or rush-hour traffic), certain seasons (e.g. spring runoff or summer motorboat activities), or certain stochastic events (e.g. earthquakes, volcanoes, and outdoor concerts).

Statistical noise levels (often denoted L10, L20, L30, etc.) are a useful set of parameters to understand the percentage of time that a particular sound pressure level was exceeded. An L10 measurement of 60 dBA, for example, means that the sound pressure level was 60 dBA or higher, 10% of the time. This measure will include any sudden or abrupt peaks of noise in an acoustic environment. L90 measurements, on the other hand, give you the sound pressure level which was exceeded 90% of the time. This measurement often results in a much lower dB value, and likely excludes sudden peaks of noise. Similarly, L50 measures give you the median SPL.

APPENDIX B

Supplementary information for the ‘Phantom Rivers’ experiment

Noise playback setup:

We suspended speakers from tripods made of 4.5 m metal conduit to elevate them 3-3.5 m from the ground to improve noise propagation (Figure B.2). River noise was broadcast at each site via two Octasound SP820A speakers (35 Hz to 20 kHz ± 10 dB; KDM Electronics Incorporated, Ajax, ON, Canada), whereas shifted noise was broadcast at each site via three Octasound SP800A speakers (40 Hz to 20 kHz ± 12 dB; KDM Electronics Incorporated). This discrepancy was designed to account for differences in propagation due to attenuation of the different spectra of our playbacks. That is, we estimated a similar amount of land area would be exposed to the noise treatments (Figure B.3). To account for differences in infrastructure between treatments, river noise sites had an additional dummy tower (Figure B.3; B.4) and dummy solar panel placed in the same location as found on shifted-noise sites. Control sites consisted of three dummy towers each paired with a dummy solar panel, placed according to the same spacing as treatment sites. We constructed dummy speaker towers by hanging large metal speaker horns (0.41 m diameter; Dayton Audio RPH16) from tripods made of 4.5 m PVC piping (Figure B.4). We used particle board (1 x 1.5 m) spray-painted glossy black to mimic solar panels (see below for use of solar panels).

Each speaker was powered by an amplifier (AD1200.1, PRV audio) connected to two 12V deep cycle RV/marine batteries (DURDC12-100P; Duracell) connected in parallel. Solar panels (Suniva OPT285-60-4-100; MidNite Solar Inc., WA, USA; Figure B.2) charged the deep cycle batteries via solar controllers (The Kid 30A MPPT; MidNite Solar Inc., WA, USA), which also relayed power from the batteries to the amplifier. Roland R05 players relayed sound files from SD cards to the amplifiers, and were powered for multiple weeks at a time via LiFePO3 (3.3V, Batteryspace, CA, USA) batteries. Amplifier settings were as follows: 'over clip' was set to "off" position, 'H.P.F.' was set to minimum value (10 Hz), 'L.P.F.' was set to maximum value (25 kHz), and all three equalizer settings were set to 0 dB.

Creating acoustic environment playback files:

We recorded natural river noise to produce field playback files in June of 2016. We recorded river noise at three locations along Trail and Hyndman creeks near Sun Valley, ID using a Zoom H4N Pro recorder (Zoom North America Inc., Hauppauge, NY, USA) connected to a Rode NT1A condenser microphone (Rode, Silverwater, NSW, Australia) positioned approximately 5 m from the river's edge. This resulted in three, approximately 1-hour long files saved in an uncompressed WAV format with a 48 kHz sample rate and 16-bit depth. We screened all files for all non-river noise (e.g. insects, birds) in the program Audacity (Audacity Team 2017) and removed these instances using the cross-fade function. We standardized the runtime of all river files to 45 minutes, as this was the length of the shortest playback file following the removal of non-relevant sounds. Finally, each file was normalized to an amplitude of -2 dB.

To create the "shifted" playbacks we applied a high-pass filter to each playback file at 2 kHz in Adobe Audition CC 2017 (Adobe Systems, San Jose, CA, USA), then used the Frequency Band Splitter to apply band-specific amplifications to two bands: 2-14 kHz and 14-24 kHz. Each band received a +4 and +5 dB amplification, respectively, following power calculations below.

Next, we compared the power spectra of each playback file to a 'typical' songbird audiogram to ensure that normal and shifted playback files presented a similar sensory impact on the local bird community. We created an audiogram for birds based on values adapted from Dooling (Dooling, 2002) for songbird species whose ranges overlapped our study sites. We extracted threshold values for American robin (*Turdus migratorius*), brown-headed cowbird (*Molothrus ater*), chipping sparrow (*Spizella passerina*), dark-eyed junco (*Junco hyemalis*), red-winged blackbird (*Agelaius phoeniceus*), song sparrow (*Melospiza melodia*), and western meadowlark (*Sturnella neglecta*) as exemplars. We fit the consolidated values with a quadratic function (Dooling, 2002), providing audiograms against which the power spectra of the playback files could be compared.

To compare the power of normal and shifted playbacks with respect to songbird hearing, we played the first two minutes of each playback file in an anechoic room at Boise State University at approximate field amplitudes (i.e. ~97 dBA for shifted, ~95 dBA for phantom at 2 m) using our field playback equipment: a Roland R05 player linked to a AD1200.1-2 amplifier (PRV Audio, Fort Lauderdale, FL, USA) and an Octasound SP820A speaker. We recorded these playbacks as uncompressed WAVs at a 44.1 kHz sample rate and 16 bit-depth using a Rode NT1A condenser microphone positioned 2 m from the speaker, connected to a PC computer running Audacity 2017. We then used custom Matlab code (Daniel Mennitt) to calculate the power within each third-octave band for each file, and used these values to calculate the difference in power for each band to the area under the curve for the respective songbird audiogram between 160 Hz and 16 kHz. Each shifted file was compared to its phantom counterpart and deemed equal if the total power difference was within 3 dB (i.e. the standard error of the microphone). All shifted playbacks were within 1.38 dB of their phantom counterparts.

We used Adobe Audition CC 2017 to create the full-length playback files to be used in the field. These playback files consisted of each 45-minute recording arranged linearly in a random order, with each individual river recording used twice per playback file (no file occurred back-to-back). The order of shifted recordings matched those of their phantom counterparts. We applied a 5 s crossfade between each subsequent recording and applied a 7 s fade in/out to the full-length file to avoid clipping when looped. These files were once again exported in uncompressed WAV format at a sample rate of 48 kHz and a 16-bit depth. In total, this resulted in four playback files – phantom and shifted river – each of approximately 4:30:00 in duration.

Environmental parameter quantification

Acoustic environment quantification:

The acoustic environment was quantified with long-term recordings from Roland R05 recorders (hereafter referred to as an ARU: acoustic recording unit). ARU settings were as follows: 44.1 kHz sampling rate, 128 kbps MP3 recording mode, input gain was set to 55, mic gain = ‘H’, limiter = ‘off’, and low cut = ‘off.’

Sound pressure level (SPL):

We converted 106,769 hours of long-term ARU recordings into daily-averaged median sound pressure levels (L50; measured as dBA rel. 20 µPa; see Cinto Mejia, McClure & Barber, 2019; Levenhagen et al., 2020) using custom software ‘AUDIO2NVSPL’ and ‘Acoustic Monitoring Toolbox’ (Damon Joyce, Natural Sounds and Night Skies Division, National Park Service).

Acoustic environment spectrum:

We used custom software (Gomes, 2020b) in the programming language R and the package 'FFmpeg' in command prompt to convert 106,769 hours of long-term recordings into 71,282 individual 3-minute files starting each hour of the day (Figure B.5). Thus 24, 3-minute files were created per acoustic recording location per day (one for every hour). We then used the packages \`tuneR\` and \`seewave\` to read in and measure the median frequency of sound files, respectively (Sueur, Aubin & Simonis, 2008; Ligges, 2013; Gomes, 2020b). These hourly metrics were then averaged by date to create a daily metric.

We used different timeframes to quantify the local acoustic environment for analyses of bird abundance and bat activity, reflecting taxa-specific differences in behavior and space use. Given that birds establish breeding territories that they inhabit almost exclusively throughout the breeding season (and thus, territorial birds on our site would be experiencing a full day's variance in the acoustic environment's frequency and amplitude values), we intended to use integrated 24-hour measurements of both SPL and spectrum in our models of bird abundance. However, dawn chorus will be full of singing birds - increasing both the amplitude and frequency of background noise. In order to avoid circular findings (i.e., more singing birds equals more birds), we excluded these times of high bird activity (0600-1100). Bats, on the other hand, are likely travelling to/through these sites from their day roosts elsewhere, and likely experience the sites' acoustic environments for only a number of hours each night. Thus, we used nightly averaged SPL and frequency values when modelling bat activity. We quantified 'nightly' hours as those between 2100 and 0600, corresponding roughly to sunrise and sunset times in the region during the course of the study.

Percent riparian vegetation:

The local amount of riparian vegetation may influence both bird abundances (Sanders & Edge, 1998) and bat activity (Grindal, Morissette & Brigham, 1999). Thus, we quantified the proportion of riparian vegetation surrounding sampling locations as a location-specific parameter in our models. We used high spatial resolution land-cover data to manually create polygon vertices surrounding all patches of riparian vegetation (defined as non-coniferous trees and non-*Artemisia* ground cover) within a 100-meter radius of each sampling location. Following riparian vegetation classification, we calculated the proportion of land-cover within a 100 m radius of each sampling location that was riparian vegetation using 'Tabulate Intersection' in ArcMap 10.2 (Esri, CA, USA).

Moon phase:

The phase of the moon is known to affect the activity of at least some species of bats (Appel et al., 2017, 2019). Thus, we included the phase of the moon (represented by the proportion of the moon visible at midnight), by date, in our models of bat activity. We sourced these data from the U.S. Naval Observatory.

Bird abundance

Issues of detectability in avian point counts:

The detection of birds during point counts can be problematic when hoping to estimate the abundance of birds on the landscape. We employed various techniques that we describe below to correct for both standard detection issues, and detection issues in background noise.

Detectability over distance - distance truncation

We truncated our counts to 50 m, because at this limit it is likely that most birds can be reliably detected (Pacifici, Simons & Pollock, 2008; Hutto, 2016), given that they are singing (see next paragraph). We opted to not use a distance-based model for detectability given the nature of our river sites. Because the habitat is not homogenous, the probability that a bird is detected will not fall off evenly with distance. This situation violates the assumptions of distance-based models. Distance truncation also ensured that birds counted in one location did not overlap with birds counted in another (see *'Data collection locations'* above for distances between locations).

Observer detectability in noise

Counting birds in noisy places raises a critical problem that can be difficult to overcome. Here, we turned speakers off during counts. This largely eliminates high sound level environments that are disruptive to detecting birds (Figure B.6; Ortega & Francis, 2012). Additionally, we used three different methods to triangulate on whether or not the patterns we have measured are real, or some artefact of detection probabilities. Firstly, we included background noise levels during point counts as a covariate in a removal model. This allowed the data to tell us how varying sound levels affected our ability to detect birds. Secondly, we created a point-count experiment with our observers to directly calculate these same detection probabilities under various noise conditions. Thirdly, all of our 'regular' point count efforts in the field were paired with an equal number of 'unimodal', vision-only point counts. That is, we significantly limited our ability to detect birds auditorily, and focused on visual detections. All three of these methods consistently converge on the same results (see Table B.1).

Detectability over time - removal models

An additional issue when counting birds is that the detection probability changes with species and/or location due to the probability that a bird will sing (Sólymos et al., 2013). It is well-known that the probability that a bird will sing can vary seasonally and daily. Thus, we used various combinations of ordinal date, time after sunrise, and scaled quadratic versions of those as predictors to explain the singing rate (see Table B.11). Additionally, the probability of detecting a singing bird can change with the acoustic environment. Loud rivers can partially mask singing birds, and make them less detectable. Thus, we included background sound pressure level (3-min Leq dBA; hereafter 'LEQ') as an additional covariate. Then we used AIC to select the best fitting model, which included the quadratic time after sunrise term and the LEQ term (Sólymos et al., 2018). Thus, this detection probability \`p\`, was modelled with a conventional removal model, and \`p\` was used as an offset in our negative binomial (NB) generalized linear mixed effects models (Sólymos et al., 2013, 2018; Sólymos, Moreno & Lele, 2014).

Point count experiment

The ability of human observers to detect birds during loud point counts is a known issue (Pacifici, Simons & Pollock, 2008), yet some sound pressure levels are acceptable for point counting (Ortega & Francis, 2012). In our experiment we turned off speakers at our noise treatment sites for point counts. This alleviated differences in background sound levels (and thus detectability) between control and treatment sites (Figure B.6).

Because playback speakers were turned off during counts, most of our point counts were conducted in relatively quiet conditions (mean = 48.7 dBA, sd = 9.2 dBA, median = 47 dBA; Figure B.6). However, some point-count locations (such as positive control sites) were naturally loud (up to 78.8 dBA). Thus, as one approach to control for this problem, we estimated the ability of our point count observer to correctly identify birdsong in such locations by performing a controlled detectability experiment under varying background sound levels.

We created six playback files consisting of songs from seven of the most-common birds detected during point counts in the 2017 season, sourced from the Macaulay Library: American robin (*Turdus migratorius*; ML 203260), house wren (*Troglodytes aedon*; ML 144011), lazuli bunting (*Passerina amoena*; ML 49753), northern flicker (*Colaptes auratus*; ML 63068), song sparrow (*Melospiza melodia*; ML 144005), spotted towhee (*Pipilo maculatus*; ML 177208), and warbling vireo (*Vireo gilvus*; ML 110999). Each birdsong playback was six minutes in length (to mimic two, three-minute point counts), with 21 songs/speaker, three songs per species/speaker, for a total of 42 songs across two speakers. Each instance of birdsong was separated by at least one second of silence, and all were normalized to 0.1 dB.

For this experiment, point count observers were situated in an open landscape at a time of year when birdsong had largely ceased (e.g. following the breeding season) to minimize the occurrence of natural birdsong during the experiment. In 2017, two point counters performed the experiment in sagebrush steppe in autumn, and in 2018 four point counters performed the experiment in an alfalfa field in late July. Two FoxPro speakers (Wildfire; Lewistown, PA, USA) were placed on each side of the point counter – one at 25 m from the point counter and the other at 50 m (i.e. within our truncation distance) – that broadcast birdsong during each experimental trial. We calibrated the volume of each bird playback speaker such that birdsong was broadcast at biologically relevant amplitudes of 90 dBA at 1 m. An Octasound SP820A was suspended approximately 2-3 m from the point counters to broadcast river noise (using the same playback file broadcast in the primary study). Point counters performed birdsong identification under several acoustic conditions: natural ambient levels (i.e. no river playback), as well as river noise broadcast at 47 dBA, 51 dBA, 63 dBA, and 73 dBA - the highest sound pressure level (1 hr LEQ) recorded at positive control sites in 2017. We calibrated river playback amplitudes and ambient condition sound pressure levels as a 30 second Leq (dBA) using a Larson Davis (model 824; Depew, NY, USA).

Each point count observer performed bird identification for a randomly selected (without replacement) combination of birdsong playlist and river-playback amplitude. The order in which these point counts were performed was also randomly determined. Misidentified or unheard instances of birdsong by the point counter were recorded as a 0, while correct identifications were marked as a 1. To model how river noise affected birdsong identification, we used the software JMP v14.2 (SAS Institute) to perform a logistic regression on the pooled results of all point counters, with sound level as the predictor. This generated a probability formula for the correct identification of birdsong with the following equation:

$$\text{Detection probability} = \left(1 + e^{-(a-bx)}\right)^{-1}$$

where a = 11.84; b = 0.154; x = 3-min Leq (dBA)

During each point count we recorded sound pressure levels (dBA) as a 3-min Leq (MicW; i436; Beijing, China), which was then used in the equation above to calculate detection probabilities in the various acoustic environments (see Figure B.7). We used this probability as an offset in generalized linear mixed effects models with raw point count data.

Earplugs & earmuffs

Observers wore earplugs and over-the-ear earmuffs for approximately half of the point counts to limit the observer to visual-only observations in an acoustically-challenging environment (Table B.12). This served as a comparison of detectability, since birdsong is more difficult to hear in some sites but not others, whereas vision-only detectability should not vary with sound level.

We ran the same bird abundance models with vision-only counts to exclude the possibility of auditory detections being disrupted by varying levels of noise as an additional way to validate our findings. When this vision-only model is run, daily sound pressure level (SPL; dBA L50) and spectral overlap between background frequency and birdsong are again significant predictors, further validating the directions of these patterns in our global model (Table B.1).

Species-level analyses

We created similar abundance models (as the global model presented in the main text) for 26 individual species of birds. Dusky flycatchers and song sparrows both avoid high sound levels. Yet, Brewer's sparrows were more abundant in high intensity environments (Table B.2), even though the same species avoided energy-extraction noise in another experimental study (Cinto Mejia, McClure & Barber, 2019). This result suggests that Brewer's sparrows might use river noise as a source of information to predict the presence of habitat shielded from predators, as birds that stay in noisy areas can experience reduced nest predation (Francis et al., 2012b). It is also possible that this sagebrush-specialist species benefits from adjacent riparian areas, which can be predicted by the sounds of running water. Indeed, other taxa show attraction to such habitat selection cues (Zhao et al., 2017).

In our model that included all species, birds did not respond to the median frequency of the acoustic environment, yet nine individual species did – with seven of these species responding negatively to increasing background frequency. These patterns may be a result of deficits to sound localization behavior as small-headed songbirds rely upon higher frequencies for inter-aural level cues (4 kHz and above; Klump & Larsen, 1992).

When testing the effects of masking on birdsong, lazuli buntings definitively avoided background noise that spectrally overlaps their song, and other species trended in that direction as well (Table B.2). Counter-intuitively, orange-crowned warblers and spotted towhees were more abundant with greater spectral overlap – as if they were attracted to background spectra that were similar to their song. It is possible that these birds use frequencies similar to their own vocalizations (e.g. conspecifics) as indirect information about habitat quality. In this case, river noise could be acting as a misleading cue (Dominoni et al., 2020) by attracting birds to habitat that is not higher quality.

Alternatively, these animals may be seeking acoustic refuge from eavesdropping predators, as has been suggested for frogs that call near waterfalls to avoid bat predation (Tuttle & Ryan, 1982).

Bird foraging trials

Caterpillar scoring

We checked caterpillars on the second, fourth, and fifth days (the first day being the placement day and the fifth day being the last day) for signs of predation. Thus, we totaled 3600 caterpillar-days during the experiment. When signs of predation were present, caterpillars were removed from the substrate and all remaining caterpillars were removed from each site and scored on the fifth day. The type of predator was assessed separately by 2-3 individuals who were blind as to which site the caterpillars came from. If the assessments did not match across observers, predation values were averaged (Roslin et al., 2017). That is, if two of the three observers scored the caterpillar as being predated by birds, then that caterpillar received a score of 0.67 instead of 1. Each observer scored whether the caterpillars were not predated (NP), predated by birds (B), predated by arthropods (A), or predated by mammals (M), which were all rodents. Here we focus on avian predation (Figure B.8), since the focus of this paper is on bird and bat predators, not arthropods or other non-bat mammals.

Bat activity

Each SM3 was programmed to automatically record bat activity for five and a half hours each night. However, the timing of these recordings differed between the 2017 and 2018 seasons. Triggered recording began 30 minutes before sunset in both years, but extended for two hours following sunset in 2017 and three hours following sunset in

2018. Triggered recording resumed three hours before dawn in both years, continuing until sunrise in 2017. However, a one-hour long recording break was programmed to occur two hours before sunrise in the 2018 season to accommodate sonic recording for a separate study (Figure B.10). Ultrasonic recordings were made at a 256 kHz sample rate.

We used SonoBat v4.3 (SonoBat, CA, USA) to categorize bat calls to the species level using the Western Wyoming classifier set. Acceptable call quality was set to 0.8, a maximum of 32 calls were considered per sequence, and a 10 kHz high pass filter applied. We aggregated call sequence identifications from the "1^{st}" column of all resultant SonoBat output sheets by sample night for each detected species to use as a metric of species-level activity in further analyses, as laboratory tests showed this classification to be the most robust for files with high background noise (see below). We excluded 122 bat nights (66 in 2017, 56 in 2018) from the resulting dataset as the placement of the SM3 coincided with nighttime insect trapping using a UV bucket trap, which have been shown to decrease the activity of light-averse bat species (Froidevaux, Fialas & Jones, 2018).

Bat detection probabilities in noise

We employed two control experiments to ensure that neither the SM3 recording units nor SonoBat were impaired by the acoustic environment playbacks. First, we performed playbacks of echolocation calls from two relatively low-frequency species that are common on our study sites under similar acoustic environment conditions as found on experimental sites. This was to confirm that the detectors were properly triggered under field-playback conditions. Second, we tested the ability of the classification software we used, SonoBat, to correctly classify bats in varying noise conditions.

Passive acoustic monitor ‘triggering’ in noise

We chose *Antrozous pallidus* and *Eptesicus fuscus* (peak frequency approximately 30 and 28 kHz, respectively) sonar calls to playback in this experiment as our speakers were capable of faithfully reproducing the frequencies of these bats’ echolocation cries. We selected two call sequences per species from our datasets – one of high amplitude and one of low amplitude – to ensure that even distant or off-axis bat passes were still able to trigger a recording under high background sound levels.

We performed playbacks in an anechoic room at Boise State University. We broadcast all echolocation call sequences using an UltraSoundGate Player (BL Pro; Avisoft Bioacoustics; Glienicke/Nordbahn, Germany). Both the SM3 microphone and the UltraSoundGate Player were positioned on tripods 1 m from the floor. For *A. pallidus* calls the microphone and speaker were positioned 80 cm apart, while for *E. fuscus* they were positioned 40 cm apart. These spacings were determined by the quality of the recorded call in silence, with the speaker and microphone on-axis with each other.

To simulate the most difficult acoustic conditions under which the SM3 would be required to trigger in the field, we used Adobe Audition CC 2017 to isolate a ~1 s clip of the highest sound level sections found in each of the river and shifted-river playback files and created two “peak” playback files (i.e. peak phantom river and peak shifted river) that consisted only of these sections on loop. We broadcast these files from an Octasound SP820A speaker (suspended approximately 3 m above the ground) using a Roland R05 player and a PRV Audio AD1200.1-2 amplifier at an amplitude of 80 dB(A) as measured at the SM3 microphone using a Larson Davis 824 sound level meter. This amplitude approximates some of the highest sound level playback conditions under which the SM3 operated in the field, as the highest 1hr LEQ values recorded at SM3 locations on phantom river and shifted river playback sites during the entire study were 77.0 and 82.6 dB(A), respectively.

We played each bat call sequence directly at the SM3 microphone in four directions – facing head on, 90 degrees to the left, 90 degrees to the right, and directly behind. We broadcast each call at as high of an amplitude as was possible without clipping, resulting in the following dB values, as measured at 10 cm from the speaker: *A. pallidus*: 82.1 and 79.1 dB and *E. fuscus*: 78.5 and 73.5 dB. Given that bats of the family Vespertillionidae have been recorded producing echolocation cries of over 122 dB at 10 cm from the bat's mouth (Surlykke & Kalko, 2008), our playbacks therefore approximate bats that are either off-axis or much further away (upwards of 28 m) from the microphone. We broadcast these call sequences under three acoustic environment conditions: ambient (i.e. no playback; 33.5 dBA), peak phantom river, and peak shifted river. We manually confirmed that the SM3 triggered and recorded the full echolocation call sequence following playbacks.

SonoBat classification in noise

To investigate if the classification ability of SonoBat was compromised by high background noise we performed a second control experiment wherein we applied shifted-river noise to call sequences recorded under relatively quiet conditions. We isolated a section of shifted-river noise recorded by the ultrasonic channel of the SM3 at our highest sound level SM3 location and used the Mix Paste function of Adobe Audition CC 2017 to combine this file with every call sequence identified to the species level from our control sites in both 2017 and 2018 – a total of 15,403 files. These files were re-run through SonoBat using the program settings described above. A total of 50 files (approximately 0.3%) were misidentified or unidentifiable using the "1st" classifier, whereas SonoBat's "SppAccp" classifier returned 1,056 mis- or unidentified sequences. Thus, we used the "1st" classifier in subsequent analyses. Given the extremely low error rate, it is unlikely that background noise could alter our inference from the generalized linear mixed effects models.

Bat foraging trials

We assessed foraging-modality switching in free-flying bats using an experimental paradigm that mimicked both terrestrial and aerial prey. We hypothesized that aerial prey would be preferred under higher ambient sound levels, which was more likely to mask the cues produced by walking and calling insects (Figure B.11).

