Experimental playback study investigating effects of oil infrastructure noise on migratory grassland songbirds

by

Patricia Rosa

A thesis submitted to the Faculty of Graduate Studies of

the University of Manitoba

in partial fulfillment of the requirements of the degree of

DOCTOR OF PHILOSOPHY

Clayton H. Riddell Faculty of Environment, Earth, and Resources

Natural Resources Institute

University of Manitoba

Winnipeg

ABSTRACT

Anthropogenic noise has become widespread across all biomes, resulting in significant concern about its potentially detrimental impacts on wildlife and natural systems. Due to the increasing demand for crude oil in prairie habitats, grassland songbirds may be particularly vulnerable to projected increases in associated acoustic footprints. To isolate effects of different oil infrastructures from physical disturbances associated with the noise sources, I designed and implemented a novel large-scale, spatially and temporally replicated experimental playback study. By implementing this study design, I found that anthropogenic noise constrains animal communication across a much larger surface area when considering interferences with attentional processes in addition to energetic masking of signals. Further, I showed that oil infrastructure noise and infrastructure can decouple habitat use from habitat quality for three of my four focal grassland songbird species. Overall, intermittent drilling noise proved to be more detrimental to grassland songbirds than predictable, chronic noise, and both noise and above-ground infrastructure reduced habitat quality for specialist and threatened species, emphasising the importance of constructing studies that are able to disentangle effects of noise from physical infrastructure. Current noise mitigation recommendations to reduce impact of oil activities on migratory grassland songbirds are too broad, inaccurate, and can be easily circumvented. However, my results show that noise presents a threat to several species, and thus mitigation of noise produced by oil development would be beneficial to grassland songbirds.

ACKNOWLEDGEMENTS

This study was made possible thanks to funding from Cenovus Energy, the Natural Sciences and Engineering Research Council of Canada (NSERC), the Canadian Foundation for Innovation, the Manitoba Research and Innovation Fund, and the University of Manitoba Clayton Riddell Faculty of Environment, Earth, and Resources. Thanks to Susan Patey-LeDrew (Cenovus Energy), and Rick Martin (Eastern Irrigation District) for their help with planning, logistics, and securing access to study sites.

Thank you to my academic advisor, Dr. Nicola Koper, for her invaluable support, continuous encouragement, and for the great opportunities she has provided me. I would also like to thank my committee members, Dr. Marty Leonard and Dr. Jane Waterman, for their help in improving my research and dissertation, and for their enthusiasm regarding my work.

I am very appreciative of Dr. Claire M. Curry and Dr. Lionel Leston who have both been excellent mentors to me throughout this research. Thank you to my colleagues for their contribution to data collection and for their valuable insight: Bridget Antze, Jacy Bernath-Plaisted, Marie-Ève Cyr, Jody Daniel, Paul Des Brisay, Alex Heathcote, Jennifer Horvat, Heather Nenninger, Christoph Ng, and Jenny Yoo. Thank you to my field crews who worked diligently during the field seasons, particularly: Tyne Baker, Mathias Fenton, Renée Huntley, Amanda J. Mosca, Lynnea Parker, Marina Richardson, and Gordon Smith.

Thank you to my family and friends for their support, advice, and thoughtfulness throughout this process. Special thanks to my parents, Chantal and Denis Rosa, for their unwavering support, encouragement, and guidance.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 2

CHAPTER 3

Figure 3.1 Publications including research studies, reviews, and perspectives focused on potential effects of noise on animal communication that reference energetic and informational masking, auditory scene analysis, multimodal communication, and cross-modal effects since 2010 (see Appendix S3.1). Most studies consider only one perspective on effects of noise on communication, with more ecologists considering effects of energetic masking than all other impacts combined.