Prey-sound speaker playback

We standardized all prey-cue recordings to an amplitude of -0.1 dB, and all to a length of four minutes, with a sample rate of 48 kHz with 16-bit depth (WAV format). To create the field playbacks, we used Adobe Audition CC 2017 to create a one-hour file which linearly combined each of the cues in random order, such that each cue was played three times per hour without occurring twice in a row. A five-second crossfade was applied between each file transition, and a five-second fade at the beginning and end of each playback. We used weatherproof speakers (Eco Extreme, Grace Digital Inc., CA, USA) and an LS-7 player (Olympus, Shinjuku, Japan) powered by a LiFePO4 battery (AA Portable Power Corp, CA, USA) housed in waterproof plastic containers to deliver the acoustic cues for passive listening bats in the field (Figure B.13). Audio cues were looped continuously from dusk to dawn. Insect rustling sounds were less intense (52.1

dBF / 33.3 dBA) than cricket playback (86.4 dBF / 87.0 dBA), and the integrated hourly sound pressure level of prey playback speakers was 71.1 dBF / 71.6 dBA rel 20 µPa at 1 m in an anechoic room.

A note on treatment vs continuous analyses

There may be concerns that overall patterns in bird abundance or bat activity in relation to sound pressure levels may be driven by latent variables that are linked to river noise. For example, high sound level streams may be larger or higher sloped and thus may have different vegetation, relative humidity, or consequently communities of insect prey. Background frequency does not logically track linearly with these same variables (quiet and loud streams both may produce higher frequency measures for different reasons. Whitewater rivers can contain higher frequencies if they are intense, but slow-moving streams can as well due to leaves blowing in the wind). For this reason we focus here on sound pressure levels for the obvious connections to the above latent variables.

We first address logically why we do not believe this to be an issue, and then explore quantitative methods for addressing the potential concern. Figure B.6 shows nicely that all sites were strongly overlapping in sound levels (pre noise exposure), with the majority of the sound levels between 35 and 60 dB. When the experiment is turned “on”, the majority of the energy in those experimental sites is now between 60 and 80 dB (right panel in Figure B.6). Thus, nearly all of the high sound level sites came from the experiment. If there were confounding latent variables at the sites, we wouldn’t expect to see such a strong signature of sound level in our analysis, since the streams that were experimentally made to have high sound levels originally had lower levels (Figure B.6), thus the confounds of having larger streams and more humidity would not track linearly with sound levels – hence the power of the experiment. We do recognize that it is possible in control sites that the effects of sound level are correlated with a latent variable related to stream size, but those data are so much more sparse at the high end than the experimental data.

Additional confounding variables that almost certainly share some correlation to stream size and flow (and thus can absorb some of this variation in the model) are date (day of year), a quadratic version of date, riparian vegetation, and elevation – all of which were in our models, which help separate the effects of noise measures from other confounds. Thus, with this experimental design and analysis, we find it extremely unlikely that the effects would be due to a stream size confound.

There are also issues with designating these so called ‘treatments’. We broadcast noise at some locations and not others. While this would seem, on the face of it, that there are clear designations of treatments, there certainly are not. We chose locations that were some distance from each noise playback area to create a continuum of sound pressure levels and background frequencies. Thus, at many locations one can hear the river or shifted river broadcasted files, but nothing near the intensities at the playback locations themselves. So it appears that we have created continua of treatments – or *realized treatments*. We instead quantify the acoustic environment (Gomes, Francis & Barber, 2021) and ask specifically what different components of noise (i.e. sound levels and frequency) do to drive wildlife populations and behavior, which also happen to help with the mechanistic understanding of the system. We would argue that a categorical analysis of a gradient is almost always going to be a more crude approach than a continuous one, and should only be used when continuous data are not available or when categories actually do not differ in the values that one would measure continuously.

One possible quantitative approach to alleviate any concerns are to include an interaction term between sound pressure levels and treatment in each of the bird and bat models. We cannot include this interaction here because the term is highly collinear. That is, the slope (estimate) of sound levels for control data is highly predictive of (and thus also predicted by) the slopes for the interaction of the treatments by sound level. In this situation, calculations regarding these predictors cannot be trusted, given such high variance inflation factor (VIF) scores for these parameters (Bird abundance: VIF = 23.7 for sound level by treatment interaction; Bat activity: VIF = 19.2 for sound level by treatment interaction; both of these scores are considered high by any assessment).

Thus, plotting model predicted lines (as we do in the main text; see Figures 2.2 and 2.3) are not necessarily going to reflect accurate estimates *when we include this interaction term*. For this reason, it seems the only viable way to check inferences from experimental data line up with the overall inferences from the entire study is to create models that include only experimental data.

At the top of Table B.1, the first global bird model presented includes estimates for sound pressure level of -0.067 with a standard error of 0.018. The same model including only experimental sites (included at the bottom of Table B.1) produces an estimate of -0.052 with a standard error of 0.019. Both of these estimates return p values below 0.01 and are overlapping estimates considering the standard errors presented here.

At the top of Table B.5, the first global bat model presented includes estimates for sound pressure level of -0.082 with a standard error of 0.018. The same model including only experimental sites (included at the bottom of Table B.5) produces an estimate of -0.097 with a standard error of 0.019. Both of these estimates return p values below 0.001 and are overlapping estimates considering the standard errors presented here.

We would conclude that it is very unlikely that estimates of how sound variables affect bird and bat abundance and activity are somehow confounded with stream properties at the control sites.

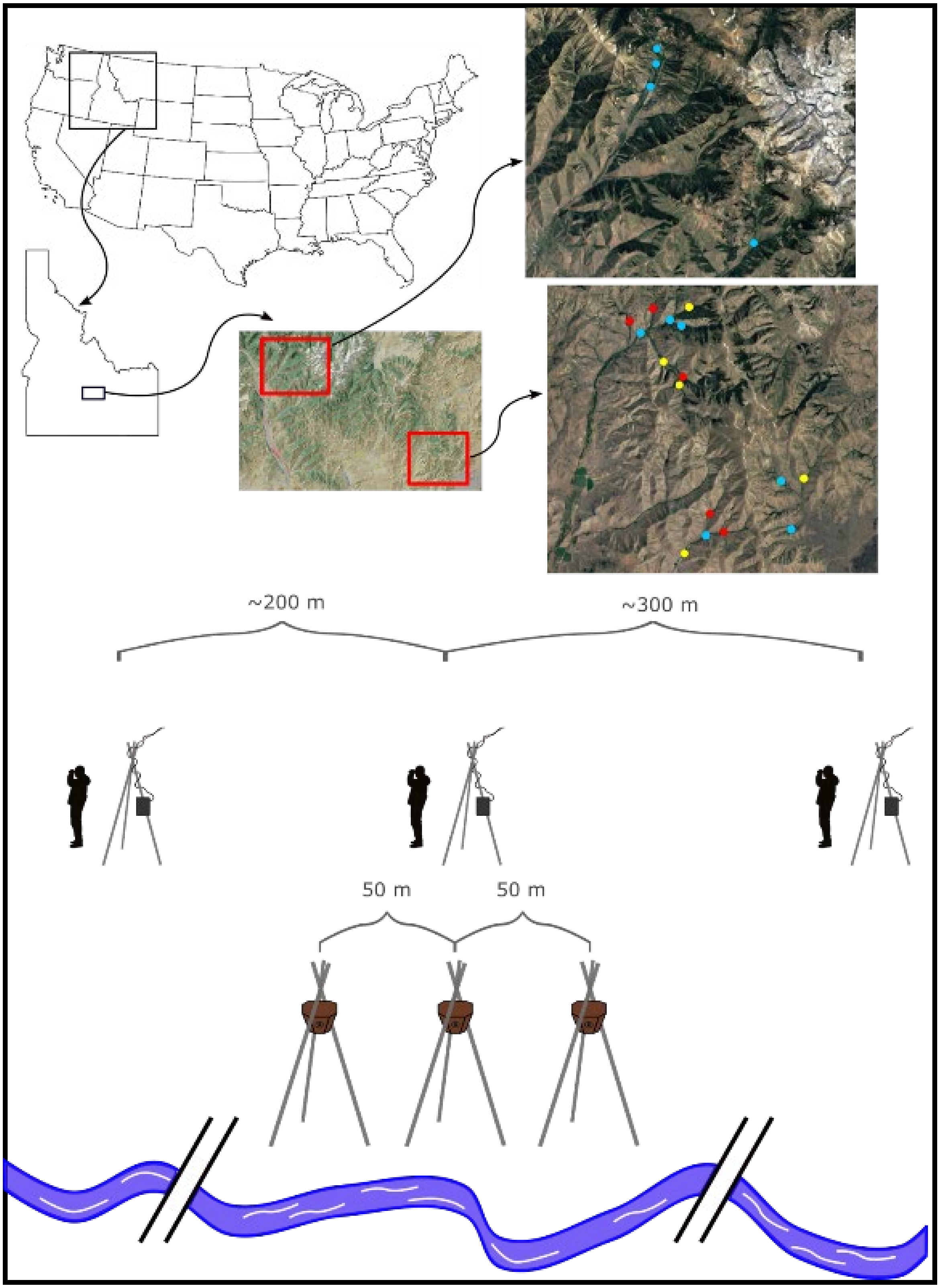


Figure B.1 Field site layout.

Twenty stream sites in the Pioneer Mountains of Idaho were selected for the experiment (top). Blue dots represent control sites that naturally ranged in sound pressure levels and frequency. Yellow dots represent treatment sites that were exposed to experimental whitewater river noise. Red dots represent treatment sites that were exposed to spectrally-shifted whitewater river noise. At each site, three speaker towers (dummy speakers at controls) were set up 50 m apart in the riparian zone (layout not to scale). Three locations within each site (with a range of acoustic environments) were monitored for bird abundance (point counts) and bat activity (passive acoustic monitoring).

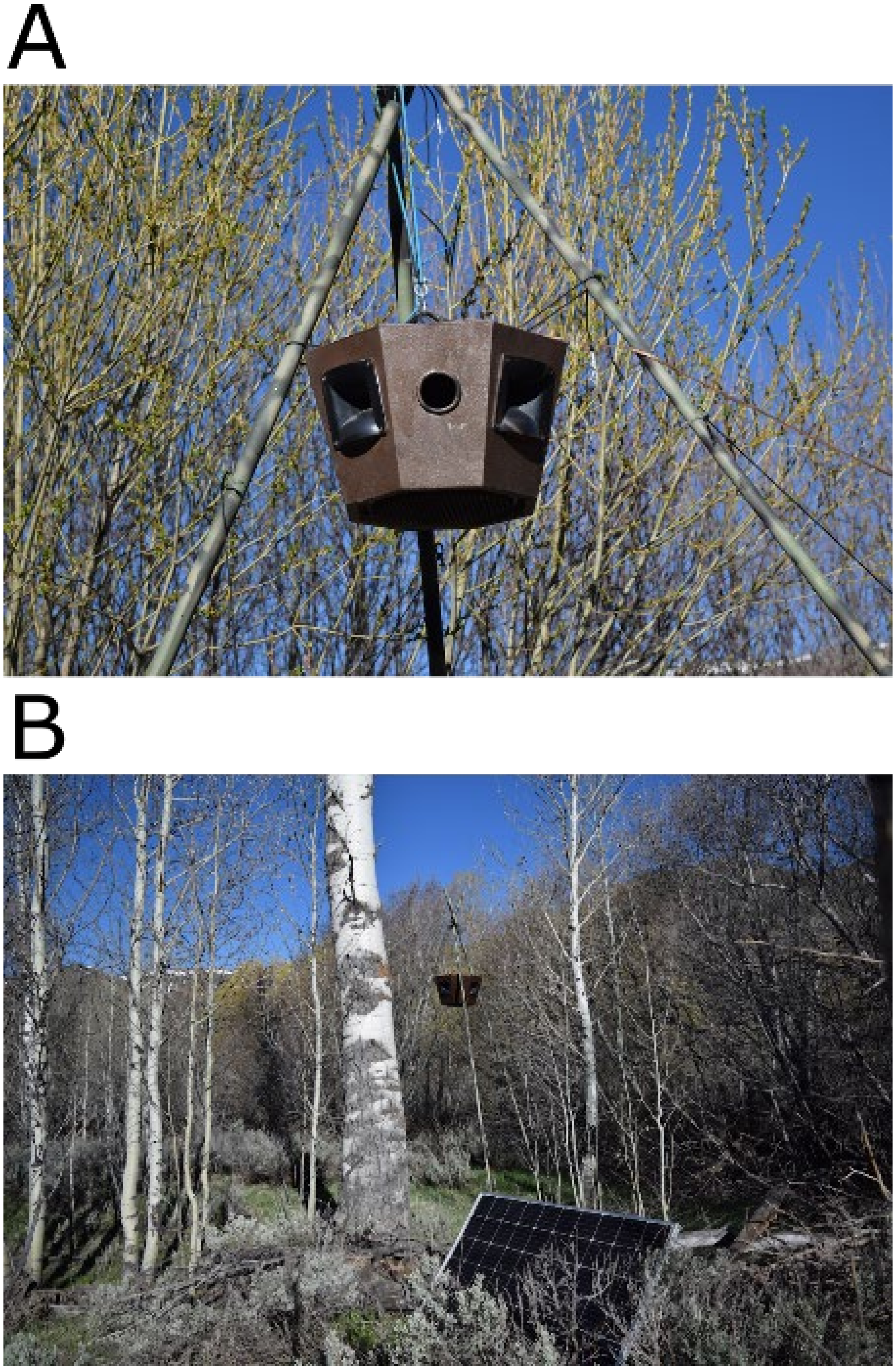


Figure B.2 Phantom rivers speakers.

Panel A: Octasound SP820A speaker broadcasting phantom river noise. Panel B: The same speaker, with solar panel, in the riparian area.

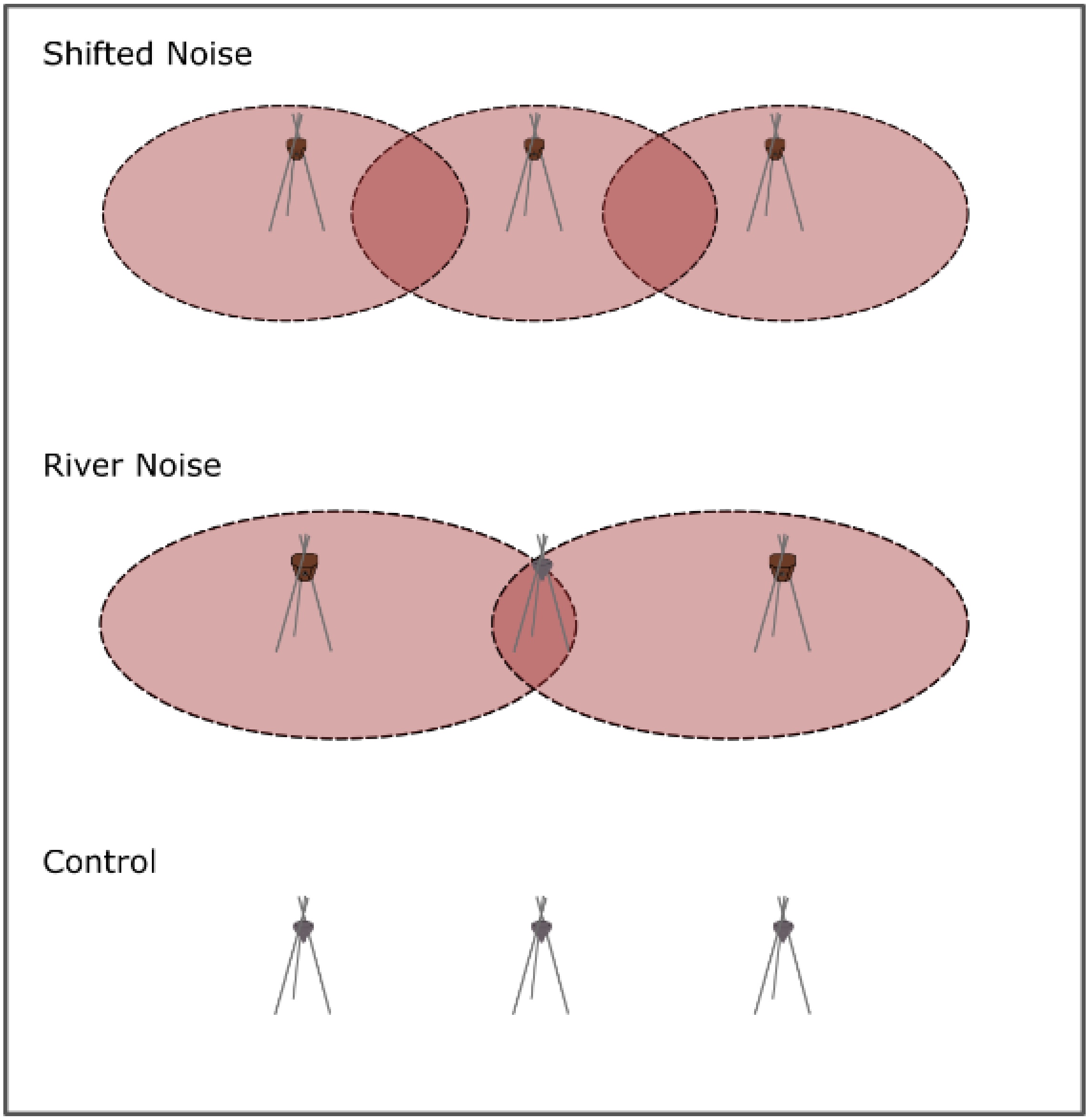
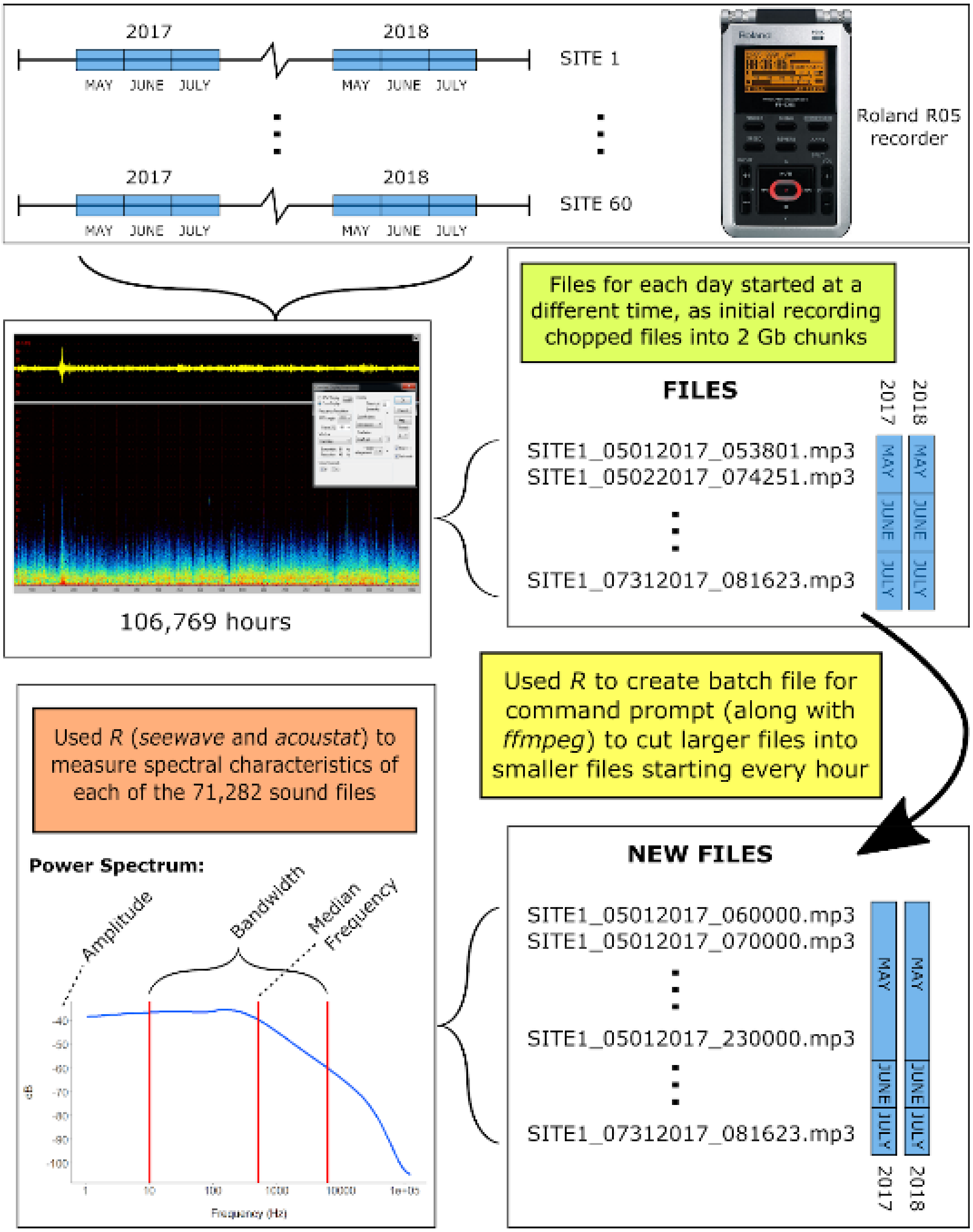


Figure B.3 Experimental site layout of the three types of sites.

Red ovals are a heuristic depiction of sound exposure from speakers. ‘Dummy’ speakers are grey, with no ovals around them. Note that ‘Shifted’ noise was produced by three speakers that impacted slightly smaller areas, whereas ‘River’ noise was produced by two speakers that had a larger spatial footprint.

Figure B.4 Phantom rivers speaker towers photos.

Comparison of Octasound SP820A (left) and Octasound SP800A (center) speakers which broadcast phantom- and shifted-river noise, respectively, to a control 'dummy' speaker (right) that matched the approximate dimensions of the treatment speakers. Phantom and shifted speakers were suspended from metal conduit, while control speakers were suspended from PVC pipe. Each control speaker was paired with a dummy solar panel constructed from black particle board matching the dimensions of the treatment solar panels (not pictured).



Files for each day started at a different time, as initial recording chopped files into 2 Gb chunks

SITE1_05012017_053801.mp3
SITE1_05022017_074251.mp3
⋮
SITE1_07312017_081623.mp3

Used *R* to create batch file for command prompt (along with *ffmpeg*) to cut larger files into smaller files starting every hour

SITE1_05012017_060000.mp3
SITE1_05012017_070000.mp3
⋮
SITE1_05012017_230000.mp3
⋮
SITE1_07312017_081623.mp3

Used *R* (*seewave* and *acoustat*) to measure spectral characteristics of each of the 71,282 sound files

Figure B.5 Heuristic of scale and pipeline of acoustic environment quantification.

Acoustic environments were continuously monitored at 60 locations, for two summers (2017 and 2018), totaling 100,000+ hours of recordings. Files were then analyzed by hour to obtain sound pressure level (not pictured) and median background frequency.

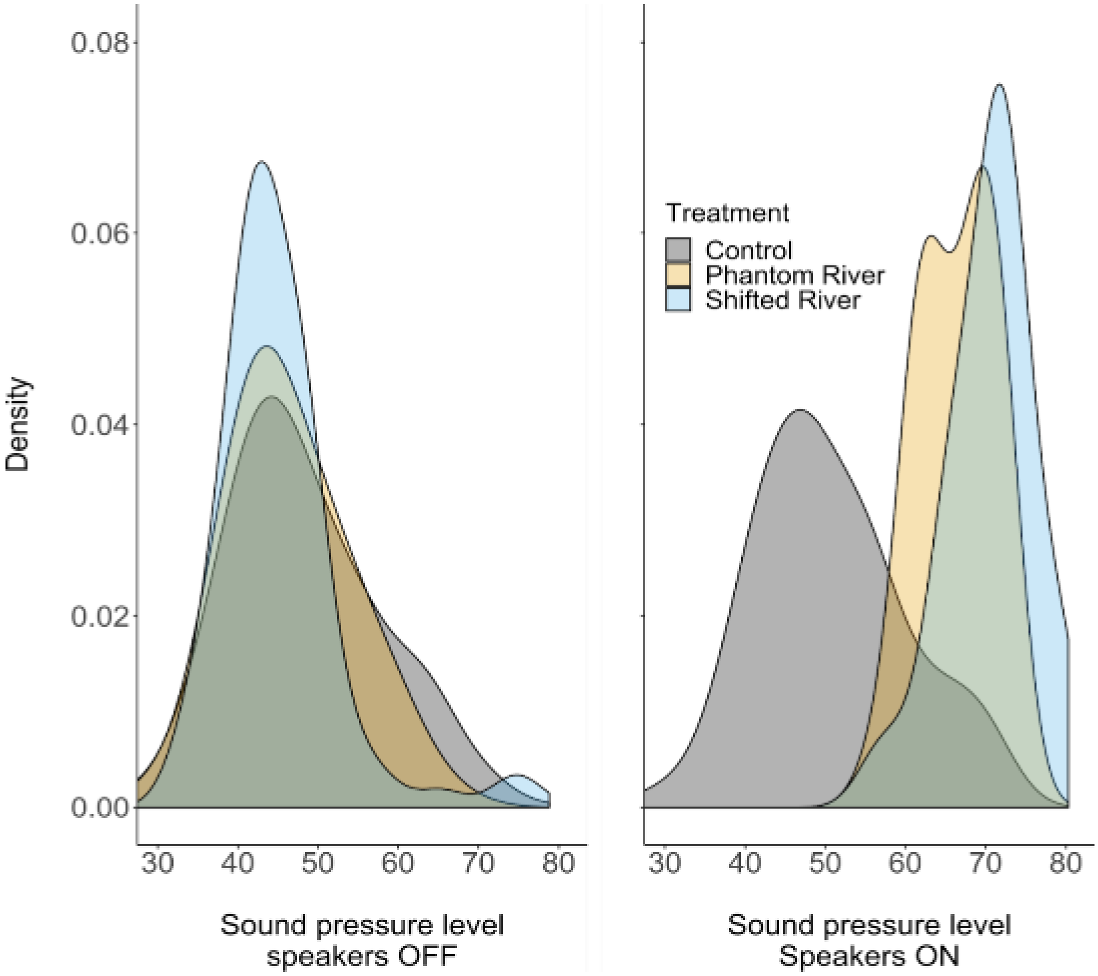


Figure B.6 Sound pressure levels of sites with speakers off and on.

The sound pressure levels (dBA) of our sites showed little variation before broadcasting noise (left). However, when we experimentally added noise to 10 of these sites sound levels dramatically increased (right).

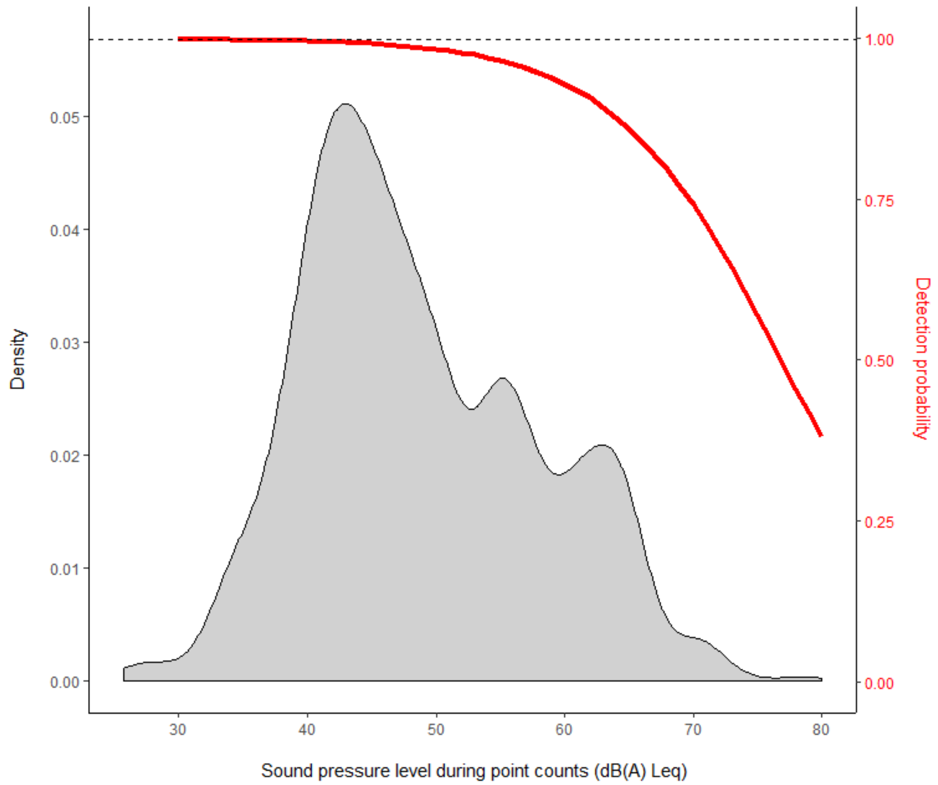


Figure B.7 The sound pressure level during point counts.

Most counts fall below 55 dB(A), where the detection probability is calculated to be nearly 1. Detection probability (in red) is informed by a birdsong playback experiment with 6 individual observers.

Figure B.8 Clay caterpillar.

Clay caterpillars were glued to branches in the riparian area to test foraging rates of birds in various acoustic environments. Note the bird beak mark in the upper portion of the caterpillar.

Figure B.9 Bat detector

Wildlife Acoustics Song Meter 3 (bat detector) at a monitoring location near sunset. Bat detector was fixed to a tripod made out of ~3 m long metal conduit.

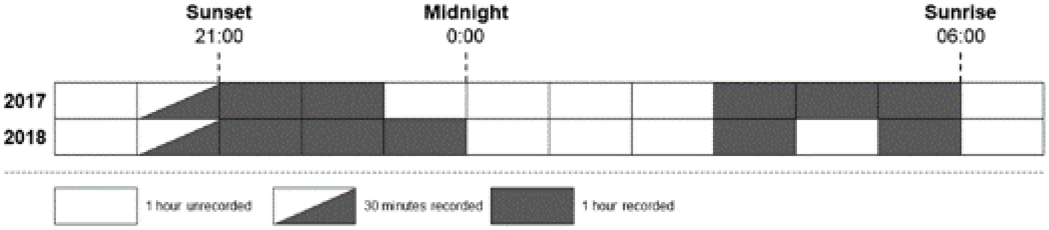


Figure B.10 Recording schedules for bat detectors

Schedules slightly differ due to other experiments that occurred in tandem.

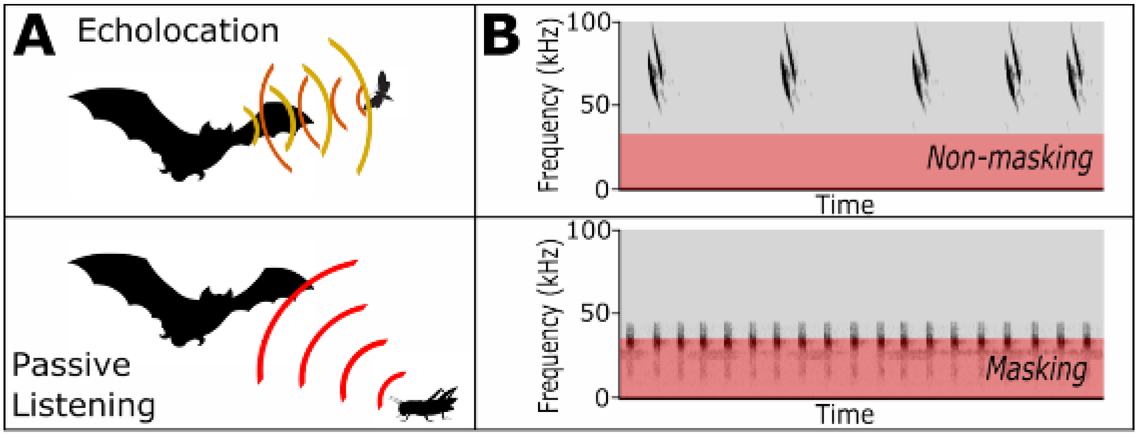


Figure B.11 Spectral overlap during echolocation and passive listening foraging strategies.

A) Depiction of two foraging styles, aerial hawking via echolocation (active listening) in the top and passive listening (to prey generated sounds) in the bottom. B) We predict, based on spectral overlap, that aerial hawking tasks would not be masked, whereas passive listening would be.

Figure B.12 Robotic insect wing

We used robotic insect wings to test foraging strategy switching in flexible bats. Ultrasonic microphone on a tripod, with Wildlife Acoustics SM2 recording unit in bottom of photo.

Figure B.13 Insect prey-sound speaker

Prey-sound speaker (small black box) was used to test foraging strategy switching in flexible bats. Ultrasonic microphone and wildlife acoustics SM2 recording unit (green box), powered by Lithium batteries (grey box) also pictured.

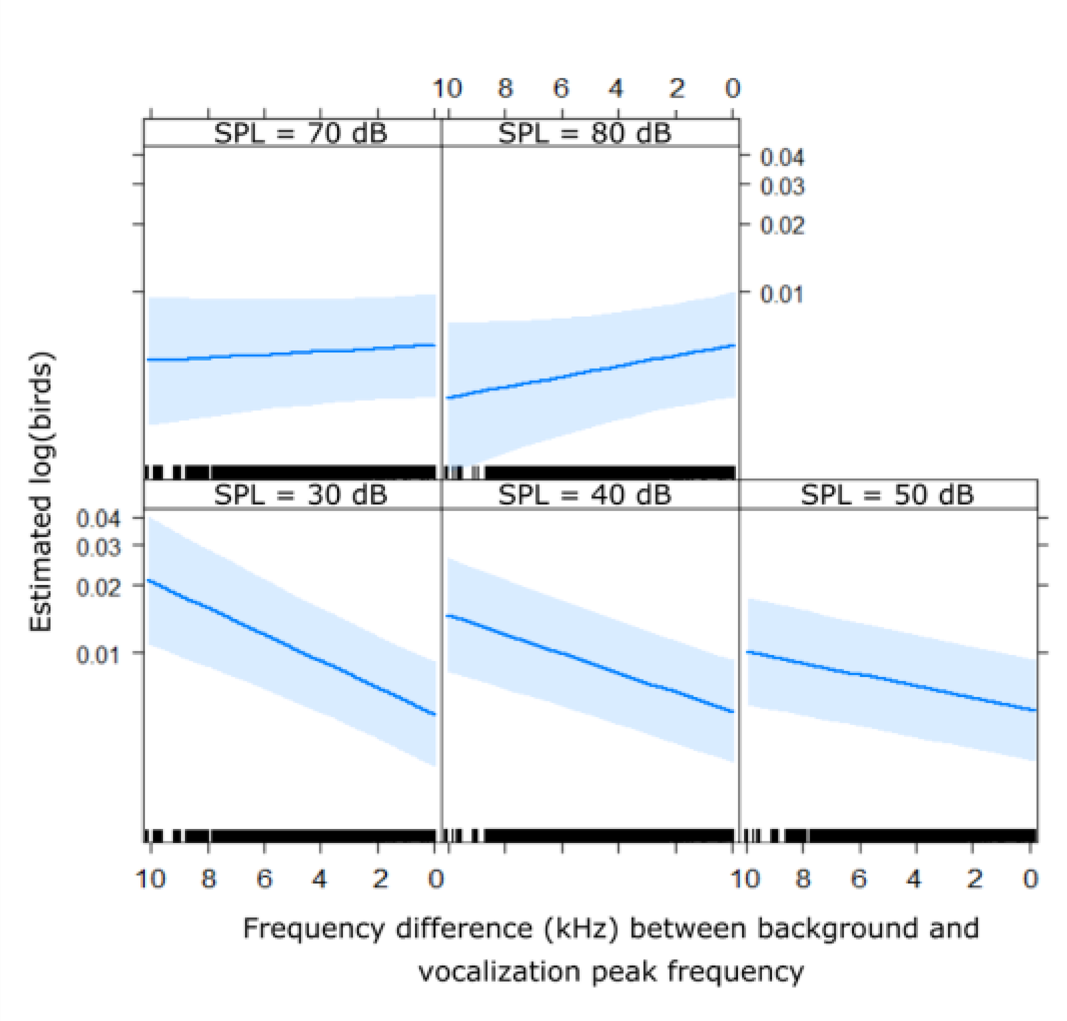


Figure B.14 Avian frequency difference and sound level interaction plots.

When sound levels are low (e.g. 30 dB), the amount of spectral overlap is important in determining bird abundance. That is, the higher the difference in frequency was between the background acoustic environment and the peak frequency of a given species' vocalization, the higher the estimated count of birds would be (high negative slopes within these flipped x-axis plots). Yet, when sound pressure level was high (e.g. 70 and 80 dB), the effect of frequency difference was negligible (flat lines in top two panels).

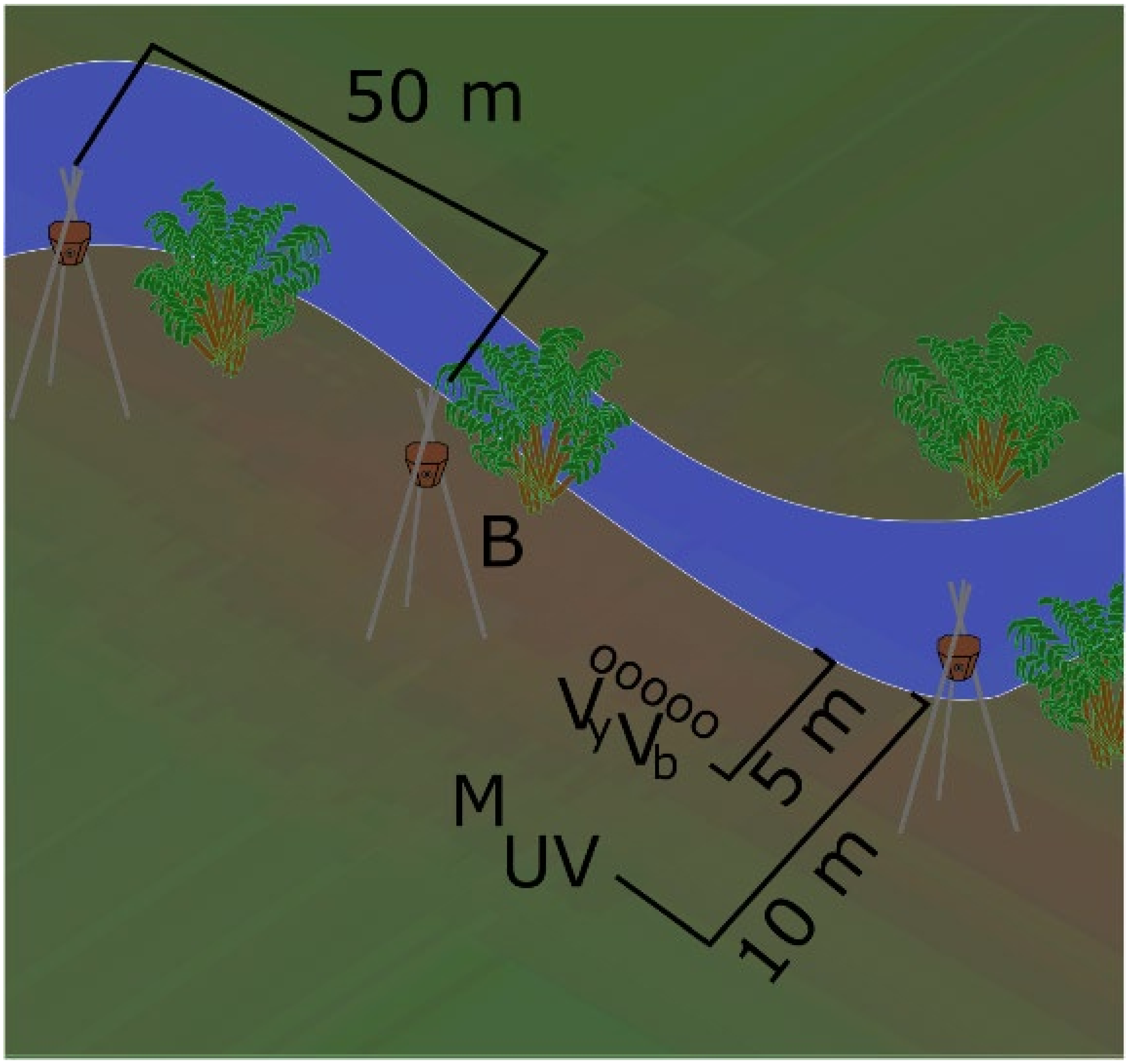


Figure B.15 A schematic of arthropod sampling at a typical site.

Towers are placed 50 m apart parallel to the stream at all sites, but only experimental sites have speakers (see Figure B.3). B = beat-netting sampling of a willow tree (*Salix* sp.); o = an individual pitfall trap (all five are parallel to, and 5 m from, the stream); V_y = yellow vane traps; V_b = blue vane traps; M = Malaise traps; UV = ultraviolet light bucket traps. This sampling scheme occurred at all 20 sites in the Pioneer Mountains of Idaho (see Figure 2.1A).

Table B.1 Bird abundance model summary tables.

All continuous variables are centered to the mean, and standardized to one standard deviation. Abundance data are analyzed with a negative binomial distribution (log link).

Model: Global	Noise control: Observer experiment				
Variable	Estimate	SE	*CI*	z value	*p*
Intercept	-4.978	0.263	-5.492 – -4.460	-18.959	<0.001
Sound pressure (SPL)	-0.067	0.018	-0.102 – -0.030	-3.764	<0.001
Background freq. (BF)	-0.031	0.021	-0.072 – 0.010	-1.480	0.139
Spectral overlap (SO)	0.066	0.016	0.034 – 0.100	4.031	<0.001
Riparian vegetation	0.127	0.026	0.077 – 0.180	4.917	<0.001
Elevation	0.113	0.085	-0.053 – 0.280	1.331	0.183
Ordinal date	0.044	0.017	0.012 – 0.080	2.671	0.008
Ordinal date^2	-0.107	0.018	-0.143 – -0.070	-5.776	<0.001
Year	0.253	0.037	0.180 – 0.330	6.765	<0.001
SPL:BF	0.033	0.018	-0.003 – 0.070	1.817	0.069
SPL:SO	-0.057	0.016	-0.088 – -0.030	-3.549	<0.001

Model: Global	Noise control: Noise removal model				
Variable	Estimate	SE	*CI*	z value	*p*
Intercept	-5.007	0.265	-5.527 – -4.490	-18.895	<0.001
Sound pressure (SPL)	-0.069	0.018	-0.103 – -0.030	-3.863	<0.001
Background freq. (BF)	-0.032	0.021	-0.073 – 0.010	-1.554	0.120
Spectral overlap (SO)	0.066	0.016	0.034 – 0.100	4.049	<0.001
Riparian vegetation	0.131	0.026	0.080 – 0.180	5.038	<0.001
Elevation	0.118	0.084	-0.047 – 0.280	1.404	0.160
Ordinal date	0.256	0.037	0.183 – 0.330	6.837	<0.001
Ordinal date^2	0.047	0.017	0.015 – 0.080	2.844	0.004
Year	-0.108	0.018	-0.144 – -0.070	-5.84	<0.001
SPL:BF	0.034	0.018	-0.002 – 0.070	1.859	0.063
SPL:SO	-0.056	0.016	-0.087 – -0.020	-3.477	0.001

Model: Visual counts	Noise control: Observer ear plugs				
Variable	Estimate	SE	*CI*	z value	*p*
Intercept	-5.755	0.281	-6.305 – -5.200	-20.49	<0.001
Sound pressure (SPL)	-0.139	0.043	-0.223 – -0.050	-3.212	0.001
Background freq. (BF)	0.009	0.044	-0.077 – 0.090	0.208	0.835
Spectral overlap (SO)	0.102	0.034	0.036 – 0.170	3.027	0.002
Riparian vegetation	0.150	0.053	0.047 – 0.250	2.844	0.004
Elevation	-0.222	0.094	-0.405 – -0.040	-2.369	0.018
Ordinal date	0.037	0.037	-0.034 – 0.110	1.019	0.308
Ordinal date^2	-0.060	0.041	-0.140 – 0.020	-1.459	0.145

Year	0.039	0.083	-0.125 – 0.200	0.464	0.642
SPL:BF	0.148	0.040	0.069 – 0.230	3.689	<0.001
SPL:SO	-0.012	0.033	-0.078 – 0.050	-0.367	0.714

Model: Control sites	Noise control: Observer experiment				
Variable	Estimate	SE	*CI*	z value	*p*
Intercept	-5.206	0.296	-5.786 – -4.630	-17.596	<0.001
Sound pressure (SPL)	-0.123	0.058	-0.237 – -0.010	-2.117	0.034
Background freq. (BF)	-0.095	0.042	-0.178 – -0.010	-2.236	0.025
Spectral overlap (SO)	0.062	0.030	0.004 – 0.120	2.094	0.036
Riparian vegetation	-0.04	0.051	-0.140 – 0.060	-0.778	0.436
Elevation	-0.301	0.111	-0.519 – -0.080	-2.704	0.007
Ordinal date	0.034	0.027	-0.019 – 0.090	1.255	0.210
Ordinal date^2	-0.105	0.029	-0.162 – -0.050	-3.582	<0.001
Year	0.215	0.058	0.100 – 0.330	3.670	<0.001
SPL:BF	0.023	0.045	-0.065 – 0.110	0.512	0.608
SPL:SO	-0.146	0.032	-0.209 – -0.080	-4.502	<0.001

Model: Experimental sites only	Noise control: Observer experiment				
Variable	Estimate	SE	*CI*	z value	*p*
Intercept	-5.01	0.3	-5.597 - -4.42	-16.716	<0.001
Sound pressure (SPL)	-0.052	0.02	-0.09 - -0.01	-2.668	0.008
Background freq. (BF)	-0.008	0.026	-0.059 - 0.04	-0.304	0.761
Spectral overlap (SO)	0.04	0.021	-0.001 - 0.08	1.898	0.058
Riparian vegetation	0.129	0.022	0.085 - 0.17	5.735	<0.001
Elevation	0.159	0.129	-0.094 - 0.41	1.233	0.218
Ordinal date	0.057	0.021	0.016 - 0.10	2.714	0.007
Ordinal date^2	-0.104	0.024	-0.151 - -0.06	-4.272	<0.001
Year	0.29	0.05	0.192 - 0.39	5.824	<0.001
SPL:BF	-0.008	0.022	-0.051 - 0.03	-0.378	0.706
SPL:SO	0.036	0.023	-0.008 - 0.08	1.587	0.113

Table B.2 Individual bird species models.

All continuous variables are centered to the mean, and standardized to one standard deviation. Abundance data are analyzed with a negative binomial distribution (log link).