Figure 3.2 Effects of noise on animal communication from the perspective of multiple disciplines. Communication components (a) are based on Wiley's (2015) adaptation of communication in the presence of noise, where noise affects each component instead of only interfering during signal transmission as previously proposed (see Shannon 1948). Examples of physical and environmental properties affecting signal transmission in noise (b), and potential negative noise impacts at the physiological and neurological levels (c), and psychological level (d) are compared to highlight contributions from these different fields to ecological noise assessment studies. Physical and environmental properties (b) likely do not directly affect signal transmitter, receiver criterion, or response. Negative physiological and neurological consequences on communication in noisy environments (c) influence all components related to the sender and receiver, while psychological consequences (d) have a greater impact on the receiver compared to the sender and do not target signal receptors. [1](Shannon 1948, Shannon and Weaver 1963, Wiley 2013, 2015). [2](e.g., Embleton 1996, Wiley 2015, Erbe et al. 2016). [3](e.g., Johnstone 1996, Kastner and Ungerleider 2000, Lentz and Leek 2001, Lohr et al. 2003, Moore 2007, Luther and Gentry 2013). [4](e.g., Dukas 2004, Appeltants et al. 2005, Beaman 2005, Kidd et al. 2008, Blumstein 2014, Halfwerk and Slabbekoorn 2015).

Figure 3.3 Relationship between the power of a signal (P_{signal}) and the power of background noise (P_{noise}; a). Corresponding signal-to-noise ratio (SNR = $P_{\text{signal}}/P_{\text{noise}}$; c). Area between dashed lines indicates active space of signal where it can be perceived by a receiver. Extent of signal perception (i.e., detection, discrimination, and identification) is highly reliant on SNR.

Figure 3.4 Spatial propagation of noise from four different oil infrastructure types and their estimated acoustic footprint for Baird's Sparrow (*Ammodramus bairdii*; a), Chestnut-collared Longspur (*Calcarius ornatus*; b), and Savannah Sparrow (*Passerculus sandwichensis*; c). Informational masking (i.e., lighter circles) generally covers a greater surface area than energetic masking (i.e., darker circles) and thus has the potential to result in greater functional habitat loss due to energy development. Masking threshold values were estimated by conducting spectral analyses of one-third octave bands using ISO standard calculation methods (Appendix S3.2).

CHAPTER 4

Figure 4.1 Shallow gas well pads (a), which are abundant across this region, have a very similar footprint (average 23.1 m^2) and height (1.44 m; Rodger and Koper 2017) to playback units (b) designed for the present study (footprint: 35.8 m^2, height: 1.25 m; Rosa et al. 2015), and are composed of some of the same materials (i.e., identical technical fencing). Both are diminutive in comparison with oil well drilling rigs (height: 24 m; c) and pumpjacks (height: 4.5 m; d).

Figure 4.2 Acoustic footprint of intermittent (purple) and chronic (yellow and blue) oil development noise for Chestnut-collared Longspur (a), Savannah Sparrow (b), Sprague's Pipit (c), and Vesper Sparrow (d). Inner circles indicate surface area where noise can energetically mask signals (noise levels within peak frequency exceed ambient levels). Outer circles represent surface area where noise can interfere with signal transmission (noise levels within frequency range of vocalisation exceed ambient levels; see Appendix S4.1; Rosa and Koper 2018).

Figure 4.3 Effects of intermittent (drilling rig) and chronic (generator and power-grid pumpjack) playback noise and of presence of the playback unit at the local scale on abundance of four species of grassland songbirds for each experimental treatment, from 2013 to 2015, in Alberta, Canada. All treatments were compared to both infrastructure-only (blue line) and control treatments (solid black line). Significant differences ($P < 0.1$) compared to infrastructure-only are indicated by * and compared to control by †, for each species: Chestnut-collared Longspur (a), Savannah Sparrow (b), Sprague's Pipit (c), and Vesper Sparrow (probability of occurrence; d). To facilitate interpretation of graphs, 90% confidence intervals were omitted from this figure (for confidence intervals see Fig. S4.2.2 in Appendix S4.2).

Figure 4.4 Effects of intermittent (drilling rig) and chronic (generator and power-grid pumpjack) playback noise and of presence of playback unit at the site scale on overall probability of nest survival (%) for four species of grassland songbirds at each experimental treatment, from 2013 to 2015, in Alberta, Canada. Noise-producing treatments were compared both to infrastructure-only (blue) and control (white) treatment. Significant differences ($P < 0.1$) compared to infrastructure-only are indicated by * and compared to control by †. Errors bars indicate 90% confidence intervals.

Figure 4.5 Nestling body condition of Savannah Sparrow (*Passerculus sandwichensis*; a) for and clutch size of Chestnut-collared Longspur (*Calcarius ornatus*; b) as a function of log-transformed distance from playback unit or centre-point at control treatments. Significant site-scale effects ($P < 0.1$) are denoted by an asterisk (*).

LIST OF APPENDICES

CONTRIBUTIONS OF AUTHORS

CHAPTER 1: PR led the writing of the chapter. NK contributed to editing.

CHAPTER 2: PR led the writing of the manuscript. PR, LL, and CRS helped collect field data and contributed to statistical analyses. PR, CRS, and NK contributed to the design of the experiment. All authors contributed to drafts and gave final approval for publication.

CHAPTER 3: PR developed the initial concept, conducted the literature review and statistical analyses, and wrote the manuscript. NK contributed to editing and study design. Both authors contributed to drafts and gave final approval for publication.

CHAPTER 4: PR and NK designed the experiment; PR collected and analyzed field data, and led the writing of the manuscript; NK supervised all work and the overall research program. Both authors contributed to drafts and gave final approval for submission.

CHAPTER 5: PR led the writing of the chapter. NK contributed to editing.

PERMISSIONS FOR COPYRIGHTED MATERIAL

CHAPTER 2: Rosa, P., C. R. Swider, L. Leston, and N. Koper. 2015. Disentangling effects of noise from presence of anthropogenic infrastructure: design and testing of system for large-scale playback experiments. Wildlife Society Bulletin 39:364–372.

CHAPTER 3: Rosa, P., and N. Koper. 2018. Integrating multiple disciplines to understand effects of anthropogenic noise on animal communication. Ecosphere 9:e02127.

RESEARCH PERMITS

This research was completed under University of Manitoba animal care protocol, Canadian Wildlife Service permit, and Alberta Environment and Sustainable Research Development research permit.

CHAPTER 1. INTRODUCTION

BACKGROUND

Anthropogenic noise has become widespread across all biomes. Noise affects wildlife occupying urban areas (e.g., Warren et al. 2006), habitats surrounding roads and energy development (e.g., McClure et al. 2013), and even protected areas (Buxton et al. 2017). With the intensification of acoustic pollution, researchers are increasingly concerned about detrimental impacts on wildlife and natural habitats (McGregor et al. 2013), and a growing body of scientific findings demonstrate that anthropogenic noise can be harmful to species residing in these disturbed habitats (Dooling and Popper 2007, Barber et al. 2010, Shannon et al. 2016). However, studies report varying and sometimes even conflicting results regarding behavioural and ecological responses of animals to noise. This inconsistency may be because anthropogenic noise is usually accompanied by a suite of other disturbances (e.g., above-ground structures, linear features such as roads and powerlines, chemical pollution), which makes it difficult to assess whether noise, or correlated human disturbances such as structures and roads, account for responses observed in wild populations (Summer et al. 2011). Experimental playback studies where noise is broadcast at sites without other forms of anthropogenic disturbances are an essential approach to disentangle impacts of noise on wildlife from effects associated with these other confounding factors.

Controlled playback studies show that noise can decrease habitat quality (Ware et al. 2015), alter predator-prey dynamics (Francis et al. 2009), and induce a physiological stress response (Blickley et al. 2012) in birds. However, most playback studies are not conducted at a landscape scale or have been replicated across study sites and years, making it difficult to determine whether responses found are representative of lasting effects at the population and community levels (Shannon et al. 2016). Large-scale, multi-species studies replicated in space and time can allow researchers to better assess complex interacting effects of noise alone on animal behaviour and ecology (Shannon et al. 2016). Further, research that characterises noise from a range of different anthropogenic noise sources can help in identifying which noise sources should be prioritized and what amount of noise reduction is required for effective mitigation (Francis and Barber 2013). Additionally, integrating knowledge from multiple disciplines to understand effects of anthropogenic noise would allow us to better evaluate responses to anthropogenic noise, and enable us to implement more appropriate management practices (Shannon et al. 2016).