	Common		Latin		
	American crow		*Corvus brachyrhynchos*		
Predictors	Estimates	SE	*CI*	Z	*p*
Intercept	-5.57	0.75	-4.10 – -7.04	-7.44	<0.01
SPL	0.26	0.31	0.87 – -0.35	0.83	0.41
Background Freq	-0.72	1.02	1.28 – -2.72	-0.7	0.48
Spectral Overlap	0.57	1.10	2.73 – -1.59	0.52	0.60
Vegetation	0.19	0.29	0.76 – -0.38	0.65	0.51
Elevation	-1.71	0.57	-0.59 – -2.83	-2.97	<0.01
Ordinal date	-0.30	0.24	0.17 – -0.77	-1.22	0.22
Ordinal date^2	0.08	0.26	0.59 – -0.43	0.32	0.75
Year	0.08	0.58	1.22 – -1.06	0.14	0.89
SPL:Background Freq	1.03	1.78	4.52 – -2.46	0.58	0.56
SPL:Spectral Overlap	-0.83	1.83	2.76 – -4.42	-0.45	0.65

	Common		Latin		
	American Kestrel		*Falco sparverius*		
Predictors	Estimates	SE	*CI*	Z	*p*
Intercept	-5.05	0.51	-4.05 – -6.05	-9.98	<0.01
SPL	-0.01	0.26	0.50 – -0.52	-0.05	0.96
Background Freq	0.37	0.22	0.80 – -0.06	1.69	0.09
Spectral Overlap	-0.12	0.18	0.23 – -0.47	-0.68	0.49
Vegetation	-0.06	0.25	0.43 – -0.55	-0.24	0.81
Elevation	-0.81	0.34	-0.14 – -1.48	-2.40	0.02
Ordinal date	-0.55	0.22	-0.12 – -0.98	-2.56	0.01
Ordinal date^2	0.71	0.23	1.16 – 0.26	3.10	<0.01
Year	-1.09	0.57	0.03 – -2.21	-1.92	0.05
SPL:Background Freq	<0.00	0.21	0.41 – -0.41	-0.02	0.98
SPL:Spectral Overlap	-0.11	0.20	0.28 – -0.50	-0.56	0.58

	Common		Latin		
	American robin		*Turdus migratorius*		
Predictors	Estimates	SE	*CI*	Z	*p*
Intercept	-2.70	0.26	-2.19 – -3.21	-10.56	<0.01
SPL	0.01	0.09	0.19 – -0.17	0.13	0.90

Background Freq	-0.18	0.20	0.21 – -0.57	-0.92	0.36
Spectral Overlap	0.33	0.18	0.68 – -0.02	1.86	0.06
Vegetation	0.13	0.13	0.38 – -0.12	0.99	0.32
Elevation	-0.03	0.21	0.38 – -0.44	-0.17	0.87
Ordinal date	-0.19	0.09	-0.01 – -0.37	-2.14	0.03
Ordinal date^2	-0.13	0.09	0.05 – -0.31	-1.43	0.15
Year	0.09	0.19	0.46 – -0.28	0.47	0.64
SPL:Background Freq	-0.29	0.22	0.14 – -0.72	-1.32	0.19
SPL:Spectral Overlap	0.25	0.21	0.66 – -0.16	1.21	0.22

Common	Latin
Black-capped Chickadee	*Poecile atricapillus*

Predictors	Estimates	SE	*CI*	Z	*p*
Intercept	-6.14	0.83	-4.51 – -7.77	-7.42	<0.01
SPL	-0.08	0.18	0.27 – -0.43	-0.43	0.67
Background Freq	0.04	0.22	0.47 – -0.39	0.17	0.87
Spectral Overlap	0.25	0.20	0.64 – -0.14	1.23	0.22
Vegetation	-0.13	0.30	0.46 – -0.72	-0.43	0.67
Elevation	0.56	0.48	1.50 – -0.38	1.15	0.25
Ordinal date	-0.16	0.18	0.19 – -0.51	-0.93	0.35
Ordinal date^2	0.85	0.21	1.26 – 0.44	4.11	<0.01
Year	0.02	0.46	0.92 – -0.88	0.05	0.96
SPL:Background Freq	0.01	0.20	0.40 – -0.38	0.05	0.96
SPL:Spectral Overlap	-0.13	0.22	0.30 – -0.56	-0.61	0.54

Common	Latin
Brown-headed cowbird	*Molothrus ater*

Predictors	Estimates	SE	*CI*	Z	*p*
Intercept	-4.89	0.45	-4.01 – -5.77	-10.77	<0.01
SPL	-0.34	0.26	0.17 – -0.85	-1.29	0.20
Background Freq	-0.14	0.49	0.82 – -1.10	-0.29	0.77
Spectral Overlap	0.19	0.43	1.03 – -0.65	0.44	0.66
Vegetation	0.41	0.18	0.76 – 0.06	2.22	0.03
Elevation	-1.26	0.25	-0.77 – -1.75	-5.12	<0.01
Ordinal date	0.05	0.21	0.46 – -0.36	0.22	0.83
Ordinal date^2	-0.39	0.24	0.08 – -0.86	-1.64	0.10
Year	0.66	0.49	1.62 – -0.30	1.35	0.18
SPL:Background Freq	-0.07	0.54	0.99 – -1.13	-0.13	0.90
SPL:Spectral Overlap	-0.60	0.51	0.40 – -1.60	-1.19	0.24

Common	Latin

	Brewer's Sparrow		*Spizella breweri*		
Predictors	Estimates	SE	*CI*	Z	*p*
Intercept	-10.1	1.81	-6.55 – -13.65	-5.59	<0.01
SPL	0.77	0.26	1.28 – 0.26	3.01	<0.01
Background Freq	-0.39	0.34	0.28 – -1.06	-1.17	0.24
Spectral Overlap	-0.01	0.31	0.60 – -0.62	-0.04	0.97
Vegetation	-1.3	0.58	-0.16 – -2.44	-2.23	0.03
Elevation	-3.25	1.03	-1.23 – -5.27	-3.15	<0.01
Ordinal date	-0.90	0.36	-0.19 – -1.61	-2.53	0.01
Ordinal date^{2}	-0.11	0.27	0.42 – -0.64	-0.40	0.69
Year	0.90	0.62	2.12 – -0.32	1.45	0.15
SPL:Background Freq	-0.14	0.25	0.35 – -0.63	-0.54	0.59
SPL:Spectral Overlap	0.84	0.28	1.39 – 0.29	2.95	<0.01

	Common		Latin		
	Bullock's Oriole		*Icterus bullockii*		
	Estimates	SE	*CI*	Z	*p*
Intercept	-5.62	0.67	-4.31 – -6.93	-8.35	<0.01
SPL	0.33	0.36	1.04 – -0.38	0.93	0.35
Background Freq	0.54	0.60	1.72 – -0.64	0.91	0.36
Spectral Overlap	-0.12	0.42	0.70 – -0.94	-0.29	0.77
Vegetation	0.26	0.29	0.83 – -0.31	0.89	0.38
Elevation	-0.91	0.45	-0.03 – -1.79	-2.01	0.04
Ordinal date	0.23	0.19	0.60 – -0.14	1.18	0.24
Ordinal date^{2}	-0.75	0.21	-0.34 – -1.16	-3.63	<0.01
Year	1.08	0.41	1.88 – 0.28	2.62	0.01
SPL:Background Freq	-0.50	0.69	0.85 – -1.85	-0.72	0.47
SPL:Spectral Overlap	0.03	0.50	1.01 – -0.95	0.06	0.95

	Common		Latin		
	Chipping Sparrow		*Spizella passerina*		
Predictors	Estimates	SE	*CI*	Z	*p*
Intercept	-5.11	0.65	-3.84 – -6.38	-7.86	<0.01
SPL	-0.11	0.37	0.62 – -0.84	-0.31	0.76
Background Freq	-1.95	2.18	2.32 – -6.22	-0.89	0.37
Spectral Overlap	-1.19	1.62	1.99 – -4.37	-0.73	0.46
Vegetation	-0.55	0.31	0.06 – -1.16	-1.77	0.08
Elevation	0.39	0.32	1.02 – -0.24	1.22	0.22
Ordinal date	0.18	0.20	0.57 – -0.21	0.87	0.38
Ordinal date^{2}	0.31	0.21	0.72 – -0.10	1.50	0.13
Year	-0.54	0.44	0.32 – -1.40	-1.23	0.22

SPL:Background Freq	1.56	1.55	4.60 – -1.48	1.01	0.31
SPL:Spectral Overlap	0.88	1.16	3.15 – -1.39	0.76	0.45

Common	Latin
Dark-eyed Junco	*Junco hyemalis*

Predictors	Estimates	SE	*CI*	Z	*p*
Intercept	-4.85	0.49	-3.89 – -5.81	-9.83	<0.01
SPL	0.03	0.19	0.40 – -0.34	0.16	0.88
Background Freq	-0.52	0.62	0.70 – -1.74	-0.83	0.41
Spectral Overlap	-0.60	0.49	0.36 – -1.56	-1.23	0.22
Vegetation	-0.21	0.22	0.22 – -0.64	-0.95	0.34
Elevation	0.42	0.32	1.05 – -0.21	1.31	0.19
Ordinal date	-0.49	0.20	-0.10 – -0.88	-2.51	0.01
Ordinal date^2	0.09	0.19	0.46 – -0.28	0.49	0.62
Year	-0.14	0.42	0.68 – -0.96	-0.33	0.74
SPL:Background Freq	0.42	0.63	1.65 – -0.81	0.68	0.50
SPL:Spectral Overlap	0.42	0.49	1.38 – -0.54	0.85	0.39

Common	Latin
Dusky Flycatcher	*Empidonax oberholseri*

Predictors	Estimates	SE	*CI*	Z	*p*
Intercept	-3.80	0.26	-3.29 – -4.31	-14.49	<0.01
SPL	-0.39	0.14	-0.12 – -0.66	-2.83	<0.01
Background Freq	-0.07	0.21	0.34 – -0.48	-0.36	0.72
Spectral Overlap	0.07	0.18	0.42 – -0.28	0.42	0.67
Vegetation	-0.11	0.14	0.16 – -0.38	-0.78	0.43
Elevation	0.58	0.17	0.91 – 0.25	3.44	<0.01
Ordinal date	0.05	0.12	0.29 – -0.19	0.42	0.68
Ordinal date^2	-0.28	0.13	-0.03 – -0.53	-2.12	0.03
Year	0.73	0.27	1.26 – 0.20	2.68	0.01
SPL:Background Freq	-0.13	0.22	0.30 – -0.56	-0.62	0.54
SPL:Spectral Overlap	0.22	0.18	0.57 – -0.13	1.22	0.22

Common	Latin
European starling	*Sturnus vulgaris*

Predictors	Estimates	SE	*CI*	Z	*p*
Intercept	-7.11	1.46	-4.25 – -9.97	-4.88	<0.01
SPL	-0.32	0.63	0.91 – -1.55	-0.51	0.61
Background Freq	-0.05	1.28	2.46 – -2.56	-0.04	0.97
Spectral Overlap	-0.51	0.88	1.21 – -2.23	-0.58	0.56

Vegetation	-0.33	0.45	0.55 – -1.21	-0.73	0.46
Elevation	-1.06	0.59	0.10 – -2.22	-1.81	0.07
Ordinal date	-3.23	1.50	-0.29 – -6.17	-2.15	0.03
Ordinal date^2	-1.88	0.89	-0.14 – -3.62	-2.12	0.03
Year	1.04	1.21	3.41 – -1.33	0.86	0.39
SPL:Background Freq	-1.15	1.22	1.24 – -3.54	-0.95	0.34
SPL:Spectral Overlap	-0.51	0.76	0.98 – -2.00	-0.68	0.50

Common	Latin
House wren	*Troglodytes aedon*

Predictors	Estimates	SE	*CI*	Z	*p*
Intercept	-2.09	0.35	-1.4 – -2.78	-5.96	<0.01
SPL	-0.02	0.06	0.1 – -0.14	-0.33	0.74
Background Freq	0.19	0.07	0.33 – 0.05	2.9	<0.01
Spectral Overlap	-0.07	0.05	0.03 – -0.17	-1.4	0.16
Vegetation	0.53	0.10	0.73 – 0.33	5.42	<0.01
Elevation	0.33	0.29	0.9 – -0.24	1.13	0.26
Ordinal date	-0.24	0.05	-0.14 – -0.34	-4.34	<0.01
Ordinal date^2	-0.07	0.06	0.05 – -0.19	-1.23	0.22
Year	0.16	0.12	0.4 – -0.08	1.35	0.18
SPL:Background Freq	-0.08	0.06	0.04 – -0.2	-1.3	0.19
SPL:Spectral Overlap	-0.11	0.05	-0.01 – -0.21	-2.33	0.02

Common	Latin
Lazuli Bunting	*Passerina amoena*

Predictors	Estimates	SE	*CI*	Z	*p*
Intercept	-1.77	0.18	-1.42 – -2.12	-9.84	<0.01
SPL	0.08	0.06	0.20 – -0.04	1.37	0.17
Background Freq	-0.16	0.08	0.00 – -0.32	-1.97	0.05
Spectral Overlap	-0.16	0.07	-0.02 – -0.30	-2.36	0.02
Vegetation	-0.01	0.08	0.15 – -0.17	-0.13	0.90
Elevation	-0.32	0.15	-0.03 – -0.61	-2.12	0.03
Ordinal date	1.34	0.10	1.54 – 1.14	13.79	<0.01
Ordinal date^2	-0.71	0.08	-0.55 – -0.87	-8.54	<0.01
Year	0.40	0.11	0.62 – 0.18	3.67	<0.01
SPL:Background Freq	-0.07	0.07	0.07 – -0.21	-0.95	0.34
SPL:Spectral Overlap	-0.01	0.07	0.13 – -0.15	-0.14	0.89

Common	Latin
MacGillivray's Warbler	*Geothlypis tolmiei*

Predictors	Estimates	SE	*CI*	Z	*p*
Intercept	-2.53	0.25	-2.04 – -3.02	-10.13	<0.01
SPL	0.12	0.08	0.28 – -0.04	1.55	0.12
Background Freq	-0.53	0.15	-0.24 – -0.82	-3.53	<0.01
Spectral Overlap	-0.08	0.11	0.14 – -0.30	-0.75	0.45
Vegetation	0.08	0.12	0.32 – -0.16	0.69	0.49
Elevation	0.21	0.20	0.6 – -0.18	1.04	0.30
Ordinal date	0.71	0.11	0.93 – 0.49	6.69	<0.01
Ordinal date^2	-0.79	0.11	-0.57 – -1.01	-7.01	<0.01
Year	0.53	0.16	0.84 – 0.22	3.29	<0.01
SPL:Background Freq	0.40	0.11	0.62 – 0.18	3.62	<0.01
SPL:Spectral Overlap	0.15	0.10	0.35 – -0.05	1.54	0.12

Common	Latin
Northern flicker	*Colaptes auratus*

Predictors	Estimates	SE	*CI*	Z	*p*
Intercept	-3.75	0.29	-3.18 – -4.32	-12.76	<0.01
SPL	-0.16	0.15	0.13 – -0.45	-1.06	0.29
Background Freq	-0.01	0.25	0.48 – -0.50	-0.06	0.95
Spectral Overlap	0.14	0.22	0.57 – -0.29	0.65	0.52
Vegetation	0.08	0.16	0.39 – -0.23	0.54	0.59
Elevation	-0.81	0.23	-0.36 – -1.26	-3.61	<0.01
Ordinal date	-0.06	0.10	0.14 – -0.26	-0.57	0.57
Ordinal date^2	0.30	0.12	0.54 – 0.06	2.55	0.01
Year	-0.11	0.27	0.42 – -0.64	-0.39	0.69
SPL:Background Freq	0.20	0.30	0.79 – -0.39	0.66	0.51
SPL:Spectral Overlap	-0.14	0.26	0.37 – -0.65	-0.55	0.58

Common	Latin
Orange-crowned Warbler	*Vermivora celata*

Predictors	Estimates	SE	*CI*	Z	*p*
Intercept	-4.38	0.35	-3.69 – -5.07	-12.54	<0.01
SPL	-0.10	0.09	0.08 – -0.28	-1.13	0.26
Background Freq	0.63	0.15	0.92 – 0.34	4.33	<0.01
Spectral Overlap	0.39	0.14	0.66 – 0.12	2.79	0.01
Vegetation	0.20	0.14	0.47 – -0.07	1.42	0.16
Elevation	0.49	0.22	0.92 – 0.06	2.25	0.02
Ordinal date	-1.07	0.17	-0.74 – -1.40	-6.18	<0.01
Ordinal date^2	0.15	0.14	0.42 – -0.12	1.09	0.28
Year	0.72	0.32	1.35 – 0.09	2.26	0.02

SPL:Background Freq	0.19	0.18	0.54 – -0.16	1.07	0.29
SPL:Spectral Overlap	0.08	0.15	0.37 – -0.21	0.52	0.60

Common	Latin
Red-breasted Nuthatch	*Sitta canadensis*

Predictors	Estimates	SE	*CI*	Z	*p*
Intercept	-7.74	1.10	-5.58 – -9.90	-7.06	<0.01
SPL	-0.19	0.19	0.18 – -0.56	-0.98	0.33
Background Freq	-0.25	0.36	0.46 – -0.96	-0.70	0.49
Spectral Overlap	0.56	0.40	1.34 – -0.22	1.39	0.17
Vegetation	-0.14	0.27	0.39 – -0.67	-0.53	0.60
Elevation	0.31	0.30	0.90 – -0.28	1.04	0.30
Ordinal date	-0.55	0.19	-0.18 – -0.92	-2.86	<0.01
Ordinal date^2	0.78	0.25	1.27 – 0.29	3.17	<0.01
Year	2.22	1.08	4.34 – 0.10	2.05	0.04
SPL:Background Freq	-0.36	0.38	0.38 – -1.10	-0.96	0.34
SPL:Spectral Overlap	0.68	0.44	1.54 – -0.18	1.55	0.12

Common	Latin
Ruby-crowned Kinglet	*Regulus calendula*

Predictors	Estimates	SE	*CI*	Z	*p*
Intercept	-6.77	0.78	-5.24 – -8.30	-8.69	<0.01
SPL	0.21	0.20	0.60 – -0.18	1.06	0.29
Background Freq	-0.46	0.47	0.46 – -1.38	-0.98	0.32
Spectral Overlap	-0.41	0.32	0.22 – -1.04	-1.25	0.21
Vegetation	-0.01	0.19	0.36 – -0.38	-0.05	0.96
Elevation	0.85	0.22	1.28 – 0.42	3.88	<0.01
Ordinal date	-1.22	0.29	-0.65 – -1.79	-4.18	<0.01
Ordinal date^2	0.38	0.23	0.83 – -0.07	1.63	0.10
Year	1.41	0.79	2.96 – -0.14	1.80	0.07
SPL:Background Freq	0.50	0.29	1.07 – -0.07	1.73	0.08
SPL:Spectral Overlap	0.35	0.27	0.88 – -0.18	1.29	0.20

Common	Latin
Red-naped Sapsucker	*Sphyrapicus nuchalis*

Predictors	Estimates	SE	*CI*	Z	*p*
Intercept	-4.05	0.43	-3.21 – -4.89	-9.32	<0.01
SPL	-0.03	0.26	0.48 – -0.54	-0.12	0.91
Background Freq	-0.72	0.36	-0.01 – -1.43	-2.02	0.04

Spectral Overlap	0.73	0.38	1.47 – -0.01	1.91	0.06
Vegetation	0.23	0.27	0.76 – -0.30	0.86	0.39
Elevation	-0.18	0.31	0.43 – -0.79	-0.59	0.56
Ordinal date	0.14	0.22	0.57 – -0.29	0.63	0.53
Ordinal date^2	0.14	0.22	0.57 – -0.29	0.62	0.53
Year	-0.80	0.46	0.10 – -1.7	-1.72	0.08
SPL:Background Freq	0.03	0.54	1.09 – -1.03	0.05	0.96
SPL:Spectral Overlap	0.33	0.54	1.39 – -0.73	0.61	0.54

	Common		Latin		
	Song sparrow		*Melospiza melodia*		
Predictors	Estimates	SE	*CI*	Z	*p*
Intercept	-2.57	0.30	-1.98 – -3.16	-8.65	<0.01
SPL	-0.35	0.09	-0.17 – -0.53	-3.92	<0.01
Background Freq	-0.42	0.16	-0.11 – -0.73	-2.57	0.01
Spectral Overlap	-0.13	0.13	0.12 – -0.38	-0.97	0.33
Vegetation	0.27	0.09	0.45 – 0.09	2.89	<0.01
Elevation	-0.49	0.23	-0.04 – -0.94	-2.11	0.04
Ordinal date	0.07	0.06	0.19 – -0.05	1.16	0.25
Ordinal date^2	0.11	0.07	0.25 – -0.03	1.59	0.11
Year	-0.16	0.14	0.11 – -0.43	-1.15	0.25
SPL:Background Freq	-0.23	0.16	0.08 – -0.54	-1.46	0.15
SPL:Spectral Overlap	-0.08	0.13	0.17 – -0.33	-0.63	0.53

	Common		Latin		
	Spotted Towhee		*Pipilo maculatus*		
Predictors	Estimates	SE	*CI*	Z	*p*
Intercept	-4.35	0.40	-3.57 – -5.13	-10.73	<0.01
SPL	-0.13	0.11	0.09 – -0.35	-1.14	0.25
Background Freq	-0.27	0.12	-0.03 – -0.51	-2.26	0.02
Spectral Overlap	0.19	0.09	0.37 – 0.01	2.05	0.04
Vegetation	0.19	0.17	0.52 – -0.14	1.17	0.24
Elevation	-1.18	0.29	-0.61 – -1.75	-4.03	<0.01
Ordinal date	0.01	0.08	0.17 – -0.15	0.11	0.91
Ordinal date^2	0.14	0.11	0.36 – -0.08	1.33	0.18
Year	0.76	0.24	1.23 – 0.29	3.12	<0.01
SPL:Background Freq	-0.07	0.11	0.15 – -0.29	-0.63	0.53
SPL:Spectral Overlap	-0.13	0.09	0.05 – -0.31	-1.47	0.14

	Common		Latin		
	Warbling vireo		*Vireo gilvus*		
Predictors	Estimates	SE	*CI*	Z	*p*
Intercept	-1.84	0.22	-1.41 – -2.27	-8.22	<0.01
SPL	0.03	0.06	0.15 – -0.09	0.42	0.68
Background Freq	-0.25	0.09	-0.07 – -0.43	-2.89	<0.01
Spectral Overlap	-0.02	0.07	0.12 – -0.16	-0.33	0.74
Vegetation	0.06	0.09	0.24 – -0.12	0.71	0.48
Elevation	0.02	0.20	0.41 – -0.37	0.08	0.94
Ordinal date	0.68	0.08	0.84 – 0.52	8.51	<0.01
Ordinal date^2	-0.85	0.09	-0.67 – -1.03	-9.69	<0.01
Year	0.57	0.13	0.82 – 0.32	4.48	<0.01
SPL:Background Freq	0.03	0.07	0.17 – -0.11	0.48	0.63
SPL:Spectral Overlap	0.11	0.07	0.25 – -0.03	1.50	0.13

	Common		Latin		
	Western Meadowlark		*Sturnella neglecta*		
Predictors	Estimates	SE	*CI*	Z	*p*
Intercept	-6.02	0.50	-5.04 – -7.00	-12.05	<0.01
SPL	0.13	0.17	0.46 – -0.20	0.73	0.46
Background Freq	-0.01	0.25	0.48 – -0.50	-0.04	0.97
Spectral Overlap	-0.02	0.24	0.45 – -0.49	-0.10	0.92
Vegetation	-0.31	0.17	0.02 – -0.64	-1.78	0.07
Elevation	-1.76	0.27	-1.23 – -2.29	-6.54	<0.01
Ordinal date	-0.53	0.16	-0.22 – -0.84	-3.28	<0.01
Ordinal date^2	0.55	0.18	0.90 – 0.20	3.15	<0.01
Year	0.32	0.46	1.22 – -0.58	0.69	0.49
SPL:Background Freq	0.10	0.29	0.67 – -0.47	0.33	0.74
SPL:Spectral Overlap	0.16	0.27	0.69 – -0.37	0.60	0.55

	Common		Latin		
	Western Tanager		*Piranga ludoviciana*		
Predictors	Estimates	SE	*CI*	Z	*p*
Intercept	-4.17	0.33	-3.52 – -4.82	-12.55	<0.01
SPL	-0.41	0.23	0.04 – -0.86	-1.81	0.07
Background Freq	-0.61	0.26	-0.1 – -1.12	-2.35	0.02
Spectral Overlap	-0.17	0.26	0.34 – -0.68	-0.65	0.52
Vegetation	-0.26	0.20	0.13 – -0.65	-1.30	0.19
Elevation	-0.10	0.22	0.33 – -0.53	-0.45	0.65

Ordinal date	0.56	0.18	0.91 – 0.21	3.08	<0.01
Ordinal date^2	-0.57	0.20	-0.18 – -0.96	-2.83	<0.01
Year	0.44	0.34	1.11 – -0.23	1.28	0.20
SPL:Background Freq	-0.11	0.27	0.42 – -0.64	-0.40	0.69
SPL:Spectral Overlap	-0.15	0.31	0.46 – -0.76	-0.48	0.63

	Common		Latin		
	Yellow Warbler		*Dendroica petechia*		
Predictors	Estimates	SE	*CI*	Z	*p*
Intercept	-1.56	0.26	-1.05 – -2.07	-6.08	<0.01
SPL	-0.09	0.07	0.05 – -0.23	-1.28	0.20
Background Freq	-0.17	0.12	0.07 – -0.41	-1.43	0.15
Spectral Overlap	0.02	0.11	0.24 – -0.20	0.22	0.83
Vegetation	0.11	0.09	0.29 – -0.07	1.23	0.22
Elevation	0.26	0.23	0.71 – -0.19	1.11	0.27
Ordinal date	0.04	0.07	0.18 – -0.10	0.59	0.56
Ordinal date^2	-0.61	0.08	-0.45 – -0.77	-7.89	<0.01
Year	-0.07	0.12	0.17 – -0.31	-0.56	0.58
SPL:Background Freq	-0.16	0.13	0.09 – -0.41	-1.23	0.22
SPL:Spectral Overlap	-0.14	0.12	0.10 – -0.38	-1.18	0.24

	Common		Latin		
	Yellow-rumped Warbler		*Dendroica coronata*		
Predictors	Estimates	SE	*CI*	Z	*p*
Intercept	-3.65	0.29	-3.08 – -4.22	-12.63	<0.01
SPL	0.13	0.13	0.38 – -0.12	1.03	0.30
Background Freq	0.28	0.20	0.67 – -0.11	1.43	0.15
Spectral Overlap	-0.21	0.16	0.10 – -0.52	-1.28	0.20
Vegetation	-0.17	0.14	0.10 – -0.44	-1.19	0.23
Elevation	0.76	0.19	1.13 – 0.39	3.99	<0.01
Ordinal date	-0.37	0.13	-0.12 – -0.62	-2.81	<0.01
Ordinal date^2	-0.44	0.14	-0.17 – -0.71	-3.14	<0.01
Year	1.18	0.28	1.73 – 0.63	4.18	<0.01
SPL:Background Freq	0.04	0.19	0.41 – -0.33	0.19	0.85
SPL:Spectral Overlap	0.04	0.16	0.35 – -0.27	0.24	0.81

Table B.3 Bird trait analyses summary tables.

Phylogenetic generalized least squares models combined species abundance model outputs with traits to elucidate larger patterns. The top (dAIC <4) models are shown here. Bolded values indicate that variables are significant at the 95% confidence level.