Oil development provides a compelling system in which to conduct a large-scale, multi-year, controlled playback experiment on effects of different noise sources on bird communities. Different types of oil infrastructure produce different noise stimuli that vary in frequency composition, amplitude, and duration (i.e., chronic and intermittent) and, therefore, may have different effects on birds present in surrounding habitats (Francis and Barber 2013). In Western Canada, the demand for drilling new oil wells is estimated to have increased 70% in 2017 compared to the previous year and the supply of crude oil is predicted to increase 39% by 2030 (Canadian Association of Petroleum Producers 2017). This addition of new oil infrastructure results in an increased acoustic footprint due to anthropogenic noise on the prairie landscape, and therefore, studies investigating oil infrastructure noise are particularly timely.

Grassland songbirds have endured the most extensive declines compared to birds of any another ecosystem in North America (Knopf 1992, Murphy 2003), and are highly dependent on acoustic communication (Rendall et al. 2009), which could be hindered in noisy habitats (Lohr et al. 2003). Grassland songbirds are protected under the *Migratory Birds Convention Act*, which prohibits the disruption and damage to nests and eggs of migratory birds (Migratory Birds Convention Act 1994) and has significant implications for the management of the oil and gas industry. Since noise can be mitigated relatively easily using commercially available equipment (e.g., Bayne et al. 2008), a manipulative experiment that successfully isolates noise impacts from other potential confounding factors related to oil extraction activities (e.g., access roads, traffic, powerlines, above-ground structure) can help industry and conservation management make appropriate, effective and immediate management decisions.

PURPOSE AND OBJECTIVES

The purpose of this study was to directly assess the effects of noise alone on the behaviour and ecology of grassland songbirds. If noise was found to have a negative effect, my goal was to also determine which noise sources associated with oil extraction activities are most detrimental, and therefore, most necessary to mitigate. Specifically, the objectives of this study were to:

1. Develop an experimental playback design that allows researchers to disentangle effects of noise from confounding factors associated with the presence of infrastructure. Ensure that the soundscape produced by different chronic oil well noise and acute drilling activities is reproduced accurately (Rosa et al. 2015, Chapter 2).
2. Propose a theoretical framework for understanding and evaluating species' responses to noise by integrating multiple disciplines to assess impacts on animal communication (Rosa and Koper 2018, Chapter 3).
3. Compare relative abundance and nesting success among acute and chronic oil development playback noise treatments to assess effects of noise on the ability of several grassland songbird species to select high quality habitats. For the two most abundant

species, evaluate whether noise affects reproductive output measured by clutch size and nestling body condition (Chapter 4).

4. Suggest feasible and appropriate mitigation measures to industry based on effects caused by oil infrastructure noise on grassland songbirds (Chapter 5).

LITERATURE CITED

Barber, J. R., K. R. Crooks, and K. M. Fristrup. 2010. The costs of chronic noise exposure for terrestrial organisms. Trends in Ecology & Evolution 25:180–189.

Bayne, E. M., L. Habib, and S. Boutin. 2008. Impacts of chronic anthropogenic noise from energy-sector activity on abundance of songbirds in the boreal forest. Conservation Biology 22:1186–1193.

Blickley, J. L., K. R Word, A. H. Krakauer, J. L. Phillips, S. N Sells, C. C. Taff, et al. 2012. Experimental chronic noise is related to elevated fecal corticosteroid metabolites in lekking male greater sage-grouse (*Centrocercus urophasianus*). PLoS ONE 7:e50462.

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

Canadian Association of Petroleum Producers. 2017. 2017 CAPP Crude oil forecast, markets & transportation. Canada’s Oil & Natural Gas Producers, Calgary, AB, Canada. http://www.capp.ca/publications-and-statistics/publications/303440.

Dooling, R. J., and A. N. Popper. 2007. The effects of highway noise on birds. The California Department of Transportation, Division of Environmental Analysis, Sacramento, California, USA.

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

Francis, C. D., C. P. Ortega, and A. Cruz. 2009. Noise pollution changes avian communities and species interactions. Current Biology 19:1415–1419.

Knopf, F. L. 1992. Faunal mixing, fauna integrity, and the biopolitical template for diversity conservation. Transactions of the North American Wildlife and Natural Resources Conference 57:30–342.

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

McClure, C. J., H. E. Ware, J. Carlisle, G. Kaltenecker, and J. R. Barber. 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.