Model	Intercept	Flexible	Ground	Mass	Insectivory	Peak frequency	*K*	logLik	AICc	delta	weight
SPL	-0.022	NA	NA	NA	NA	NA	2	-3.633	11.788	0.000	0.242
SPL	0.211	NA	NA	NA	NA	-0.059	3	-2.770	12.632	0.844	0.159
SPL	0.769	NA	0.003	-0.127	NA	**-0.129**	5	-0.221	13.443	1.655	0.106
SPL	-0.069	NA	0.001	NA	NA	NA	3	-3.352	13.795	2.007	0.089
SPL	-0.116	NA	NA	NA	0.024	NA	3	-3.612	14.315	2.528	0.068
SPL	0.007	NA	NA	-0.009	NA	NA	3	-3.616	14.323	2.535	0.068
SPL	-0.021	-0.002	NA	NA	NA	NA	3	-3.633	14.356	2.569	0.067
SPL	0.174	NA	0.001	NA	NA	-0.064	4	-2.315	14.535	2.747	0.061
SPL	0.448	NA	NA	-0.046	NA	-0.079	4	-2.360	14.624	2.836	0.059
SPL	0.074	NA	NA	NA	0.036	-0.060	4	-2.720	15.345	3.558	0.041
SPL	0.205	0.017	NA	NA	NA	-0.060	4	-2.758	15.420	3.633	0.039
SO	0.882	NA	NA	NA	NA	**-0.242**	3	-14.124	35.339	0.000	0.160
SO	-0.623	NA	**-0.008**	**0.273**	NA	NA	4	-12.739	35.382	0.043	0.157
SO	0.162	NA	**-0.006**	0.166	NA	-0.132	5	-11.396	35.792	0.453	0.128
SO	0.983	NA	-0.003	NA	NA	**-0.231**	4	-12.948	35.801	0.462	0.127
SO	0.219	NA	NA	NA	0.180	**-0.251**	4	-13.534	36.972	1.633	0.071
SO	-1.796	NA	**-0.007**	**0.314**	0.252	NA	5	-12.073	37.145	1.806	0.065
SO	-0.755	0.148	**-0.009**	**0.296**	NA	NA	5	-12.329	37.659	2.320	0.050
SO	0.774	NA	NA	0.020	NA	**-0.232**	4	-14.091	38.087	2.748	0.041
SO	-0.908	NA	-0.005	0.209	0.219	-0.124	6	-10.844	38.108	2.769	0.040
SO	0.888	-0.021	NA	NA	NA	**-0.240**	4	-14.116	38.136	2.797	0.040
SO	-1.128	NA	NA	0.126	0.358	**-0.194**	5	-12.693	38.387	3.048	0.035
SO	0.016	0.124	**-0.007**	0.191	NA	-0.126	6	-11.079	38.579	3.240	0.032
SO	0.826	NA	-0.003	NA	0.040	**-0.234**	5	-12.929	38.858	3.519	0.028

Model	**Intercept**	**Flexible**	**Ground**	**Mass**	**Insectivory**	**Peak frequency**	***K***	**logLik**	**AICc**	**delta**	**weight**
SPL:SO	1.693	**0.366**	0.004	**-0.397**	NA	**-0.167**	6	-0.033	16.487	0.000	0.444
SPL:SO	1.260	**0.441**	NA	**-0.299**	NA	**-0.110**	5	-2.312	17.623	1.137	0.252
SPL:SO	2.250	**0.444**	NA	**-0.355**	-0.188	**-0.127**	6	-1.381	19.182	2.696	0.115
SPL:SO	0.634	**0.413**	NA	**-0.236**	NA	NA	4	-4.763	19.431	2.944	0.102
SPL:SO	2.165	**0.377**	0.003	**-0.414**	-0.100	**-0.170**	7	0.234	19.753	3.267	0.087

Table B.4 Clay caterpillar predation model summary table.

All continuous variables are centered to the mean, and standardized to one standard deviation. Predation data are analyzed with a binomial distribution (logit link).

Variable	Estimate	SE	CI	z value	p
Intercept	-2.315	0.151	-2.611 – -2.02	-15.38	<0.001
SPL	-0.441	0.101	-0.639 – -0.24	-4.375	<0.001
Background freq.	0.108	0.133	-0.153 – 0.37	0.813	0.416
Elevation	-0.027	0.178	-0.376 – 0.32	-0.150	0.880
Vegetation	-0.037	0.140	-0.311 – 0.24	-0.262	0.793
Ordinal date	0.302	0.176	-0.043 – 0.65	1.716	0.086
Bird Abundance	0.439	0.149	0.147 – 0.73	2.955	0.003
SPL:Background freq.	0.136	0.111	-0.082 – 0.35	1.233	0.217

Table B.5 Bat activity model summary tables.

All continuous variables are centered to the mean, and standardized to one standard deviation. Activity count data are analyzed with a negative binomial distribution (log link).

Model: Global Bat	Frequency variable: Background frequency				
Variable	Estimate	SE	*CI*	z value	*p*
Intercept	0.063	0.569	-1.052 – 1.180	0.112	0.911
SPL	-0.082	0.018	-0.117 – -0.050	-4.631	<0.001
Background freq.	-0.206	0.020	-0.245 – -0.170	-10.291	<0.001
Year	-0.079	0.030	-0.138 – -0.020	-2.657	0.008
Elevation	0.089	0.084	-0.076 – 0.250	1.066	0.286
Vegetation	-0.229	0.030	-0.288 – -0.170	-7.768	<0.001
Moon Phase	-0.114	0.014	-0.141 – -0.090	-8.395	<0.001
Ordinal date	0.581	0.015	0.552 – 0.610	37.662	<0.001
Ordinal date^2	0.036	0.015	0.007 – 0.070	2.451	0.014
SPL:Background freq.	-0.024	0.016	-0.055 – 0.010	-1.493	0.135

Model: Global Bat	Frequency variable: Spectral difference				
Variable	Estimate	SE	*CI*	z value	*p*
Intercept	0.044	0.582	-1.097 – 1.180	0.076	0.940
SPL	-0.122	0.020	-0.161 – -0.080	-6.213	<0.001
Spectral Overlap	0.505	0.086	0.336 – 0.670	5.835	<0.001
Year	-0.006	0.028	-0.061 – 0.050	-0.202	0.840
Elevation	0.178	0.084	0.013 – 0.340	2.124	0.034
Vegetation	-0.245	0.030	-0.304 – -0.190	-8.299	<0.001
Moon Phase	-0.114	0.014	-0.141 – -0.090	-8.378	<0.001
Ordinal date	0.546	0.015	0.517 – 0.580	37.628	<0.001

Ordinal date^2	0.035	0.015	0.006 – 0.060	2.386	0.017
SPL:Spectral Overlap	-0.141	0.015	-0.170 – -0.110	-9.571	<0.001

Model: Control-only	Frequency variable: Background frequency				
Variable	Estimate	SE	*CI*	z value	*p*
Intercept	0.375	0.641	-0.881 – 1.630	0.586	0.558
SPL	0.274	0.051	0.174 – 0.370	5.410	<0.001
Background freq.	-0.215	0.038	-0.289 – -0.140	-5.651	<0.001
Year	-0.246	0.044	-0.332 – -0.160	-5.578	<0.001
Elevation	-0.235	0.170	-0.568 – 0.100	-1.379	0.168
Vegetation	-0.353	0.069	-0.488 – -0.220	-5.117	<0.001
Moon Phase	-0.040	0.021	-0.081 – 0.000	-1.921	0.055
Ordinal date	0.656	0.026	0.605 – 0.710	25.431	<0.001
Ordinal date^2	0.031	0.025	-0.018 – 0.080	1.269	0.204
SPL:Background freq.	0.171	0.033	0.106 – 0.240	5.145	<0.001

Model: Control-only	Frequency variable: Spectral difference				
Variable	Estimate	SE	*CI*	z value	*p*
Intercept	0.325	0.674	-0.996 – 1.650	0.482	0.630
SPL	0.192	0.049	0.096 – 0.290	3.920	<0.001
Spectral Overlap	1.329	0.173	0.990 – 1.670	7.671	<0.001
Year	-0.240	0.044	-0.326 – -0.150	-5.502	<0.001
Elevation	-0.513	0.149	-0.805 – -0.220	-3.454	0.001
Vegetation	-0.404	0.068	-0.537 – -0.270	-5.923	<0.001
Moon Phase	-0.049	0.021	-0.090 – -0.010	-2.410	0.016
Ordinal date	0.639	0.025	0.590 – 0.690	25.213	<0.001

Ordinal date^2	0.013	0.024	-0.034 – 0.060	0.538	0.591
SPL:Spectral Overlap	-0.190	0.022	-0.233 – -0.150	-8.669	<0.001

Model: Experimental sites only	Frequency variable: Background frequency				
Variable	Estimate	SE	*CI*	z value	*p*
Intercept	-0.325	0.588	-1.477 - 0.830	-0.553	0.580
SPL	-0.097	0.019	-0.133 - -0.060	-5.151	<0.001
Background freq.	-0.077	0.026	-0.129 - -0.030	-2.918	0.004
Year	0.255	0.043	0.170 - 0.340	5.864	<0.001
Elevation	0.123	0.094	-0.061 - 0.310	1.310	0.190
Vegetation	-0.181	0.025	-0.230 - -0.130	-7.364	<0.001
Moon Phase	-0.173	0.018	-0.208 - -0.140	-9.595	<0.001
Ordinal date	0.557	0.020	0.519 - 0.600	28.476	<0.001
Ordinal date^2	0.035	0.018	-0.001 - 0.070	1.889	0.059
SPL:Background freq.	-0.116	0.020	-0.156 - -0.080	-5.660	<0.001

Table B.6 Individual bat species model summary tables.

All continuous variables are centered to the mean, and standardized to one standard deviation. Activity count data are analyzed with a negative binomial distribution (log link).

species: Antrozous pallidus

Variable	Estimate	SE	*CI*	z value	*p*
Intercept	-3.222	0.251	-3.714 – -2.73	-12.847	<0.001
SPL	-0.001	0.157	-0.309 – 0.31	-0.009	0.993
Background freq.	-0.074	0.160	-0.388 – 0.24	-0.460	0.646
Year	-0.280	0.261	-0.792 – 0.23	-1.073	0.283
Elevation	0.333	0.178	-0.016 – 0.68	1.868	0.062
Vegetation	-0.149	0.158	-0.459 – 0.16	-0.941	0.347
Moon Phase	0.042	0.115	-0.183 – 0.27	0.367	0.713
Ordinal date	0.774	0.171	0.439 – 1.11	4.536	<0.001
Ordinal date^2	-0.147	0.159	-0.459 – 0.16	-0.923	0.356
SPL:Background freq.	-0.294	0.126	-0.541 – -0.05	-2.322	0.020

species: Corynorhinus townsendii

Variable	Estimate	SE	*CI*	z value	*p*
Intercept	-3.796	0.346	-4.474 – -3.12	-10.960	<0.001
SPL	-0.446	0.192	-0.822 – -0.07	-2.323	0.020
Background freq.	-0.163	0.223	-0.60 – 0.27	-0.732	0.464
Year	0.293	0.343	-0.379 – 0.97	0.856	0.392
Elevation	0.110	0.225	-0.331 – 0.55	0.488	0.626
Vegetation	0.308	0.218	-0.119 – 0.74	1.413	0.158
Moon Phase	-0.447	0.157	-0.755 – -0.14	-2.852	0.004

Ordinal date	0.078	0.155	-0.226 – 0.38	0.502	0.616
Ordinal date^2	-0.120	0.150	-0.414 – 0.17	-0.802	0.422
SPL:Background freq.	-0.014	0.189	-0.384 – 0.36	-0.072	0.943

species: Eptesicus fuscus

Variable	Estimate	SE	*CI*	z value	*p*
Intercept	0.064	0.211	-0.35 – 0.48	0.306	0.760
SPL	-0.025	0.058	-0.139 – 0.09	-0.431	0.667
Background freq.	-0.305	0.067	-0.436 – -0.17	-4.519	<0.001
Year	-0.032	0.101	-0.23 – 0.17	-0.320	0.749
Elevation	0.640	0.177	0.293 – 0.99	3.620	<0.001
Vegetation	0.054	0.093	-0.128 – 0.24	0.580	0.562
Moon Phase	-0.068	0.047	-0.16 – 0.02	-1.453	0.146
Ordinal date	1.006	0.052	0.904 – 1.11	19.327	<0.001
Ordinal date^2	0.010	0.054	-0.096 – 0.12	0.183	0.855
SPL:Background freq.	-0.094	0.051	-0.194 – 0.01	-1.835	0.066

species: Lasiurus cinereus

Variable	Estimate	SE	*CI*	z value	*p*
Intercept	-1.333	0.278	-1.878 – -0.79	-4.792	<0.001
SPL	-0.017	0.079	-0.172 – 0.14	-0.217	0.828
Background freq.	-0.338	0.093	-0.52 – -0.16	-3.617	<0.001
Year	-0.271	0.141	-0.547 – 0.01	-1.915	0.055
Elevation	-0.099	0.220	-0.53 – 0.33	-0.450	0.653
Vegetation	-0.121	0.125	-0.366 – 0.12	-0.966	0.334
Moon Phase	0.065	0.062	-0.057 – 0.19	1.045	0.296

Ordinal date	1.032	0.077	0.881 – 1.18	13.339	<0.001
Ordinal date^2	-0.080	0.078	-0.233 – 0.07	-1.029	0.304
SPL:Background freq.	-0.131	0.069	-0.266 – 0.00	-1.891	0.059

species: Lasionycteris noctivagans

Variable	Estimate	SE	*CI*	z value	*p*
Intercept	0.331	0.379	-0.412 – 1.07	0.875	0.381
SPL	0.011	0.051	-0.089 – 0.11	0.209	0.834
Background freq.	-0.266	0.065	-0.393 – -0.14	-4.081	<0.001
Year	0.147	0.093	-0.035 – 0.33	1.575	0.115
Elevation	0.689	0.227	0.244 – 1.13	3.037	0.002
Vegetation	0.037	0.089	-0.137 – 0.21	0.411	0.681
Moon Phase	0.074	0.043	-0.01 – 0.16	1.696	0.090
Ordinal date	0.704	0.048	0.61 – 0.80	14.799	<0.001
Ordinal date^2	-0.065	0.047	-0.157 – 0.03	-1.370	0.171
SPL:Background freq.	-0.031	0.048	-0.125 – 0.06	-0.643	0.520

species: Myotis californicus

Variable	Estimate	SE	*CI*	z value	*p*
Intercept	0.520	0.199	0.13 – 0.91	2.607	0.009
SPL	-0.275	0.062	-0.397 – -0.15	-4.467	<0.001
Background freq.	-0.328	0.067	-0.459 – -0.20	-4.919	<0.001
Year	-0.113	0.099	-0.307 – 0.08	-1.139	0.255
Elevation	-0.306	0.172	-0.643 – 0.03	-1.774	0.076
Vegetation	-0.234	0.096	-0.422 – -0.05	-2.422	0.015
Moon Phase	-0.227	0.044	-0.313 – -0.14	-5.100	<0.001

Ordinal date	0.052	0.049	-0.044 – 0.15	1.045	0.296
Ordinal date^2	-0.068	0.048	-0.162 – 0.03	-1.416	0.157
SPL:Background freq.	0.055	0.052	-0.047 – 0.16	1.060	0.289

species: Myotis ciliolabrum

Variable	Estimate	SE	*CI*	z value	*p*
Intercept	1.477	0.172	1.140 – 1.810	8.611	<0.001
SPL	-0.186	0.047	-0.278 – -0.090	-3.914	<0.001
Background freq.	-0.309	0.051	-0.409 – -0.210	-6.015	<0.001
Year	-0.176	0.080	-0.333 – -0.020	-2.201	0.028
Elevation	-0.776	0.159	-1.088 – -0.460	-4.885	<0.001
Vegetation	-0.068	0.073	-0.211 – 0.080	-0.926	0.354
Moon Phase	-0.139	0.035	-0.208 – -0.070	-3.985	<0.001
Ordinal date	0.260	0.039	0.184 – 0.340	6.604	<0.001
Ordinal date^2	-0.025	0.037	-0.098 – 0.05	-0.666	0.506
SPL:Background freq.	-0.001	0.038	-0.075 – 0.07	-0.039	0.969

species: Myotis evotis

Variable	Estimate	SE	*CI*	z value	*p*
Intercept	1.695	0.201	1.301 – 2.09	8.431	<0.001
SPL	-0.002	0.042	-0.084 – 0.08	-0.043	0.965
Background freq.	0.008	0.046	-0.082 – 0.1	0.176	0.860
Year	-0.058	0.068	-0.191 – 0.08	-0.849	0.396
Elevation	-0.202	0.142	-0.48 – 0.08	-1.419	0.156
Vegetation	-0.276	0.068	-0.409 – -0.14	-4.067	<0.001
Moon Phase	-0.240	0.031	-0.301 – -0.18	-7.819	<0.001

Ordinal date	0.606	0.034	0.539 – 0.67	17.610	<0.001
Ordinal date^2	-0.004	0.033	-0.069 – 0.06	-0.120	0.904
SPL:Background freq.	0.028	0.037	-0.045 – 0.1	0.748	0.454

species: Myotis lucifugus

Variable	Estimate	SE	*CI*	z value	*p*
Intercept	1.934	0.162	1.616 – 2.25	11.953	<0.001
SPL	-0.209	0.039	-0.285 – -0.13	-5.299	<0.001
Background freq.	-0.135	0.045	-0.223 – -0.05	-3.023	0.003
Year	-0.391	0.069	-0.526 – -0.26	-5.644	<0.001
Elevation	-0.413	0.126	-0.66 – -0.17	-3.276	0.001
Vegetation	-0.345	0.061	-0.465 – -0.23	-5.660	<0.001
Moon Phase	-0.099	0.030	-0.158 – -0.04	-3.285	0.001
Ordinal date	0.781	0.036	0.71 – 0.85	21.937	<0.001
Ordinal date^2	0.014	0.034	-0.053 – 0.08	0.409	0.683
SPL:Background freq.	-0.096	0.035	-0.165 – -0.03	-2.747	0.006

species: Myotis thysanodes

Variable	Estimate	SE	*CI*	z value	*p*
Intercept	-2.886	0.267	-3.409 – -2.36	-10.802	<0.001
SPL	0.188	0.102	-0.012 – 0.39	1.837	0.066
Background freq.	0.108	0.094	-0.076 – 0.29	1.140	0.254
Year	0.189	0.166	-0.136 – 0.51	1.139	0.255
Elevation	-0.908	0.207	-1.314 – -0.5	-4.376	<0.001
Vegetation	-0.359	0.147	-0.647 – -0.07	-2.441	0.015
Moon Phase	0.080	0.074	-0.065 – 0.23	1.075	0.282

Ordinal date	0.748	0.075	0.601 – 0.9	10.015	<0.001
Ordinal date^2	0.416	0.079	0.261 – 0.57	5.257	<0.001
SPL:Background freq.	0.066	0.072	-0.075 – 0.21	0.909	0.363

species: Myotis volans

Variable	Estimate	SE	*CI*	z value	*p*
Intercept	2.055	0.217	1.63 – 2.48	9.451	<0.001
SPL	0.008	0.041	-0.072 – 0.09	0.191	0.849
Background freq.	-0.165	0.044	-0.251 – -0.08	-3.771	<0.001
Year	-0.143	0.068	-0.276 – -0.01	-2.089	0.037
Elevation	-0.870	0.179	-1.221 – -0.52	-4.858	<0.001
Vegetation	-0.155	0.066	-0.284 – -0.03	-2.343	0.019
Moon Phase	-0.206	0.032	-0.269 – -0.14	-6.534	<0.001
Ordinal date	0.432	0.034	0.365 – 0.5	12.619	<0.001
Ordinal date^2	0.027	0.032	-0.036 – 0.09	0.825	0.409
SPL:Background freq.	-0.021	0.038	-0.095 – 0.05	-0.560	0.576

species: Myotis yumanensis

Variable	Estimate	SE	*CI*	z value	*p*
Intercept	-0.351	0.126	-0.598 – -0.1	-2.797	0.005
SPL	-0.199	0.059	-0.315 – -0.08	-3.391	0.001
Background freq.	-0.188	0.067	-0.319 – -0.06	-2.785	0.005
Year	-0.144	0.104	-0.348 – 0.06	-1.384	0.167
Elevation	-0.211	0.103	-0.413 – -0.01	-2.043	0.041
Vegetation	-0.067	0.089	-0.241 – 0.11	-0.747	0.455
Moon Phase	-0.214	0.048	-0.308 – -0.12	-4.410	<0.001

Ordinal date	0.120	0.052	0.018 – 0.22	2.307	0.021
Ordinal date^2	-0.047	0.048	-0.141 – 0.05	-0.988	0.323
SPL:Background freq.	-0.077	0.053	-0.181 – 0.03	-1.464	0.143

Table B.7 Bat foraging style switching model summary tables.

All continuous variables are centered to the mean, and standardized to one standard deviation. Activity counts are analyzed with a negative binomial distribution (log link).

Model: Prey playback speaker bat visits

Variable	Estimate	SE	*CI*	z value	*p*
Intercept	-2.777	1.104	-4.941 - -0.61	-2.516	0.012
SPL	0.421	0.228	-0.026 - 0.87	1.846	0.065
Background freq.	-0.148	0.271	-0.679 - 0.38	-0.549	0.583
Spectral Overlap	-0.499	1.082	-2.620 - 1.62	-0.461	0.645
Elevation	0.098	0.242	-0.376 - 0.57	0.406	0.685
Moon Phase	-0.025	0.243	-0.501 - 0.45	-0.102	0.919
Vegetation	0.344	0.218	-0.083 - 0.77	1.576	0.115
Ordinal date	0.726	0.244	0.248 - 1.20	2.981	0.003
Ordinal date^2	0.500	0.329	-0.145 - 1.14	1.519	0.129
Predicted bats in area	0.295	0.266	-0.226 - 0.82	1.108	0.268
SPL:Background freq.	-0.376	0.143	-0.656 - -0.10	-2.637	0.008
SPL:Spectral Overlap	0.249	0.236	-0.214 - 0.71	1.052	0.293

Model: Robotic moth bat visits

Variable	Estimate	SE	*CI*	z value	*p*
Intercept	-2.096	1.499	-5.034 - 0.84	-1.398	0.162
SPL	0.492	0.254	-0.006 - 0.99	1.938	0.053
Background freq.	0.568	0.291	-0.002 - 1.14	1.949	0.051
Spectral Overlap	0.471	1.514	-2.496 - 3.44	0.311	0.756
Elevation	-0.513	0.305	-1.111 - 0.08	-1.685	0.092
Moon Phase	0.377	0.215	-0.044 - 0.80	1.753	0.080
Vegetation	-0.038	0.448	-0.916 - 0.84	-0.085	0.932
Ordinal date	1.236	0.362	0.526 - 1.95	3.413	0.001
Ordinal date^2	-0.032	0.194	-0.412 - 0.35	-0.163	0.870
Predicted bats in area	-0.184	0.337	-0.845 - 0.48	-0.546	0.585
SPL:Background freq.	0.747	0.310	0.139 - 1.35	2.411	0.016
SPL:Spectral Overlap	0.560	0.422	-0.267 - 1.39	1.328	0.184

Table B.8 Bat trait analyses summary tables.

Phylogenetic generalized least squares models combined species activity model outputs with traits to elucidate larger patterns. The top (dAIC <4) models are shown here. Bolded values indicate that variables are significant at the 95% confidence level. Flexible indicates that bats are able to forage via both active echolocation and passive listening.

Model	Intercept	Flexible	Mass	Peak Frequency	*K*	logLik	AICc	delta	weight
SPL	0.638	NA	NA	**-0.019**	3	9.951	-10.901	0.000	0.605
SPL	1.064	NA	-0.132	**-0.022**	4	11.880	-10.045	0.856	0.395
Freq	-0.059	**-0.216**	NA	NA	3	12.576	-16.153	0.000	0.830
Freq	0.067	**-0.224**	-0.054	NA	4	13.347	-12.979	3.174	0.170
SPL:Freq	0.284	NA	**-0.151**	NA	3	15.376	-21.752	0.000	0.849
SPL:Freq	0.459	NA	**-0.181**	-0.003	4	16.005	-18.295	3.457	0.151

Table B.9 Bird observation summary tables.

Observations columns are sums of total number of times a species was observed. Unique site-days are the number of times a given species was observed as present (0 or 1) during each sampling visit (per site per day).