McGregor, P. K., A. G. Horn, M. L. Leonard, and F. Thomsen. 2013. Anthropogenic noise and conservation. Pages 409–444 *in* H. Brumm, editor. Animal communication and noise (Vol. 2). Springer Science & Business Media, Berlin.

Migratory Birds Convention Act. 1994. (S.C. 1994, c.22). Minister of Justice, Government of Canada, current to August 27, 2017, http://laws-lois.justice.gc.ca/PDF/M-7.01.pdf.

Murphy, M. T. 2003. Avian population trends within the evolving agricultural landscape of eastern and central United States. The Auk 120:20–34.

Rendall, D., M. J. Owren, and M. J. Ryan. 2009. What do animal signals mean? Animal Behaviour 78:233–240.

Rosa, P., and N. Koper. 2018. Integrating multiple disciplines to understand effects of anthropogenic noise on animal communication. Ecosphere 9:e02127.

Rosa, P., C. R. Swider, L. Leston, and N. Koper. 2015. Disentangling effects of noise from presence of anthropogenic infrastructure: Design and testing of system for large-scale playback experiments. Wildlife Society Bulletin 39:364–372.

Shannon, G., M. F. McKenna, L. M. Angeloni, K. R. Crooks, K. M. Fristrup, E. Brown, et al. 2016. A synthesis of two decades of research documenting the effects of noise on wildlife. Biological Reviews 91:982–1005.

Ware, H. E., C. J. McClure, J. D. Carlisle, and J. R. Barber. 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.

Warren, P. S., M. Katti, M. Ermann, and A. Brazel. 2006. Urban bioacoustics: it's not just noise. Animal Behaviour 71:491–502.

CHAPTER 2. DISENTANGLING EFFECTS OF NOISE FROM PRESENCE OF ANTHROPOGENIC INFRASTRUCTURE: DESIGN AND TESTING OF SYSTEM FOR LARGE-SCALE PLAYBACK EXPERIMENTS

ABSTRACT

Anthropogenic noise may be detrimental to many bird species, and manipulative experiments would help us understand these effects. I present the design and validation of a self-sustaining solar-powered broadcasting system that will allow researchers to disentangle acute or chronic effects of noise from effects of the presence of infrastructure, even in remote areas. I tested the broadcasting system using a case study on noise from oil well infrastructure in southern Alberta, Canada. Recordings from two types of oil wells were obtained and then broadcasted through six independent playback units continuously for a period of three months in 2013, at sites undisturbed by oil development. Sound measurements at real oil wells and at sites with broadcasting systems simulating the noise from these oil wells demonstrated that real and projected noise had very similar sound pressure levels, attenuation trends, and spectral composition. Throughout this long-term playback experiment, the system produced power and noise reliably and consistently. In conjunction with bird surveys, this experimental design and infrastructure can be used to allow researchers to dissociate the presence of anthropogenic development from associated noise, providing us with information that will help decrease the environmental impacts of human activities.

INTRODUCTION

Many ecological soundscapes are influenced by noise produced by human activities and this novel selection pressure may negatively affect some wildlife populations (Barber et al. 2010). Anthropogenic noise may be particularly detrimental to species that rely on acoustic signals to communicate and may contribute to bird population declines (Patricelli and Blickley 2006, Bayne et al. 2008, Slabbekoorn and Ripmeester 2008) by masking communication signals, although some species may alter their songs in noisy urban landscapes (Slabbekoorn and Peet 2003). Anthropogenic noise is also frequently louder and occurs over longer time periods than natural noises, and can be a source of physiological stress for many organisms, affecting their metabolism and cardiovascular health (Kight and Swaddle 2011). However, it can be difficult to distinguish between effects of anthropogenic noise from the effects of anthropogenic infrastructure, given that the two factors usually co-occur. For example, the degree to which noise has contributed to the rapid population declines of many species of birds (Sauer et al. 2008) is not well-understood (Kight et al. 2012) because of the difficulty of isolating effects of noise from potential confounding factors associated with infrastructure (e.g., chemical pollution, visual stimuli, habitat alterations; Reijnen et al. 1995, Warren et al. 2006, Bayne et al. 2008). Manipulative experimentation may be an important tool for allowing researchers to dissociate the effects of noise from the presence of infrastructure.