Common name	*Latin name*	Observations	Unique site-days
American crow	*Corvus brachyrhynchos*	88	39
American dipper	*Cinclus mexicanus*	21	6
American goldfinch	*Spinus tristis*	10	7
American kestrel	*Falco sparverius*	83	50
American robin	*Turdus migratorius*	409	176
Black-billed magpie	*Pica hudsonia*	47	17
Black-capped chickadee	*Poecile atricapillus*	75	27
Brown-headed cowbird	*Molothrus ater*	80	36
Black-headed grosbeak	*Pheucticus melanocephalus*	21	19
Brewer's blackbird	*Euphagus cyanocephalus*	52	17
Brown creeper	*Certhia americana*	5	2
Brewer's sparrow	*Spizella breweri*	52	29
Bullock's oriole	*Icterus bullockii*	109	54
Cassin's finch	*Haemorhous cassinii*	1	1
Canada goose	*Branta canadensis*	1	1
Cassin's vireo	*Vireo cassinii*	4	4
Cedar waxwing	*Bombycilla cedrorum*	22	5
Chipping sparrow	*Spizella passerina*	60	26
Cordilleran flycatcher	*Empidonax occidentalis*	9	4
Common merganser	*Mergus merganser*	2	2
Dark-eyed junco	*Junco hyemalis*	63	40
Downy woodpecker	*Dryobates pubescens*	6	4
Dusky flycatcher	*Empidonax oberholseri*	126	83
Dusky grouse	*Dendragapus obscurus*	2	2
Eastern kingbird	*Tyrannus tyrannus*	12	3
European starling	*Sturnus vulgaris*	129	26
Fox sparrow	*Passerella iliaca*	10	9
Golden-crowned kinglet	*Regulus satrapa*	4	2
Golden eagle	*Aquila chrysaetos*	1	1
Gray catbird	*Dumetella carolinensis*	2	1
Green-tailed towhee	*Pipilo chlorurus*	16	12
Hammond's flycatcher	*Empidonax hammondii*	31	17
Hairy woodpecker	*Dryobates villosus*	9	9
Hermit thrush	*Catharus guttatus*	13	6
House wren	*Troglodytes aedon*	864	280
Lazuli bunting	*Passerina amoena*	758	266
Lesser goldfinch	*Spinus psaltria*	1	1

Common name	*Latin name*	Observations	Unique site-days
Lewis's woodpecker	*Melanerpes lewis*	139	57
Lincoln's sparrow	*Melospiza lincolnii*	3	3
Mallard	*Anas platyrhynchos*	7	3
MacGillivray's warbler	*Geothlypis tolmiei*	293	137
Mountain bluebird	*Sialia currucoides*	4	1
Mountain chickadee	*Poecile gambeli*	55	22
Mourning dove	*Zenaida macroura*	60	29
Northern flicker	*Colaptes auratus*	287	127
Northern harrier	*Circus hudsonius*	4	4
Orange-crowned warbler	*Vermivora celata*	192	102
Pine siskin	*Spinus pinus*	12	5
Pilleated woodpecker	*Dryocopus pileatus*	1	1
Red-breasted nuthatch	*Sitta canadensis*	57	33
Ruby-crowned kinglet	*Regulus calendula*	89	53
Red-naped sapsucker	*Sphyrapicus nuchalis*	77	39
Rock wren	*Salpinctes obsoletus*	2	1
Red-tailed hawk	*Buteo jamaicensis*	3	2
Red-winged blackbird	*Agelaius phoeniceus*	136	21
song sparrow	*Melospiza melodia*	461	207
Spotted sandpiper	*Actitis macularius*	9	4
Spotted towhee	*Pipilo maculatus*	238	116
Steller's jay	*Cyanocitta stelleri*	1	1
Swainson's thrush	*Catharus ustulatus*	11	7
Tree swallow	*Tachycineta bicolor*	40	20
Vesper sparrow	*Pooecetes gramineus*	5	4
Violet-green swallow	*Tachycineta thalassina*	67	16
Warbling vireo	*Vireo gilvus*	542	225
Western kingbird	*Tyrannus verticalis*	1	1
Western meadowlark	*Sturnella neglecta*	131	61
Western tanager	*Piranga ludoviciana*	82	46
Western wood-pewee	*Contopus sordidulus*	7	5
Willow flycatcher	*Empidonax traillii*	4	3
Wilson's snipe	*Gallinago delicata*	2	1
Wilson's warbler	*Cardellina pusilla*	26	15
Yellow warbler	*Dendroica petechia*	576	246
Yellow-rumped warbler	*Dendroica coronata*	192	79
	Total	**7014**	**2981**

Table B.10 Bat observation summary tables.

Total passes indicate the number of times a bat species was identified over the course of the study, whereas "site-night occurrences" indicates how many times a species occurred in a unique night and site.

Latin name	Total passes	Site-night occurrences
Antrozous pallidus	116	94
Corynorhinus townsendii	91	65
Eptesicus fuscus	6111	923
Lasiurus cinereus	1822	474
Lasionycteris noctivagans	10520	1085
Myotis californicus	4871	989
Myotis ciliolabrum	16215	1440
Myotis evotis	18025	1619
Myotis lucifugus	21889	1636
Myotis thysanodes	554	279
Myotis volans	21439	1682
Myotis yumanensis	1587	694
Total	**103240**	**10980**

Table B.11 AIC table for bird removal model.

Model 19, the scaled, quadratic version of time after sunrise and the background sound pressure level during counts (LEQ) was most predictive of when birds were more likely to be singing (dAIC =0). Additionally, Model 5, is the best fit model that doesn't contain LEQ, which was paired with our point count detectability experiment as an alternative method of controlling for background noise levels during counts.

Mod	Predictors					*K*	AIC	dAIC
0	1	-	-	-	-	1	854.55	4.39
1	ordinal date	-	-	-	-	2	856.41	6.25
2	-	TASR	-	-	-	2	856.52	6.35
3	ordinal date	TASR	-	-	-	3	858.37	8.21
4	-	-	(ordinal date)^2	-	-	2	856.35	6.19
5	-	-	-	**(TASR)^2**	-	**2**	**851.27**	**1.11**
6	-	-	(ordinal date)^2	(TASR)^2	-	3	853.12	2.95
7	ordinal date	-	(ordinal date)^2	-	-	3	856.94	6.78
8	ordinal date	-	-	(TASR)^2	-	3	853.11	2.95
9	-	TASR	(ordinal date)^2	-	-	3	858.32	8.16
10	-	TASR	-	(TASR)^2	-	3	852.92	2.75
11	ordinal date	TASR	-	(TASR)^2	-	4	854.75	4.58
12	ordinal date	TASR	(ordinal date)^2	-	-	4	858.93	8.77
13	ordinal date	TASR	(ordinal date)^2	(TASR)^2	-	5	855.2	5.03
14	-	-	-	-	LEQ	2	853.92	3.76
15	ordinal date	-	-	-	LEQ	3	855.53	5.37
16	-	TASR	-	-	LEQ	3	855.82	5.65
17	ordinal date	TASR	-	-	LEQ	4	857.41	7.25
18	-	-	(ordinal date)^2	-	LEQ	3	855.92	5.76
19	-	-	-	**(TASR)^2**	**LEQ**	**3**	**850.16**	**0**
20	-	-	(ordinal date)^2	(TASR)^2	LEQ	4	852.16	1.99

Mod	Predictors					*K*	AIC	dAIC
21	ordinal date	-	(ordinal date)^2	-	LEQ	4	856.83	6.66
22	ordinal date	-	-	(TASR)^2	LEQ	4	851.72	1.55
23	-	TASR	(ordinal date)^2	-	LEQ	4	857.81	7.65
24	-	TASR	-	(TASR)^2	LEQ	4	851.94	1.78
25	ordinal date	TASR	-	(TASR)^2	LEQ	5	853.48	3.32
26	ordinal date	TASR	(ordinal date)^2	-	LEQ	5	858.77	8.61
27	ordinal date	TASR	(ordinal date)^2	(TASR)^2	LEQ	6	854.86	4.7

Table B.12 Number of 3-minute bird point counts.

Year	# Multimodal counts	# Vision-only counts
2017	1558	1793
2018	2079	2274
Total	**3637**	**4067**

Table B.13 Trait table for bat data

References are subscripts on foraging style. Where (1) gleaning bats, (2) behaviourally flexible bats (gleaning and aerial hawking), (3) clutter-tolerant aerial hawking bats, and (4) open space aerial hawking bats. a = Gordon et al., 2019; b = Kunz, 1982 + Barclay, 1985; c = Faure & Barclay, 1994; d = Ratcliffe & Dawson, 2003

Species	Foraging style	Recorded calls	Peak frequency Mean ± SD (kHz)	Calls per hour Mean ± SD
Antrozous pallidus	1 [a]	525	33.48 ± 4.77	8.0 ± 6.0
Corynorhinus townsendii	2 [a]	228	51.45 ± 18.21	6.0 ± 15.6
Eptesicus fuscus	4 [a]	59,536	31.54 ± 2.54	50.1 ± 190.1
Lasiurus cinereus	4 [a]	15,955	26.05 ± 3.47	59.3 ± 257.4
Lasionycteris noctivagans	3 [b]	51,785	28.69 ± 1.75	54.8 ± 163.4
Myotis californicus	3 [a]	59,539	50.80 ± 4.60	84.4 ± 350.0
Myotis ciliolabrum	3 [a]	158,789	44.68 ± 1.90	109.0 ± 341.4
Myotis evotis	2 [c]	111,936	39.20 ± 2.12	57.1 ± 168.6
Myotis lucifugus	2 [d]	105,289	43.57 ± 2.15	54.9 ± 138.3
Myotis thysanodes	2 [a]	2,039	30.38 ± 3.83	19.4 ± 19.3
Myotis volans	3 [a]	165,674	45.38 ± 2.49	71.7 ± 190.0
Myotis yumanensis	3 [a]	9,583	54.79 ± 6.43	21.8 ± 73.8

Table B.14 Model outputs from arthropod abundance models.

Abundance for each order and trap type combination (in alphabetical order) was estimated individually with Bayesian generalized linear mixed-effects models (individual models are separated by horizontal lines). Within the parameter column are all fixed effects of generalized linear mixed-effects models. Estimate = model estimate (median draw); SE = standard error; 80% CI = 80% credible intervals; 90% CI = 90% credible intervals; Probability of Direction (PD) is an index for the probability that the effect is non-zero; ESS = effective sample size; $\hat{r}$ (or Rhat) statistics above 1.1 indicates that chain has not converged yet; MCSE = Monte Carlo standard error, defined as the standard deviation of the chains divided by their effective sample size (see Lüdecke D. 2020). All Parameters were standardized by two standard deviations to make Estimates comparable to one another (Gelman 2008).

Order	Trap	Parameter	Estimate	SE	80% CI	90% CI	PD	ESS	Rhat	MCSE
Acari	Pitfall	Sound pressure level (SPL)	0.94	0.82	[-0.04, 2.07]	[-0.42, 2.29]	0.878	5508	1.000	0.011
Acari	Pitfall	Background frequency (Freq.)	-0.50	0.84	[-1.59, 0.60]	[-1.93, 0.88]	0.722	5559	1.000	0.011
Acari	Pitfall	Ordinal day	2.54	0.84	[1.39, 3.64]	[1.15, 4.08]	0.997	5880	1.000	0.012
Acari	Pitfall	Vegetation	0.31	0.73	[-0.67, 1.19]	[-0.98, 1.45]	0.665	5117	1.000	0.010
Acari	Pitfall	Elevation	-1.04	0.80	[-2.05, -0.01]	[-2.41, 0.23]	0.918	4619	1.000	0.012
Acari	Pitfall	Moon Illuminance	0.11	0.59	[-0.69, 0.88]	[-0.90, 1.14]	0.575	5775	1.001	0.008
Acari	Pitfall	Temperature	-0.34	0.93	[-1.46, 0.98]	[-1.92, 1.26]	0.638	5387	1.000	0.013
Acari	Pitfall	Year (2018)	-0.69	0.66	[-1.53, 0.16]	[-1.78, 0.43]	0.854	5350	1.000	0.009
Acari	Pitfall	SPL x Freq. interaction	-0.78	1.86	[-3.25, 1.55]	[-3.97, 2.10]	0.657	5698	1.001	0.025
Araneae	Beat-net	Sound pressure level (SPL)	0.27	0.47	[-0.30, 0.93]	[-0.47, 1.12]	0.717	6130	1.000	0.006

Order	Trap	Parameter	Estimate	SE	80% CI	90% CI	PD	ESS	Rhat	MCSE
Araneae	Beat-net	Background frequency (Freq.)	-0.39	0.43	[-0.94, 0.17]	[-1.15, 0.30]	0.817	6015	1.000	0.006
Araneae	Beat-net	Ordinal day	-0.79	0.50	[-1.38, -0.12]	[-1.62, 0.01]	0.951	5197	1.000	0.007
Araneae	Beat-net	Vegetation	0.49	0.40	[-0.03, 1.02]	[-0.16, 1.20]	0.885	5348	1.000	0.006
Araneae	Beat-net	Elevation	0.04	0.40	[-0.47, 0.57]	[-0.68, 0.69]	0.545	5465	1.001	0.006
Araneae	Beat-net	Moon Illuminance	-0.08	0.34	[-0.51, 0.36]	[-0.64, 0.48]	0.598	8246	1.000	0.004
Araneae	Beat-net	Temperature	1.33	0.55	[0.64, 2.07]	[0.36, 2.22]	0.994	5428	1.000	0.008
Araneae	Beat-net	Year (2018)	-0.38	0.34	[-0.84, 0.03]	[-0.93, 0.18]	0.869	8291	1.000	0.004
Araneae	Beat-net	SPL x Freq. interaction	1.03	0.90	[-0.09, 2.27]	[-0.43, 2.65]	0.878	7148	1.000	0.011
Araneae	Fly (Vane)	Sound pressure level (SPL)	-0.06	0.62	[-0.88, 0.76]	[-1.18, 0.95]	0.539	6293	1.000	0.008
Araneae	Fly (Vane)	Background frequency (Freq.)	-0.72	0.56	[-1.39, 0.03]	[-1.65, 0.19]	0.913	6339	1.000	0.007
Araneae	Fly (Vane)	Ordinal day	-0.23	0.68	[-1.14, 0.62]	[-1.38, 0.88]	0.636	6440	1.000	0.009
Araneae	Fly (Vane)	Vegetation	-0.62	0.57	[-1.40, 0.09]	[-1.58, 0.34]	0.858	6510	1.000	0.007
Araneae	Fly (Vane)	Elevation	-1.42	0.63	[-2.28, -0.62]	[-2.55, -0.41]	0.991	5128	1.000	0.009
Araneae	Fly (Vane)	Moon Illuminance	-0.52	0.51	[-1.20, 0.11]	[-1.35, 0.35]	0.852	8415	1.000	0.006

Order	Trap	Parameter	Estimate	SE	80% CI	90% CI	PD	ESS	Rhat	MCSE
Araneae	Fly (Vane)	Temperature	0.34	0.65	[-0.46, 1.22]	[-0.74, 1.43]	0.699	5626	1.001	0.009
Araneae	Fly (Vane)	Year (2018)	-0.80	0.48	[-1.41, -0.19]	[-1.57, -0.00]	0.952	8213	1.000	0.005
Araneae	Fly (Vane)	SPL x Freq. interaction	0.50	1.15	[-0.94, 2.03]	[-1.33, 2.47]	0.668	7858	1.000	0.013
Araneae	Malaise	Sound pressure level (SPL)	-1.62	0.70	[-2.53, -0.73]	[-2.88, -0.54]	0.991	6024	1.000	0.009
Araneae	Malaise	Background frequency (Freq.)	-0.29	0.74	[-1.19, 0.71]	[-1.56, 0.89]	0.653	5456	1.000	0.010
Araneae	Malaise	Ordinal day	0.44	0.82	[-0.64, 1.49]	[-0.96, 1.80]	0.709	5221	1.000	0.012
Araneae	Malaise	Vegetation	0.35	0.60	[-0.41, 1.17]	[-0.67, 1.37]	0.715	5715	1.000	0.008
Araneae	Malaise	Elevation	-0.69	0.73	[-1.62, 0.27]	[-1.86, 0.60]	0.830	6177	1.000	0.010
Araneae	Malaise	Moon Illuminance	0.39	0.56	[-0.36, 1.11]	[-0.51, 1.41]	0.754	8272	1.000	0.006
Araneae	Malaise	Temperature	-0.24	0.85	[-1.28, 0.92]	[-1.69, 1.11]	0.611	5639	1.000	0.012
Araneae	Malaise	Year (2018)	-0.55	0.55	[-1.30, 0.12]	[-1.46, 0.38]	0.846	8208	1.000	0.006
Araneae	Malaise	SPL x Freq. interaction	4.80	1.59	[2.93, 7.08]	[2.46, 7.78]	1.000	4845	1.000	0.023
Araneae	Pitfall	Sound pressure level (SPL)	0.71	0.43	[0.15, 1.26]	[-0.02, 1.43]	0.947	4840	1.000	0.006
Araneae	Pitfall	Background frequency (Freq.)	-0.61	0.35	[-1.08, -0.16]	[-1.21, -0.02]	0.956	5626	1.000	0.005

Order	Trap	Parameter	Estimate	SE	80% CI	90% CI	PD	ESS	Rhat	MCSE
Araneae	Pitfall	Ordinal day	0.42	0.40	[-0.08, 0.95]	[-0.25, 1.06]	0.851	5053	1.000	0.006
Araneae	Pitfall	Vegetation	1.01	0.42	[0.45, 1.54]	[0.34, 1.74]	0.988	5215	1.000	0.006
Araneae	Pitfall	Elevation	-1.00	0.42	[-1.54, -0.45]	[-1.72, -0.31]	0.990	5169	1.001	0.006
Araneae	Pitfall	Moon Illuminance	0.17	0.26	[-0.16, 0.49]	[-0.25, 0.59]	0.752	8003	1.000	0.003
Araneae	Pitfall	Temperature	0.19	0.43	[-0.31, 0.80]	[-0.55, 0.88]	0.671	5833	1.000	0.006
Araneae	Pitfall	Year (2018)	-0.31	0.27	[-0.63, 0.06]	[-0.75, 0.15]	0.864	6727	1.000	0.003
Araneae	Pitfall	SPL x Freq. interaction	-0.53	0.74	[-1.47, 0.42]	[-1.75, 0.68]	0.756	8201	1.000	0.008
Araneae	UV	Sound pressure level (SPL)	0.83	0.53	[0.13, 1.50]	[-0.07, 1.70]	0.941	6701	1.000	0.007
Araneae	UV	Background frequency (Freq.)	0.26	0.44	[-0.33, 0.82]	[-0.48, 1.01]	0.726	8345	1.001	0.005
Araneae	UV	Ordinal day	0.01	0.52	[-0.68, 0.67]	[-0.88, 0.86]	0.506	7482	1.000	0.006
Araneae	UV	Vegetation	-0.32	0.46	[-0.94, 0.24]	[-1.07, 0.48]	0.757	8530	1.000	0.005
Araneae	UV	Elevation	-0.64	0.48	[-1.28, -0.02]	[-1.43, 0.19]	0.904	8318	1.000	0.005
Araneae	UV	Moon Illuminance	-0.45	0.35	[-0.88, -0.00]	[-1.01, 0.13]	0.904	12992	1.000	0.003
Araneae	UV	Temperature	0.69	0.53	[0.02, 1.37]	[-0.20, 1.56]	0.904	7357	1.000	0.006

Order	Trap	Parameter	Estimate	SE	80% CI	90% CI	PD	ESS	Rhat	MCSE
Araneae	UV	Year (2018)	0.32	0.37	[-0.17, 0.79]	[-0.31, 0.93]	0.806	9707	1.000	0.004
Araneae	UV	SPL x Freq. interaction	-0.47	0.78	[-1.51, 0.53]	[-1.82, 0.82]	0.729	7863	1.000	0.009
Archaeognatha	Pitfall	Sound pressure level (SPL)	0.52	1.56	[-1.39, 2.54]	[-1.90, 3.28]	0.633	5027	1.000	0.022
Archaeognatha	Pitfall	Background frequency (Freq.)	-0.93	1.01	[-2.28, 0.38]	[-2.79, 0.70]	0.833	5763	1.000	0.014
Archaeognatha	Pitfall	Ordinal day	2.94	1.52	[0.88, 4.90]	[0.31, 5.53]	0.974	5232	1.000	0.022
Archaeognatha	Pitfall	Vegetation	-0.09	1.55	[-2.02, 2.07]	[-2.79, 2.53]	0.523	6447	1.000	0.020
Archaeognatha	Pitfall	Elevation	-1.10	0.94	[-2.29, 0.17]	[-2.74, 0.47]	0.886	6048	1.000	0.013
Archaeognatha	Pitfall	Moon Illuminance	1.33	0.81	[0.31, 2.39]	[-0.02, 2.72]	0.962	5605	1.000	0.011
Archaeognatha	Pitfall	Temperature	1.31	1.55	[-0.78, 3.25]	[-1.19, 4.08]	0.808	6259	1.000	0.020
Archaeognatha	Pitfall	Year (2018)	-1.10	0.87	[-2.38, -0.10]	[-2.61, 0.39]	0.902	6942	1.000	0.011
Archaeognatha	Pitfall	SPL x Freq. interaction	-1.08	2.20	[-4.1, 1.64]	[-5.14, 2.41]	0.694	6744	1.000	0.028
Coleoptera	Beat-net	Sound pressure level (SPL)	-0.16	0.70	[-1.06, 0.73]	[-1.31, 0.99]	0.591	4819	1.000	0.010
Coleoptera	Beat-net	Background frequency (Freq.)	0.17	0.53	[-0.55, 0.87]	[-0.75, 1.08]	0.620	4186	1.002	0.009
Coleoptera	Beat-net	Ordinal day	0.73	0.75	[-0.25, 1.70]	[-0.56, 1.96]	0.835	5491	1.000	0.010

Order	Trap	Parameter	Estimate	SE	80% CI	90% CI	PD	ESS	Rhat	MCSE
Coleoptera	Beat-net	Vegetation	0.03	0.56	[-0.67, 0.79]	[-0.90, 1.02]	0.522	5109	1.001	0.008
Coleoptera	Beat-net	Elevation	-1.68	0.56	[-2.40, -0.96]	[-2.61, -0.73]	0.998	4639	1.000	0.009
Coleoptera	Beat-net	Moon Illuminance	-0.59	0.48	[-1.20, 0.04]	[-1.39, 0.21]	0.887	6802	1.000	0.006
Coleoptera	Beat-net	Temperature	0.34	0.73	[-0.60, 1.26]	[-0.85, 1.53]	0.679	5265	1.000	0.010
Coleoptera	Beat-net	Year (2018)	-0.46	0.49	[-1.09, 0.15]	[-1.28, 0.33]	0.830	4725	1.000	0.007
Coleoptera	Beat-net	SPL x Freq. interaction	0.22	1.10	[-1.24, 1.59]	[-1.65, 2.02]	0.580	5108	1.001	0.016
Coleoptera	Fly (Vane)	Sound pressure level (SPL)	-0.22	0.37	[-0.69, 0.24]	[-0.83, 0.38]	0.723	6069	1.000	0.005
Coleoptera	Fly (Vane)	Background frequency (Freq.)	-0.53	0.28	[-0.87, -0.16]	[-0.99, -0.09]	0.977	7131	1.000	0.003
Coleoptera	Fly (Vane)	Ordinal day	0.50	0.33	[0.07, 0.94]	[-0.06, 1.04]	0.925	6547	1.000	0.004
Coleoptera	Fly (Vane)	Vegetation	-0.37	0.30	[-0.75, 0.01]	[-0.86, 0.13]	0.900	5910	1.000	0.004
Coleoptera	Fly (Vane)	Elevation	-1.41	0.33	[-1.81, -0.95]	[-1.94, -0.82]	1.000	6022	1.000	0.004
Coleoptera	Fly (Vane)	Moon Illuminance	0.33	0.25	[0.02, 0.67]	[-0.09, 0.73]	0.905	8225	1.000	0.003
Coleoptera	Fly (Vane)	Temperature	0.87	0.37	[0.40, 1.35]	[0.25, 1.45]	0.991	6389	1.000	0.005
Coleoptera	Fly (Vane)	Year (2018)	0.95	0.24	[0.67, 1.30]	[0.55, 1.35]	1.000	8409	1.000	0.003

Order	Trap	Parameter	Estimate	SE	80% CI	90% CI	PD	ESS	Rhat	MCSE
Coleoptera	Fly (Vane)	SPL x Freq. interaction	-0.59	0.55	[-1.3, 0.09]	[-1.51, 0.27]	0.869	6420	1.000	0.007
Coleoptera	Malaise	Sound pressure level (SPL)	0.00	0.33	[-0.44, 0.44]	[-0.61, 0.55]	0.503	3881	1.001	0.006
Coleoptera	Malaise	Background frequency (Freq.)	-0.09	0.30	[-0.48, 0.30]	[-0.59, 0.42]	0.623	5435	1.000	0.004
Coleoptera	Malaise	Ordinal day	0.05	0.37	[-0.40, 0.54]	[-0.59, 0.63]	0.551	5643	1.000	0.005
Coleoptera	Malaise	Vegetation	-0.17	0.32	[-0.61, 0.22]	[-0.72, 0.35]	0.711	4642	1.001	0.005
Coleoptera	Malaise	Elevation	-0.72	0.31	[-1.13, -0.33]	[-1.25, -0.22]	0.986	4792	1.001	0.005
Coleoptera	Malaise	Moon Illuminance	0.18	0.22	[-0.11, 0.46]	[-0.16, 0.58]	0.800	7630	1.000	0.003
Coleoptera	Malaise	Temperature	0.85	0.42	[0.34, 1.41]	[0.13, 1.51]	0.981	4852	1.000	0.006
Coleoptera	Malaise	Year (2018)	0.10	0.23	[-0.18, 0.41]	[-0.26, 0.50]	0.672	7728	1.000	0.003
Coleoptera	Malaise	SPL x Freq. interaction	0.03	0.56	[-0.67, 0.75]	[-0.87, 0.97]	0.523	4297	1.001	0.009
Coleoptera	Pitfall	Sound pressure level (SPL)	0.48	0.25	[0.17, 0.82]	[0.04, 0.89]	0.972	6451	1.000	0.003
Coleoptera	Pitfall	Background frequency (Freq.)	-0.02	0.22	[-0.30, 0.28]	[-0.40, 0.35]	0.541	6427	1.000	0.003
Coleoptera	Pitfall	Ordinal day	-0.10	0.28	[-0.46, 0.27]	[-0.57, 0.36]	0.648	6250	1.000	0.004
Coleoptera	Pitfall	Vegetation	0.36	0.25	[0.02, 0.66]	[-0.05, 0.78]	0.922	6877	1.000	0.003

Order	Trap	Parameter	Estimate	SE	80% CI	90% CI	PD	ESS	Rhat	MCSE
Coleoptera	Pitfall	Elevation	-0.37	0.24	[-0.68, -0.06]	[-0.77, 0.05]	0.941	5888	1.001	0.003
Coleoptera	Pitfall	Moon Illuminance	0.12	0.18	[-0.11, 0.35]	[-0.19, 0.41]	0.748	9389	1.000	0.002
Coleoptera	Pitfall	Temperature	0.34	0.30	[-0.02, 0.72]	[-0.12, 0.83]	0.882	5706	1.000	0.004
Coleoptera	Pitfall	Year (2018)	0.25	0.18	[0.01, 0.47]	[-0.05, 0.55]	0.912	9782	1.000	0.002
Coleoptera	Pitfall	SPL x Freq. interaction	-0.18	0.46	[-0.77, 0.39]	[-0.95, 0.56]	0.654	7163	1.000	0.005
Coleoptera	UV	Sound pressure level (SPL)	-0.36	0.50	[-0.97, 0.32]	[-1.23, 0.44]	0.780	2975	1.000	0.009
Coleoptera	UV	Background frequency (Freq.)	-0.13	0.38	[-0.60, 0.40]	[-0.76, 0.55]	0.634	5481	1.000	0.005
Coleoptera	UV	Ordinal day	0.53	0.46	[-0.05, 1.11]	[-0.22, 1.31]	0.873	5631	1.000	0.006
Coleoptera	UV	Vegetation	-0.19	0.43	[-0.75, 0.37]	[-0.92, 0.54]	0.672	4553	1.000	0.007
Coleoptera	UV	Elevation	-1.26	0.42	[-1.86, -0.75]	[-1.99, -0.54]	0.995	4807	1.000	0.006
Coleoptera	UV	Moon Illuminance	-0.01	0.29	[-0.37, 0.38]	[-0.47, 0.48]	0.509	8012	1.000	0.003
Coleoptera	UV	Temperature	1.61	0.53	[0.97, 2.32]	[0.75, 2.51]	0.999	5571	1.000	0.007
Coleoptera	UV	Year (2018)	-0.48	0.32	[-0.89, -0.05]	[-1.01, 0.07]	0.929	6374	1.000	0.004
Coleoptera	UV	SPL x Freq. interaction	1.05	0.81	[-0.01, 2.08]	[-0.34, 2.41]	0.898	3995	1.000	0.013

Order	Trap	Parameter	Estimate	SE	80% CI	90% CI	PD	ESS	Rhat	MCSE
Collembola	Pitfall	Sound pressure level (SPL)	2.43	0.80	[1.43, 3.52]	[1.01, 3.77]	0.999	7097	1.000	0.010
Collembola	Pitfall	Background frequency (Freq.)	-1.14	1.11	[-2.61, 0.22]	[-2.85, 0.85]	0.844	5275	1.000	0.015
Collembola	Pitfall	Ordinal day	0.03	1.15	[-1.41, 1.58]	[-1.95, 1.90]	0.509	4593	1.001	0.017
Collembola	Pitfall	Vegetation	-0.23	1.00	[-1.61, 0.98]	[-1.86, 1.46]	0.593	4793	1.000	0.015
Collembola	Pitfall	Elevation	-2.73	1.24	[-4.20, -1.05]	[-4.77, -0.70]	0.986	6263	1.000	0.016
Collembola	Pitfall	Moon Illuminance	0.63	1.00	[-0.74, 1.81]	[-1.02, 2.29]	0.739	5582	1.000	0.014
Collembola	Pitfall	Temperature	-1.10	1.29	[-2.70, 0.69]	[-3.26, 1.06]	0.794	4031	1.001	0.021
Collembola	Pitfall	Year (2018)	2.41	1.00	[1.07, 3.61]	[0.80, 4.08]	0.991	6360	1.001	0.013
Collembola	Pitfall	SPL x Freq. interaction	-2.52	1.98	[-5.12, -0.06]	[-5.92, 0.63]	0.907	6232	1.000	0.025
Dermaptera	Pitfall	Sound pressure level (SPL)	2.59	1.08	[1.07, 3.88]	[0.83, 4.45]	0.993	5849	1.000	0.015
Dermaptera	Pitfall	Background frequency (Freq.)	-1.24	0.84	[-2.32, -0.14]	[-2.67, 0.13]	0.927	4774	1.000	0.012
Dermaptera	Pitfall	Ordinal day	1.92	1.10	[0.49, 3.37]	[0.04, 3.81]	0.952	6489	1.000	0.014
Dermaptera	Pitfall	Vegetation	2.79	1.10	[1.29, 4.17]	[1.04, 4.80]	0.996	5564	1.000	0.016
Dermaptera	Pitfall	Elevation	-3.41	1.05	[-4.76, -2.09]	[-5.23, -1.78]	1.000	4889	1.000	0.015

Order	Trap	Parameter	Estimate	SE	80% CI	90% CI	PD	ESS	Rhat	MCSE
Dermaptera	Pitfall	Moon Illuminance	0.91	0.50	[0.28, 1.54]	[0.15, 1.80]	0.972	5508	1.001	0.007
Dermaptera	Pitfall	Temperature	-0.05	1.20	[-1.54, 1.58]	[-2.06, 1.97]	0.516	5770	1.000	0.016
Dermaptera	Pitfall	Year (2018)	-0.03	0.71	[-0.92, 0.89]	[-1.20, 1.16]	0.515	7103	1.000	0.009
Dermaptera	Pitfall	SPL x Freq. interaction	-0.21	1.65	[-2.31, 2]	[-3.01, 2.66]	0.553	6485	1.000	0.022
Dermaptera	UV	Sound pressure level (SPL)	1.80	1.20	[0.24, 3.39]	[-0.16, 3.92]	0.934	3803	1.000	0.020
Dermaptera	UV	Background frequency (Freq.)	1.10	0.92	[-0.14, 2.24]	[-0.36, 2.75]	0.887	4956	1.002	0.013
Dermaptera	UV	Ordinal day	2.83	1.33	[1.16, 4.59]	[0.55, 4.97]	0.993	4109	1.001	0.021
Dermaptera	UV	Vegetation	0.24	1.07	[-1.10, 1.67]	[-1.56, 2.04]	0.590	6369	1.000	0.014
Dermaptera	UV	Elevation	-1.77	1.03	[-3.10, -0.43]	[-3.50, -0.01]	0.953	5394	1.001	0.015
Dermaptera	UV	Moon Illuminance	-0.18	0.70	[-1.03, 0.80]	[-1.35, 1.02]	0.606	6994	1.000	0.009
Dermaptera	UV	Temperature	0.03	1.04	[-1.36, 1.37]	[-1.75, 1.80]	0.510	5343	1.001	0.015
Dermaptera	UV	Year (2018)	0.26	0.85	[-0.78, 1.43]	[-1.18, 1.73]	0.621	5077	1.002	0.013
Dermaptera	UV	SPL x Freq. interaction	2.07	1.56	[-0.01, 4.08]	[-0.61, 4.73]	0.899	6394	1.000	0.020
Diptera	Beat-net	Sound pressure level (SPL)	0.21	0.54	[-0.47, 0.94]	[-0.70, 1.14]	0.645	5798	1.001	0.007

Order	Trap	Parameter	Estimate	SE	80% CI	90% CI	PD	ESS	Rhat	MCSE
Diptera	Beat-net	Background frequency (Freq.)	0.01	0.49	[-0.65, 0.61]	[-0.80, 0.83]	0.505	6864	1.000	0.006
Diptera	Beat-net	Ordinal day	0.89	0.66	[0.05, 1.72]	[-0.17, 1.96]	0.915	6994	1.000	0.008
Diptera	Beat-net	Vegetation	0.65	0.43	[0.09, 1.23]	[-0.12, 1.38]	0.926	6800	1.000	0.006
Diptera	Beat-net	Elevation	-0.24	0.44	[-0.79, 0.35]	[-0.99, 0.49]	0.707	7477	1.000	0.005
Diptera	Beat-net	Moon Illuminance	-0.14	0.38	[-0.60, 0.37]	[-0.72, 0.53]	0.639	9226	1.000	0.004
Diptera	Beat-net	Temperature	-1.03	0.61	[-1.82, -0.23]	[-2.04, 0.01]	0.951	6798	1.000	0.008
Diptera	Beat-net	Year (2018)	-0.77	0.39	[-1.25, -0.25]	[-1.42, -0.12]	0.973	6676	1.000	0.005
Diptera	Beat-net	SPL x Freq. interaction	0.72	0.94	[-0.51, 1.91]	[-0.86, 2.24]	0.777	7824	1.000	0.011
Diptera	Fly (Vane)	Sound pressure level (SPL)	-0.13	0.29	[-0.49, 0.26]	[-0.62, 0.35]	0.679	3861	1.000	0.005
Diptera	Fly (Vane)	Background frequency (Freq.)	-0.18	0.30	[-0.55, 0.19]	[-0.62, 0.34]	0.725	4967	1.000	0.004
Diptera	Fly (Vane)	Ordinal day	0.98	0.35	[0.54, 1.45]	[0.41, 1.56]	0.997	4279	1.000	0.005
Diptera	Fly (Vane)	Vegetation	0.22	0.31	[-0.17, 0.64]	[-0.32, 0.72]	0.759	3883	1.001	0.005
Diptera	Fly (Vane)	Elevation	-0.08	0.31	[-0.47, 0.33]	[-0.61, 0.42]	0.601	4431	1.000	0.005
Diptera	Fly (Vane)	Moon Illuminance	0.86	0.22	[0.60, 1.15]	[0.51, 1.23]	1.000	5739	1.000	0.003

Order	Trap	Parameter	Estimate	SE	80% CI	90% CI	PD	ESS	Rhat	MCSE
Diptera	Fly (Vane)	Temperature	-0.25	0.37	[-0.73, 0.22]	[-0.86, 0.34]	0.749	4507	1.000	0.006
Diptera	Fly (Vane)	Year (2018)	-0.36	0.23	[-0.65, -0.07]	[-0.72, 0.02]	0.946	6261	1.000	0.003
Diptera	Fly (Vane)	SPL x Freq. interaction	0.15	0.52	[-0.53, 0.82]	[-0.74, 1.00]	0.618	5759	1.000	0.007
Diptera	Malaise	Sound pressure level (SPL)	-0.12	0.38	[-0.59, 0.39]	[-0.72, 0.55]	0.624	3898	1.001	0.006
Diptera	Malaise	Background frequency (Freq.)	-0.04	0.36	[-0.48, 0.43]	[-0.66, 0.52]	0.545	5554	1.000	0.005
Diptera	Malaise	Ordinal day	0.74	0.43	[0.17, 1.28]	[0.05, 1.47]	0.952	4426	1.000	0.007
Diptera	Malaise	Vegetation	-0.42	0.34	[-0.89, 0.00]	[-1.03, 0.15]	0.892	4342	1.000	0.005
Diptera	Malaise	Elevation	-0.14	0.39	[-0.64, 0.36]	[-0.77, 0.52]	0.630	5590	1.000	0.005
Diptera	Malaise	Moon Illuminance	1.08	0.32	[0.66, 1.47]	[0.54, 1.59]	1.000	7318	1.000	0.004
Diptera	Malaise	Temperature	0.59	0.49	[-0.06, 1.20]	[-0.23, 1.37]	0.883	4453	1.000	0.007
Diptera	Malaise	Year (2018)	-0.39	0.29	[-0.78, -0.02]	[-0.88, 0.11]	0.912	5478	1.000	0.004
Diptera	Malaise	SPL x Freq. interaction	-0.74	0.63	[-1.58, 0.08]	[-1.82, 0.32]	0.880	6366	1.001	0.008
Diptera	UV	Sound pressure level (SPL)	-0.12	0.66	[-1.03, 0.68]	[-1.24, 0.95]	0.570	3178	1.000	0.012
Diptera	UV	Background frequency (Freq.)	-0.10	0.47	[-0.71, 0.48]	[-0.86, 0.66]	0.582	5620	1.000	0.006

Order	Trap	Parameter	Estimate	SE	80% CI	90% CI	PD	ESS	Rhat	MCSE
Diptera	UV	Ordinal day	2.26	0.53	[1.57, 2.94]	[1.37, 3.15]	1.000	5351	1.001	0.007
Diptera	UV	Vegetation	-0.15	0.52	[-0.87, 0.50]	[-1.13, 0.69]	0.625	4205	1.000	0.009
Diptera	UV	Elevation	-0.44	0.58	[-1.26, 0.24]	[-1.37, 0.58]	0.776	4911	1.000	0.009
Diptera	UV	Moon Illuminance	0.52	0.34	[0.08, 0.95]	[-0.07, 1.07]	0.939	7973	1.000	0.004
Diptera	UV	Temperature	0.20	0.60	[-0.59, 0.99]	[-0.82, 1.20]	0.631	4949	1.000	0.009
Diptera	UV	Year (2018)	-0.39	0.37	[-0.86, 0.10]	[-1.00, 0.26]	0.852	6261	1.000	0.005
Diptera	UV	SPL x Freq. interaction	0.23	0.95	[-1.02, 1.44]	[-1.36, 1.81]	0.593	5665	1.000	0.013
Hemiptera	Beat-net	Sound pressure level (SPL)	-0.12	0.49	[-0.76, 0.49]	[-0.89, 0.74]	0.602	5968	1.000	0.006
Hemiptera	Beat-net	Background frequency (Freq.)	0.04	0.44	[-0.50, 0.62]	[-0.68, 0.75]	0.537	7047	1.000	0.005
Hemiptera	Beat-net	Ordinal day	-0.63	0.52	[-1.32, 0.02]	[-1.48, 0.26]	0.888	5665	1.000	0.007
Hemiptera	Beat-net	Vegetation	0.23	0.39	[-0.25, 0.75]	[-0.40, 0.90]	0.729	7061	1.000	0.005
Hemiptera	Beat-net	Elevation	-0.39	0.40	[-0.89, 0.16]	[-1.09, 0.27]	0.831	6920	1.000	0.005
Hemiptera	Beat-net	Moon Illuminance	-0.12	0.33	[-0.56, 0.29]	[-0.67, 0.44]	0.637	9690	1.000	0.003
Hemiptera	Beat-net	Temperature	0.37	0.55	[-0.35, 1.09]	[-0.58, 1.28]	0.753	5279	1.000	0.008

Order	Trap	Parameter	Estimate	SE	80% CI	90% CI	PD	ESS	Rhat	MCSE
Hemiptera	Beat-net	Year (2018)	-0.53	0.37	[-1.02, -0.09]	[-1.14, 0.06]	0.926	7821	1.000	0.004
Hemiptera	Beat-net	SPL x Freq. interaction	1.91	0.95	[0.66, 3.13]	[0.31, 3.45]	0.974	6923	1.000	0.012
Hemiptera	Fly (Vane)	Sound pressure level (SPL)	0.28	0.43	[-0.30, 0.79]	[-0.42, 0.99]	0.743	6824	1.000	0.005
Hemiptera	Fly (Vane)	Background frequency (Freq.)	-0.47	0.34	[-0.92, -0.02]	[-1.05, 0.11]	0.909	7587	1.000	0.004
Hemiptera	Fly (Vane)	Ordinal day	0.03	0.49	[-0.59, 0.69]	[-0.84, 0.82]	0.527	7877	1.000	0.006
Hemiptera	Fly (Vane)	Vegetation	0.09	0.37	[-0.37, 0.60]	[-0.54, 0.70]	0.593	7818	1.000	0.004
Hemiptera	Fly (Vane)	Elevation	-0.90	0.42	[-1.43, -0.37]	[-1.62, -0.25]	0.986	7315	1.001	0.005
Hemiptera	Fly (Vane)	Moon Illuminance	-0.12	0.27	[-0.48, 0.22]	[-0.57, 0.34]	0.672	9237	1.000	0.003
Hemiptera	Fly (Vane)	Temperature	0.72	0.53	[0.04, 1.40]	[-0.19, 1.56]	0.917	7122	1.000	0.006
Hemiptera	Fly (Vane)	Year (2018)	0.02	0.29	[-0.39, 0.36]	[-0.46, 0.49]	0.529	10080	1.000	0.003
Hemiptera	Fly (Vane)	SPL x Freq. interaction	-1.00	0.66	[-1.87, -0.18]	[-2.13, 0.08]	0.936	8690	1.000	0.007
Hemiptera	Malaise	Sound pressure level (SPL)	-0.08	0.62	[-0.93, 0.66]	[-1.17, 0.91]	0.556	3308	1.003	0.011
Hemiptera	Malaise	Background frequency (Freq.)	0.44	0.50	[-0.25, 1.06]	[-0.40, 1.29]	0.805	5136	1.000	0.007
Hemiptera	Malaise	Ordinal day	0.30	0.53	[-0.40, 0.96]	[-0.54, 1.21]	0.710	5983	1.001	0.007

Order	Trap	Parameter	Estimate	SE	80% CI	90% CI	PD	ESS	Rhat	MCSE
Hemiptera	Malaise	Vegetation	0.12	0.64	[-0.70, 0.91]	[-0.93, 1.15]	0.570	4224	1.001	0.010
Hemiptera	Malaise	Elevation	-0.28	0.62	[-1.11, 0.52]	[-1.37, 0.73]	0.674	4246	1.000	0.010
Hemiptera	Malaise	Moon Illuminance	0.43	0.31	[0.04, 0.84]	[-0.08, 0.95]	0.924	7663	1.000	0.004
Hemiptera	Malaise	Temperature	0.93	0.61	[0.06, 1.68]	[-0.11, 2.00]	0.923	5397	1.001	0.009
Hemiptera	Malaise	Year (2018)	0.34	0.32	[-0.08, 0.75]	[-0.20, 0.89]	0.859	7035	1.000	0.004
Hemiptera	Malaise	SPL x Freq. interaction	0.97	0.87	[-0.17, 2.07]	[-0.50, 2.39]	0.864	6395	1.001	0.011
Hemiptera	Pitfall	Sound pressure level (SPL)	0.41	0.35	[-0.04, 0.85]	[-0.17, 0.99]	0.881	6865	1.000	0.004
Hemiptera	Pitfall	Background frequency (Freq.)	-0.65	0.30	[-1.03, -0.26]	[-1.15, -0.16]	0.984	7840	1.000	0.003
Hemiptera	Pitfall	Ordinal day	0.73	0.43	[0.20, 1.28]	[0.08, 1.46]	0.959	7273	1.000	0.005
Hemiptera	Pitfall	Vegetation	1.58	0.32	[1.19, 2.03]	[1.03, 2.11]	1.000	7005	1.000	0.004
Hemiptera	Pitfall	Elevation	-0.80	0.31	[-1.18, -0.37]	[-1.31, -0.27]	0.994	6358	1.000	0.004
Hemiptera	Pitfall	Moon Illuminance	0.54	0.24	[0.22, 0.84]	[0.15, 0.95]	0.987	8615	1.000	0.003
Hemiptera	Pitfall	Temperature	-0.01	0.42	[-0.53, 0.54]	[-0.70, 0.69]	0.510	6447	1.000	0.005
Hemiptera	Pitfall	Year (2018)	-0.46	0.25	[-0.77, -0.12]	[-0.86, -0.03]	0.962	7873	1.000	0.003

Order	Trap	Parameter	Estimate	SE	80% CI	90% CI	PD	ESS	Rhat	MCSE
Hemiptera	Pitfall	SPL x Freq. interaction	0.45	0.60	[-0.38, 1.22]	[-0.63, 1.44]	0.770	8353	1.000	0.007
Hemiptera	UV	Sound pressure level (SPL)	1.01	0.64	[0.16, 1.79]	[-0.07, 2.04]	0.938	4684	1.001	0.010
Hemiptera	UV	Background frequency (Freq.)	0.52	0.48	[-0.08, 1.15]	[-0.31, 1.28]	0.859	8660	1.000	0.005
Hemiptera	UV	Ordinal day	1.32	0.66	[0.48, 2.16]	[0.27, 2.45]	0.977	6806	1.000	0.008
Hemiptera	UV	Vegetation	0.17	0.54	[-0.51, 0.90]	[-0.69, 1.12]	0.629	7274	1.000	0.007
Hemiptera	UV	Elevation	-1.09	0.53	[-1.78, -0.42]	[-1.99, -0.24]	0.977	7106	1.000	0.006
Hemiptera	UV	Moon Illuminance	0.13	0.39	[-0.34, 0.67]	[-0.52, 0.78]	0.637	9940	1.000	0.004
Hemiptera	UV	Temperature	1.74	0.75	[0.80, 2.71]	[0.44, 2.90]	0.991	7161	1.000	0.009
Hemiptera	UV	Year (2018)	0.47	0.44	[-0.10, 1.03]	[-0.23, 1.21]	0.862	6686	1.000	0.005
Hemiptera	UV	SPL x Freq. interaction	-0.43	1.08	[-1.85, 1.01]	[-2.27, 1.43]	0.655	5167	1.000	0.016
Hymenoptera	Beat-net	Sound pressure level (SPL)	-0.55	0.52	[-1.20, 0.12]	[-1.45, 0.27]	0.861	7071	1.000	0.006
Hymenoptera	Beat-net	Background frequency (Freq.)	-0.61	0.48	[-1.24, -0.02]	[-1.36, 0.22]	0.902	8120	1.001	0.005
Hymenoptera	Beat-net	Ordinal day	0.68	0.55	[0.02, 1.42]	[-0.23, 1.58]	0.895	7205	1.001	0.007
Hymenoptera	Beat-net	Vegetation	0.86	0.45	[0.28, 1.44]	[0.13, 1.63]	0.971	7300	1.000	0.005

Order	Trap	Parameter	Estimate	SE	80% CI	90% CI	PD	ESS	Rhat	MCSE
Hymenoptera	Beat-net	Elevation	-0.18	0.40	[-0.69, 0.36]	[-0.87, 0.51]	0.678	7085	1.000	0.005
Hymenoptera	Beat-net	Moon Illuminance	-0.07	0.38	[-0.55, 0.41]	[-0.70, 0.53]	0.573	11068	1.000	0.004
Hymenoptera	Beat-net	Temperature	-0.11	0.53	[-0.78, 0.60]	[-1.01, 0.75]	0.582	7241	1.000	0.006
Hymenoptera	Beat-net	Year (2018)	-0.75	0.35	[-1.18, -0.31]	[-1.34, -0.21]	0.986	9519	1.000	0.004
Hymenoptera	Beat-net	SPL x Freq. interaction	1.96	1.02	[0.67, 3.32]	[0.27, 3.68]	0.972	8651	1.000	0.011
Hymenoptera	Fly (Vane)	Sound pressure level (SPL)	0.13	0.26	[-0.20, 0.48]	[-0.32, 0.55]	0.695	6012	1.000	0.003
Hymenoptera	Fly (Vane)	Background frequency (Freq.)	-0.59	0.23	[-0.87, -0.30]	[-0.96, -0.21]	0.997	6110	1.000	0.003
Hymenoptera	Fly (Vane)	Ordinal day	0.03	0.29	[-0.33, 0.41]	[-0.42, 0.53]	0.544	6061	1.001	0.004
Hymenoptera	Fly (Vane)	Vegetation	0.21	0.23	[-0.07, 0.54]	[-0.15, 0.62]	0.819	5191	1.000	0.003

Order	Trap	Parameter	Estimate	SE	80% CI	90% CI	PD	ESS	Rhat	MCSE
Hymenoptera	Fly (Vane)	Elevation	-0.74	0.27	[-1.08, -0.39]	[-1.20, -0.31]	0.997	5535	1.001	0.004
Hymenoptera	Fly (Vane)	Moon Illuminance	0.16	0.20	[-0.11, 0.42]	[-0.19, 0.49]	0.786	8754	1.000	0.002
Hymenoptera	Fly (Vane)	Temperature	0.78	0.30	[0.41, 1.19]	[0.27, 1.28]	0.994	5756	1.001	0.004
Hymenoptera	Fly (Vane)	Year (2018)	-0.30	0.20	[-0.54, -0.05]	[-0.64, 0.00]	0.939	8563	1.000	0.002
Hymenoptera	Fly (Vane)	SPL x Freq. interaction	-0.29	0.44	[-0.89, 0.24]	[-1.08, 0.41]	0.757	6161	1.000	0.006
Hymenoptera	Malaise	Sound pressure level	-0.09	0.35	[-0.59, 0.34]	[-0.70, 0.52]	0.595	4955	1.000	0.005
Hymenoptera	Malaise	Background frequency	-0.25	0.31	[-0.66, 0.16]	[-0.77, 0.30]	0.782	5076	1.000	0.005
Hymenoptera	Malaise	Ordinal day	0.30	0.35	[-0.17, 0.74]	[-0.28, 0.90]	0.803	4876	1.000	0.005
Hymenoptera	Malaise	Vegetation	-0.18	0.33	[-0.63, 0.24]	[-0.75, 0.41]	0.705	4688	1.000	0.005
Hymenoptera	Malaise	Elevation	-0.12	0.35	[-0.56, 0.33]	[-0.73, 0.42]	0.637	4719	1.000	0.005