A valuable method that allows researchers to understand effects on birds of anthropogenic noise, natural noise, and conspecific and heterospecific communication involves the use of playbacks, in which recordings of sounds are broadcasted, followed by observations of avian responses to the projected noise. For example, Arroyo-Solís et al. (2013) shifted the time at which urban bird species were exposed to street noises to see if it would affect the time at which they sang at dawn, and a recent study in road ecology simulated a road by broadcasting traffic noise through speakers distributed along a transect (McClure et al. 2013). However, previous playback experiments have typically disregarded the importance of obtaining and broadcasting high-quality audio recordings and measuring appropriate acoustic metrics to ensure that projected noise is qualitatively similar to original recordings (Francis and Barber 2013), and thus the magnitude of previous estimates of effects of anthropogenic noise may be unreliable. For example, studies have reported instantaneous rather than time-averaged amplitudes (Francis and Barber 2013). Many studies use low-quality recordings and playback files (e.g., Arroyo-Solís et al. 2013, McClure et al. 2013) and low-fidelity speakers (e.g., Rabin et al. 2006, Zanette et al. 2011, Cunnington and Fahrig 2012), which can have the effect of broadcasting a sound that is significantly different from the sound originally recorded. In addition, most playback experiments have not reported on the fidelity of the playback system, or the ability of the system to accurately and representatively reproduce anthropogenic noise. Furthermore, broadcast stimuli in most studies have been intermittent or are emitted for short periods of time (e.g., Zanette et al. 2011, Cunnington and Fahrig 2012, Lackey et al. 2012, Arroyo-Solís et al. 2013, McClure et al. 2013), and thus cannot be used to assess chronic effects of noise. Therefore, there is a need for guidelines for reporting requirements for playback experiments, and for the development and evaluation of infrastructure that accurately reproduces anthropogenic noise and can withstand field conditions for long periods (e.g., continuous broadcast throughout the breeding season of focal species).

Although high-fidelity playback systems may be costly in time and resources, a need for experimental designs that accurately measure, characterise, and reproduce sound has been emphasised in noise impact studies (e.g., Pater et al. 2009, Francis and Barber 2013). Particularly during the investigation of more subtle effects of noise disturbance on wildlife populations, high-fidelity playback designs are expected to provide a more representative overview of consequences resulting from noise exposure (Francis and Barber 2013). These include fitness-related consequences that have the potential to impact a species at the population level, not just the more apparent indices of noise impacts such as site occupancy, abundance, or signal modifications (Francis and Barber 2013). Variations of sound source amplitude by a few decibels have the potential to lead to considerably different outcomes in observed behavioural responses (Grubb et al. 1998, Delaney et al. 2011). Further, masking of acoustic signals used by animals and physiological consequences of chronic noise largely depend on the frequency composition of the sound source (Dooling and Popper 2007, Francis and Barber 2013). Therefore, the accurate reproduction of the sound source in playback studies via high-fidelity systems will ensure a better estimation of the full range of threats that noise can pose for species exposed to anthropogenic noise.

My objectives were to design, validate, and demonstrate an experimental setup that accurately reproduces sound and thus contributes to the improvement of playback experimental design. I also provide recommendations for informative evaluation and reporting of sound quality and amplitude for playback studies. I used noise from oil-extraction infrastructure as a case study for assessing this experimental setup. This study is the first to combine (1) high-quality playback equipment, recordings, and sound files; (2) a verification of system fidelity to the original noise source; (3) the use of equivalent continuous sound level (L_{eq}) to characterise sound; (4) an entirely self-sustaining and self-powered system; and (5) the continuous broadcasting of sound for a long period of time (i.e., the duration of the breeding season) to allow evaluation of chronic effects of noise. This experiment was conducted within the context of a broader study in which bird response to the broadcasted noise was measured throughout the breeding season.