Order	Trap	Parameter	Estimate	SE	80% CI	90% CI	PD	ESS	Rhat	MCSE
Hymenoptera	Malaise	Moon Illuminance	0.53	0.24	[0.22, 0.84]	[0.13, 0.93]	0.988	7115	1.000	0.003
Hymenoptera	Malaise	Temperature	0.81	0.40	[0.28, 1.31]	[0.12, 1.46]	0.979	5086	1.000	0.006
Hymenoptera	Malaise	Year (2018)	0.31	0.25	[-0.02, 0.64]	[-0.15, 0.72]	0.878	6675	1.000	0.003
Hymenoptera	Malaise	SPL x Freq. interaction	0.27	0.59	[-0.51, 1.04]	[-0.73, 1.24]	0.675	6827	1.000	0.007
Hymenoptera	Pitfall	Sound pressure level (SPL)	0.09	0.51	[-0.59, 0.72]	[-0.81, 0.90]	0.575	4379	1.000	0.008
Hymenoptera	Pitfall	Background frequency (Freq.)	-0.62	0.40	[-1.14, -0.09]	[-1.28, 0.07]	0.932	5847	1.000	0.005
Hymenoptera	Pitfall	Ordinal day	0.90	0.44	[0.33, 1.46]	[0.19, 1.63]	0.974	5954	1.000	0.006
Hymenoptera	Pitfall	Vegetation	1.52	0.53	[0.83, 2.19]	[0.60, 2.36]	0.996	4248	1.001	0.008
Hymenoptera	Pitfall	Elevation	-0.40	0.53	[-1.10, 0.27]	[-1.27, 0.51]	0.779	4252	1.000	0.008
Hymenoptera	Pitfall	Moon Illuminance	0.20	0.30	[-0.17, 0.60]	[-0.27, 0.72]	0.761	7537	1.000	0.003

Order	Trap	Parameter	Estimate	SE	80% CI	90% CI	PD	ESS	Rhat	MCSE
Hymenoptera	Pitfall	Temperature	0.21	0.49	[-0.48, 0.80]	[-0.61, 1.03]	0.660	5412	1.000	0.007
Hymenoptera	Pitfall	Year (2018)	-0.58	0.32	[-0.97, -0.19]	[-1.12, -0.10]	0.969	7321	1.000	0.004
Hymenoptera	Pitfall	SPL x Freq. interaction	1.09	0.81	[0, 2.15]	[-0.33, 2.42]	0.899	6345	1.000	0.010
Hymenoptera	UV	Sound pressure level (SPL)	0.29	0.55	[-0.41, 0.99]	[-0.62, 1.20]	0.705	4242	1.000	0.009
Hymenoptera	UV	Background frequency (Freq.)	0.09	0.40	[-0.42, 0.60]	[-0.56, 0.73]	0.596	5258	1.000	0.005
Hymenoptera	UV	Ordinal day	1.11	0.40	[0.63, 1.65]	[0.47, 1.79]	0.995	5886	1.000	0.005
Hymenoptera	UV	Vegetation	-0.09	0.53	[-0.80, 0.58]	[-1.01, 0.79]	0.568	4344	1.000	0.008
Hymenoptera	UV	Elevation	-0.11	0.50	[-0.81, 0.51]	[-1.01, 0.73]	0.586	4025	1.000	0.008
Hymenoptera	UV	Moon Illuminance	0.33	0.28	[-0.02, 0.69]	[-0.12, 0.80]	0.886	6889	1.000	0.003
Hymenoptera	UV	Temperature	1.06	0.48	[0.46, 1.71]	[0.26, 1.86]	0.985	5373	1.000	0.007
Hymenoptera	UV	Year (2018)	0.88	0.29	[0.52, 1.28]	[0.39, 1.37]	0.999	6006	1.000	0.004
Hymenoptera	UV	SPL x Freq. interaction	0.02	0.79	[-1.04, 1.01]	[-1.33, 1.31]	0.507	5472	1.000	0.011

Order	Trap	Parameter	Estimate	SE	80% CI	90% CI	PD	ESS	Rhat	MCSE
Lep. larvae	Beat-net	Sound pressure level (SPL)	0.54	0.69	[-0.36, 1.40]	[-0.61, 1.66]	0.784	5871	1.001	0.009
Lep. larvae	Beat-net	Background frequency (Freq.)	0.44	0.51	[-0.24, 1.04]	[-0.35, 1.33]	0.810	6167	1.000	0.007
Lep. larvae	Beat-net	Ordinal day	-0.46	0.65	[-1.28, 0.38]	[-1.57, 0.62]	0.759	4992	1.001	0.009
Lep. larvae	Beat-net	Vegetation	-0.51	0.58	[-1.28, 0.25]	[-1.54, 0.45]	0.804	5396	1.000	0.008
Lep. larvae	Beat-net	Elevation	-0.62	0.51	[-1.26, 0.05]	[-1.48, 0.22]	0.889	6095	1.001	0.007
Lep. larvae	Beat-net	Moon Illuminance	-0.03	0.48	[-0.67, 0.58]	[-0.84, 0.77]	0.523	6750	1.000	0.006
Lep. larvae	Beat-net	Temperature	0.09	0.64	[-0.72, 0.94]	[-0.98, 1.15]	0.556	4941	1.000	0.009
Lep. larvae	Beat-net	Year (2018)	-1.16	0.43	[-1.71, -0.61]	[-1.86, -0.45]	0.995	7392	1.000	0.005
Lep. larvae	Beat-net	SPL x Freq. interaction	-1.76	1.16	[-3.37, -0.29]	[-3.87, 0.12]	0.938	6770	1.000	0.015
Lepidoptera	Fly (Vane)	Sound pressure level (SPL)	0.38	0.61	[-0.45, 1.13]	[-0.71, 1.33]	0.728	5398	1.001	0.008
Lepidoptera	Fly (Vane)	Background frequency (Freq.)	0.13	0.48	[-0.50, 0.73]	[-0.68, 0.92]	0.613	6204	1.000	0.006
Lepidoptera	Fly (Vane)	Ordinal day	3.21	0.80	[2.16, 4.17]	[1.91, 4.48]	1.000	5963	1.001	0.010
Lepidoptera	Fly (Vane)	Vegetation	0.90	0.55	[0.20, 1.59]	[0.01, 1.79]	0.954	5228	1.000	0.008

Order	Trap	Parameter	Estimate	SE	80% CI	90% CI	PD	ESS	Rhat	MCSE
Lepidoptera	Fly (Vane)	Elevation	-0.80	0.57	[-1.48, -0.01]	[-1.80, 0.10]	0.924	4546	1.000	0.009
Lepidoptera	Fly (Vane)	Moon Illuminance	0.22	0.40	[-0.32, 0.69]	[-0.45, 0.86]	0.708	6599	1.000	0.005
Lepidoptera	Fly (Vane)	Temperature	0.02	0.69	[-0.85, 0.91]	[-1.07, 1.19]	0.512	5137	1.001	0.010
Lepidoptera	Fly (Vane)	Year (2018)	0.41	0.41	[-0.08, 0.97]	[-0.23, 1.11]	0.838	7055	1.000	0.005
Lepidoptera	Fly (Vane)	SPL x Freq. interaction	-1.23	0.93	[-2.49, -0.1]	[-2.85, 0.22]	0.917	7153	1.000	0.011
Lepidoptera	Malaise	Sound pressure level (SPL)	0.54	0.44	[-0.03, 1.09]	[-0.23, 1.25]	0.887	6310	1.000	0.006
Lepidoptera	Malaise	Background frequency (Freq.)	-0.41	0.38	[-0.89, 0.08]	[-1.05, 0.22]	0.862	6832	1.000	0.005
Lepidoptera	Malaise	Ordinal day	1.34	0.48	[0.77, 1.98]	[0.54, 2.09]	0.996	7091	1.000	0.006
Lepidoptera	Malaise	Vegetation	-0.09	0.38	[-0.61, 0.37]	[-0.71, 0.55]	0.597	6851	1.000	0.005
Lepidoptera	Malaise	Elevation	-0.95	0.45	[-1.49, -0.34]	[-1.66, -0.16]	0.984	6490	1.000	0.006
Lepidoptera	Malaise	Moon Illuminance	-0.09	0.31	[-0.50, 0.28]	[-0.60, 0.43]	0.614	9872	1.000	0.003
Lepidoptera	Malaise	Temperature	1.36	0.55	[0.63, 2.01]	[0.48, 2.25]	0.996	6226	1.000	0.007
Lepidoptera	Malaise	Year (2018)	-0.10	0.32	[-0.52, 0.29]	[-0.60, 0.46]	0.626	7098	1.000	0.004
Lepidoptera	Malaise	SPL x Freq. interaction	-0.75	0.69	[-1.7, 0.12]	[-1.99, 0.37]	0.864	9262	1.000	0.007

Order	Trap	Parameter	Estimate	SE	80% CI	90% CI	PD	ESS	Rhat	MCSE
Lepidoptera	UV	Sound pressure level (SPL)	0.27	0.49	[-0.32, 0.93]	[-0.56, 1.07]	0.706	2832	1.000	0.009
Lepidoptera	UV	Background frequency (Freq.)	0.04	0.33	[-0.40, 0.44]	[-0.50, 0.58]	0.548	6782	1.000	0.004
Lepidoptera	UV	Ordinal day	0.63	0.35	[0.19, 1.10]	[0.06, 1.23]	0.959	6669	1.000	0.004
Lepidoptera	UV	Vegetation	0.10	0.41	[-0.42, 0.66]	[-0.64, 0.77]	0.598	4643	1.000	0.006
Lepidoptera	UV	Elevation	-0.80	0.44	[-1.42, -0.27]	[-1.52, -0.02]	0.951	4237	1.000	0.007
Lepidoptera	UV	Moon Illuminance	-0.33	0.24	[-0.64, -0.04]	[-0.72, 0.05]	0.914	9105	1.000	0.003
Lepidoptera	UV	Temperature	1.25	0.38	[0.74, 1.70]	[0.61, 1.85]	0.999	6265	1.000	0.005
Lepidoptera	UV	Year (2018)	-0.04	0.26	[-0.38, 0.29]	[-0.47, 0.38]	0.564	6830	1.001	0.003
Lepidoptera	UV	SPL x Freq. interaction	-0.38	0.73	[-1.28, 0.53]	[-1.55, 0.80]	0.698	4455	1.000	0.011
Neuroptera	UV	Sound pressure level (SPL)	-1.14	1.09	[-2.52, 0.33]	[-2.99, 0.71]	0.844	4900	1.000	0.016
Neuroptera	UV	Background frequency (Freq.)	2.09	1.03	[0.78, 3.48]	[0.36, 3.87]	0.980	3985	1.000	0.017
Neuroptera	UV	Ordinal day	3.36	1.44	[1.41, 5.13]	[1.00, 5.81]	0.992	5112	1.001	0.021
Neuroptera	UV	Vegetation	-3.27	1.31	[-4.85, -1.45]	[-5.51, -1.12]	0.996	4391	1.000	0.020
Neuroptera	UV	Elevation	-0.81	0.99	[-2.17, 0.45]	[-2.50, 0.97]	0.794	5499	1.000	0.014

Order	Trap	Parameter	Estimate	SE	80% CI	90% CI	PD	ESS	Rhat	MCSE
Neuroptera	UV	Moon Illuminance	-2.19	1.12	[-3.60, -0.68]	[-4.12, -0.37]	0.980	3433	1.000	0.020
Neuroptera	UV	Temperature	3.41	1.62	[1.29, 5.51]	[0.77, 6.24]	0.984	4819	1.001	0.024
Neuroptera	UV	Year (2018)	0.37	0.81	[-0.69, 1.45]	[-0.94, 1.87]	0.679	5741	1.001	0.011
Neuroptera	UV	SPL x Freq. interaction	1.12	1.89	[-1.42, 3.56]	[-2.27, 4.23]	0.716	5495	1.000	0.027
Opiliones	Pitfall	Sound pressure level (SPL)	2.09	0.78	[1.07, 3.06]	[0.89, 3.50]	0.998	4594	1.000	0.012
Opiliones	Pitfall	Background frequency (Freq.)	0.87	0.63	[0.07, 1.66]	[-0.14, 1.91]	0.921	6454	1.000	0.008
Opiliones	Pitfall	Ordinal day	3.20	0.98	[1.94, 4.48]	[1.53, 4.85]	0.999	3958	1.001	0.016
Opiliones	Pitfall	Vegetation	1.72	0.76	[0.76, 2.68]	[0.54, 3.05]	0.991	5051	1.000	0.011
Opiliones	Pitfall	Elevation	-2.84	0.78	[-3.83, -1.82]	[-4.19, -1.58]	1.000	5787	1.000	0.010
Opiliones	Pitfall	Moon Illuminance	0.22	0.49	[-0.46, 0.83]	[-0.66, 1.03]	0.672	6562	1.000	0.006
Opiliones	Pitfall	Temperature	-1.82	0.92	[-3.05, -0.68]	[-3.30, -0.26]	0.979	3991	1.001	0.015
Opiliones	Pitfall	Year (2018)	1.30	0.54	[0.56, 1.94]	[0.46, 2.24]	0.993	5572	1.001	0.007
Opiliones	Pitfall	SPL x Freq. interaction	-1.55	1.15	[-3.1, -0.12]	[-3.60, 0.28]	0.917	5617	1.000	0.016
Orthoptera	Pitfall	Sound pressure level (SPL)	0.20	1.02	[-1.02, 1.65]	[-1.55, 1.96]	0.578	2313	1.001	0.023

Order	Trap	Parameter	Estimate	SE	80% CI	90% CI	PD	ESS	Rhat	MCSE
Orthoptera	Pitfall	Background frequency (Freq.)	-1.70	0.84	[-2.78, -0.60]	[-3.05, -0.23]	0.979	3148	1.001	0.015
Orthoptera	Pitfall	Ordinal day	0.92	1.01	[-0.34, 2.28]	[-0.83, 2.56]	0.823	4338	1.001	0.016
Orthoptera	Pitfall	Vegetation	2.52	0.93	[1.39, 3.81]	[0.91, 4.06]	0.992	2552	1.001	0.019
Orthoptera	Pitfall	Elevation	-0.84	0.87	[-1.94, 0.29]	[-2.31, 0.61]	0.839	5848	1.000	0.012
Orthoptera	Pitfall	Moon Illuminance	0.80	0.61	[-0.03, 1.54]	[-0.21, 1.82]	0.919	6422	1.000	0.008
Orthoptera	Pitfall	Temperature	1.03	1.13	[-0.39, 2.50]	[-0.79, 2.90]	0.824	4568	1.001	0.017
Orthoptera	Pitfall	Year (2018)	0.16	0.66	[-0.74, 0.98]	[-1.02, 1.19]	0.595	6481	1.000	0.008
Orthoptera	Pitfall	SPL x Freq. interaction	-1.53	1.36	[-3.3, 0.22]	[-3.87, 0.71]	0.870	4064	1.000	0.022
Orthoptera	UV	Sound pressure level (SPL)	1.16	1.36	[-0.67, 2.95]	[-1.11, 3.70]	0.798	3641	1.000	0.025
Orthoptera	UV	Background frequency (Freq.)	-0.55	1.19	[-2.21, 0.95]	[-2.57, 1.55]	0.682	6361	1.000	0.016
Orthoptera	UV	Ordinal day	2.53	1.54	[0.56, 4.53]	[0.04, 5.22]	0.964	6374	1.000	0.020
Orthoptera	UV	Vegetation	0.72	1.27	[-0.98, 2.35]	[-1.44, 2.93]	0.718	5933	1.000	0.018
Orthoptera	UV	Elevation	-1.14	1.11	[-2.53, 0.45]	[-2.98, 0.99]	0.840	5413	1.000	0.016
Orthoptera	UV	Moon Illuminance	-0.68	0.85	[-1.80, 0.39]	[-2.15, 0.70]	0.792	8955	1.000	0.009

Order	Trap	Parameter	Estimate	SE	80% CI	90% CI	PD	ESS	Rhat	MCSE
Orthoptera	UV	Temperature	0.37	1.71	[-2.02, 2.42]	[-2.54, 3.31]	0.589	5070	1.000	0.026
Orthoptera	UV	Year (2018)	2.30	1.07	[0.82, 3.58]	[0.48, 4.05]	0.990	7250	1.001	0.013
Orthoptera	UV	SPL x Freq. interaction	0.63	2.66	[-2.66, 4.19]	[-3.66, 5.39]	0.593	6162	1.001	0.036
Plecoptera	Malaise	Sound pressure level (SPL)	0.00	0.81	[-1.05, 1.02]	[-1.35, 1.36]	0.502	5928	1.000	0.011
Plecoptera	Malaise	Background frequency (Freq.)	0.13	0.77	[-0.81, 1.16]	[-1.17, 1.40]	0.567	5554	1.000	0.011
Plecoptera	Malaise	Ordinal day	-0.70	0.91	[-1.86, 0.49]	[-2.25, 0.78]	0.781	6416	1.000	0.012
Plecoptera	Malaise	Vegetation	-0.97	0.82	[-2.01, 0.08]	[-2.26, 0.49]	0.878	7321	1.000	0.010
Plecoptera	Malaise	Elevation	0.16	0.79	[-0.78, 1.25]	[-1.14, 1.47]	0.580	5289	1.000	0.011
Plecoptera	Malaise	Moon Illuminance	0.68	0.63	[-0.13, 1.50]	[-0.36, 1.74]	0.870	7235	1.000	0.008
Plecoptera	Malaise	Temperature	-0.21	1.01	[-1.49, 1.02]	[-1.76, 1.47]	0.584	5493	1.000	0.013
Plecoptera	Malaise	Year (2018)	-0.12	0.58	[-0.90, 0.59]	[-1.08, 0.84]	0.586	8537	1.000	0.006
Plecoptera	Malaise	SPL x Freq. interaction	-2.59	1.52	[-4.72, -0.77]	[-5.38, -0.28]	0.967	5305	1.000	0.021
Raphidioptera	Malaise	Sound pressure level (SPL)	0.09	0.80	[-0.92, 1.17]	[-1.26, 1.44]	0.543	4005	1.001	0.013
Raphidioptera	Malaise	Background frequency (Freq.)	-2.07	0.80	[-3.04, -0.99]	[-3.38, -0.75]	0.995	5149	1.000	0.011

Order	Trap	Parameter	Estimate	SE	80% CI	90% CI	PD	ESS	Rhat	MCSE
Raphidioptera	Malaise	Ordinal day	2.39	0.83	[1.26, 3.37]	[1.03, 3.77]	0.998	6265	1.001	0.011
Raphidioptera	Malaise	Vegetation	-0.38	0.90	[-1.54, 0.79]	[-1.88, 1.14]	0.664	4682	1.001	0.014
Raphidioptera	Malaise	Elevation	-2.13	0.82	[-3.24, -1.11]	[-3.50, -0.74]	0.993	5087	1.000	0.012
Raphidioptera	Malaise	Moon Illuminance	0.56	0.44	[-0.00, 1.13]	[-0.20, 1.27]	0.898	7222	1.000	0.005
Raphidioptera	Malaise	Temperature	-0.02	0.89	[-1.14, 1.15]	[-1.47, 1.47]	0.508	6173	1.002	0.011
Raphidioptera	Malaise	Year (2018)	-0.31	0.46	[-0.93, 0.27]	[-1.09, 0.47]	0.753	6606	1.001	0.006
Raphidioptera	Malaise	SPL x Freq. interaction	0.57	1.54	[-1.43, 2.6]	[-1.99, 3.16]	0.639	6635	1.000	0.019
Thysanoptera	Fly (Vane)	Sound pressure level (SPL)	-2.21	0.87	[-3.37, -1.11]	[-3.77, -0.82]	0.994	4991	1.000	0.013
Thysanoptera	Fly (Vane)	Background frequency (Freq.)	-1.93	0.84	[-3.02, -0.85]	[-3.44, -0.60]	0.990	5090	1.000	0.012

Order	Trap	Parameter	Estimate	SE	80% CI	90% CI	PD	ESS	Rhat	MCSE
Thysanoptera	Fly (Vane)	Ordinal day	0.89	1.25	[-0.75, 2.54]	[-1.19, 3.04]	0.757	4191	1.000	0.020
Thysanoptera	Fly (Vane)	Vegetation	-0.71	0.66	[-1.51, 0.20]	[-1.90, 0.35]	0.858	6862	1.000	0.008
Thysanoptera	Fly (Vane)	Elevation	0.36	0.75	[-0.58, 1.37]	[-0.94, 1.62]	0.687	6558	1.000	0.010
Thysanoptera	Fly (Vane)	Moon Illuminance	0.35	0.62	[-0.45, 1.15]	[-0.70, 1.37]	0.709	6047	1.000	0.008
Thysanoptera	Fly (Vane)	Temperature	1.08	1.31	[-0.55, 2.86]	[-0.93, 3.40]	0.801	3757	1.000	0.022
Thysanoptera	Fly (Vane)	Year (2018)	-2.20	0.85	[-3.31, -1.13]	[-3.67, -0.82]	0.996	4020	1.000	0.014
Thysanoptera	Fly (Vane)	SPL x Freq. interaction	-0.96	1.51	[-2.98, 1]	[-3.64, 1.55]	0.736	5357	1.000	0.022

Order	Trap	Parameter	Estimate	SE	80% CI	90% CI	PD	ESS	Rhat	MCSE
Trichoptera	Malaise	Sound pressure level (SPL)	0.25	0.55	[-0.47, 0.96]	[-0.63, 1.21]	0.672	7903	1.000	0.006
Trichoptera	Malaise	Background frequency (Freq.)	-0.12	0.54	[-0.82, 0.58]	[-0.99, 0.81]	0.585	8372	1.000	0.006
Trichoptera	Malaise	Ordinal day	1.63	0.78	[0.62, 2.57]	[0.36, 2.87]	0.981	7262	1.000	0.009
Trichoptera	Malaise	Vegetation	-0.48	0.54	[-1.18, 0.20]	[-1.34, 0.43]	0.810	8787	1.001	0.006
Trichoptera	Malaise	Elevation	0.24	0.57	[-0.44, 1.05]	[-0.77, 1.14]	0.664	8247	1.000	0.006
Trichoptera	Malaise	Moon Illuminance	0.76	0.42	[0.22, 1.31]	[0.08, 1.48]	0.971	9059	1.000	0.005
Trichoptera	Malaise	Temperature	0.38	0.81	[-0.71, 1.36]	[-0.95, 1.71]	0.679	6680	1.000	0.010
Trichoptera	Malaise	Year (2018)	0.54	0.44	[-0.05, 1.10]	[-0.23, 1.25]	0.884	9184	1.000	0.005
Trichoptera	Malaise	SPL x Freq. interaction	-1.92	1.05	[-3.31, -0.62]	[-3.74, -0.27]	0.972	8726	1.000	0.011

Order	Trap	Parameter	Estimate	SE	80% CI	90% CI	PD	ESS	Rhat	MCSE
Trichoptera	UV	Sound pressure level (SPL)	-0.08	0.60	[-0.87, 0.69]	[-1.04, 0.98]	0.548	4175	1.000	0.009
Trichoptera	UV	Background frequency (Freq.)	-0.49	0.47	[-1.15, 0.07]	[-1.28, 0.29]	0.847	5061	1.000	0.007
Trichoptera	UV	Ordinal day	2.29	0.54	[1.57, 2.97]	[1.39, 3.19]	1.000	4694	1.000	0.008
Trichoptera	UV	Vegetation	0.29	0.56	[-0.43, 1.01]	[-0.64, 1.22]	0.697	4043	1.000	0.009
Trichoptera	UV	Elevation	-0.04	0.60	[-0.81, 0.74]	[-1.03, 0.98]	0.522	5024	1.000	0.009
Trichoptera	UV	Moon Illuminance	0.99	0.39	[0.46, 1.47]	[0.36, 1.65]	0.994	6408	1.000	0.005
Trichoptera	UV	Temperature	0.72	0.65	[-0.11, 1.55]	[-0.34, 1.79]	0.865	4318	1.000	0.010
Trichoptera	UV	Year (2018)	0.82	0.42	[0.28, 1.36]	[0.16, 1.54]	0.975	5116	1.000	0.006
Trichoptera	UV	SPL x Freq. interaction	0.87	0.90	[-0.35, 1.99]	[-0.70, 2.32]	0.827	6156	1.000	0.012