STUDY AREA

This study took place in nine 64-ha mixed-grass prairie sites owned by the Eastern Irrigation District in south-central Alberta, within 40 km of Brooks, Alberta, Canada (49°0′0.004″N to 50°53′56.475″N; 110°0′2.757″W to 112°28′44.473″W). Sites were predominately mixed-grass prairie plants (e.g., blue grama [*Bouteloua gracilis*], needle-and-thread [*Hesperostipa comata*], and western wheatgrass [*Pascopyrum smithii*], and were topographically flat or gently rolling. Typical avian species here included Baird’s Sparrow (*Ammodramus bairdii*), Chestnut-collared Longspur (*Calcarius ornatus*), and Sprague’s Pipit (*Anthus spragueii*). Sites with playback infrastructure were free of oil wells and associated development to ensure that all anthropogenic noise originated from playback equipment. Pumpjacks are a common and widespread type of well pumping system used for oil extraction in grasslands across North America. Pumping systems can be either connected to the power-grid (power-grid pumpjacks) or powered by a generator fueled by an adjacent propane tank (generator pumpjacks; Fig. 2.1A). Amplitudes of the infrastructure averaged 73 dB(C) (57 dB(A)) at 10 m for generator pumpjacks and 62 dB(C) (53 dB(A)) at 10 m for power-grid pumpjacks. Pumpjack noise encompasses a wide frequency range (0 Hz–21 kHz) and therefore is likely to overlap with the range pertinent to avian vocalization and hearing, which is generally best between 1 kHz and 5 kHz (Dooling 1980, 1982, 1992) and achieves a maximum threshold of approximately 10 kHz (Necker 2000, Beason 2004).

METHODS

Recording noise from infrastructure

I recorded noise from three generator pumpjacks and three power-grid pumpjacks, and broadcasted this sound at sites without any oil-related infrastructure present (Fig. 2.1A, B). Sites were chosen for recording based on isolation from other noise sources (e.g., other oil wells and roads) to ensure that recorded noise was that of the target infrastructure. Recordings were taken from 6–17 April 2013. I recorded each pumpjack for a minimum of 65 min between 0600 and 1130 hr to minimise disturbance from wind, which generally increased later in the day. I acquired all recordings in winds <7 km/hr. At each well, I took recordings with three Zoom H4N handheld recorders (Zoom, Tokyo, Japan; 48-kHz sample rate, 24-bit Waveform Audio File Format [WAV] files) placed just outside of the technical fence for safety reasons, 1.5–6 m from the loudest part of the pumpjack, typically near the crank and counter weight or the exhaust pipe. I spaced the microphones in an effort to capture the full range of sounds emanating from the pumpjacks and to maximise the signal-to-noise ratio (the amount of noise due to the pumpjack relative to ambient noise sources such as wind). I then compared the recordings from the three microphones using Cubase LE Al Elements 6 software (Steinberg Media Technologies, Hamburg, Germany), and chose the highest quality recording (best signal-to-noise ratio, least amount of other noise sources) for editing into a stimulus for broadcasting. I edited out other noise sources (i.e., bird songs and calls, wind, traffic) by listening to the recordings and deleting the segments in which they occurred. I then amplified the WAV files and loaded them onto 8-GB iPod Nanos (Apple Inc., Cupertino, CA) for use in the sound broadcasting systems. The end result was six different broadcast stimuli made from recordings of six different pumpjacks.

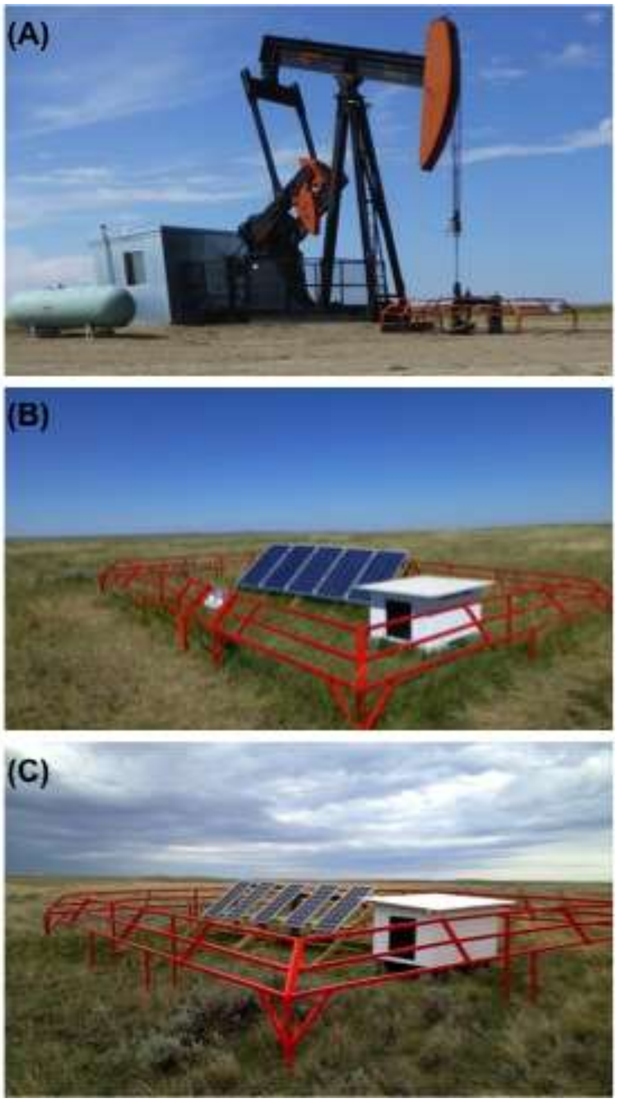


Figure 2.1 Noise of active pumpjacks (A) was recorded and broadcasted at sites without oil infrastructure using solar-powered broadcasting systems (B), in southern Alberta, Canada, 2013. Infrastructure-only units (C) were installed at other locations as a control for the presence of the broadcasting units.

Sound broadcasting system design

I projected playbacks continuously from early May until the beginning of August 2013, which was the duration of the breeding season for most grassland songbirds in this region (e.g., Robbins and Dale 1999). Six solar-powered playback systems (Figs. 2.1B, 2.2; “playback units”), each in an independent research site, reproduced the sound from generator pumpjacks and power-grid pumpjacks. Treatments consisted of (1) three sites with playback units emitting generator pumpjack noise, (2) three sites with playback units emitting power-grid pumpjack noise, and (3) three sites with infrastructure-only units, including nonfunctional solar panels, as a control to ensure there was no effect of the presence of the experimental apparatus on grassland birds (Fig. 2.1C). All six active broadcasting units played a recording of a different pumpjack, to avoid pseudoreplication.

Each playback unit was powered by an array of five 150-W (8.7-A) solar panels (SunForce Products, Montreal, QC, Canada) for a potential maximum of 750 W (43.5 A)/unit. These panels charged an array of four deep-cycle golf cart batteries, regulated by a TriStar 45 charge controller (Morningstar, Newtown, PA) to prevent overheating, overcharging, and reverse current. Current from the batteries flowed through a 410-W power inverter (Schumacher Electric, Mount Prospect, IL), which supplied two Mackie SRM350v2 loudspeakers (LOUD Technologies, Woodinville, WA) and an iPod with alternating-current power (Fig. 2.2). The batteries, speakers, iPod, charge controller, and inverter were housed together in a 1.2-m (l) × 0.9-m (w) × 0.7-m (h) plywood box adjacent to the solar panel array. Two screened holes (36 cm × 56 cm) in the boxes allowed sound to project from the speakers and an additional horizontal screened slot (75 cm × 3 cm) assisted in ventilation to prevent overheating. The system was grounded from the charge controller to a metal plate buried beneath the plywood box (see Appendix S2.1 for further technical details of the broadcasting system). The total dimensions of this infrastructure (solar array and box) were approximately 5 m (l) × 1.5 m (w) × 1.5 m (h). A 1-m-high, 7.3-m-long × 4.9-m-wide metal technical fence (Boomers Services, Brooks, AB, Canada) was installed around the apparatus to prevent damage from cattle. I broadcasted pumpjack noise through the sound system at a level consistent with real infrastructure. The noise was broadcasted continuously, 24 hour/day, throughout the breeding season, from 28 April to 10 August 2013. I monitored system function by visiting the sites every 4–6 days and recording DC voltage, which indicates charge and power consumption. I recorded environmental factors likely to impact the performance of the system, including time of day, cloud cover, and number of bird droppings on the solar panels. Each of the three silent playback units, used to control for the presence of broadcast systems, included all of the structural components of the operational playback units, with the exception of the wiring and electronics, which were not visible in operational systems. This included a wooden frame, nonfunctional solar panels, a plywood box, and a technical fence.

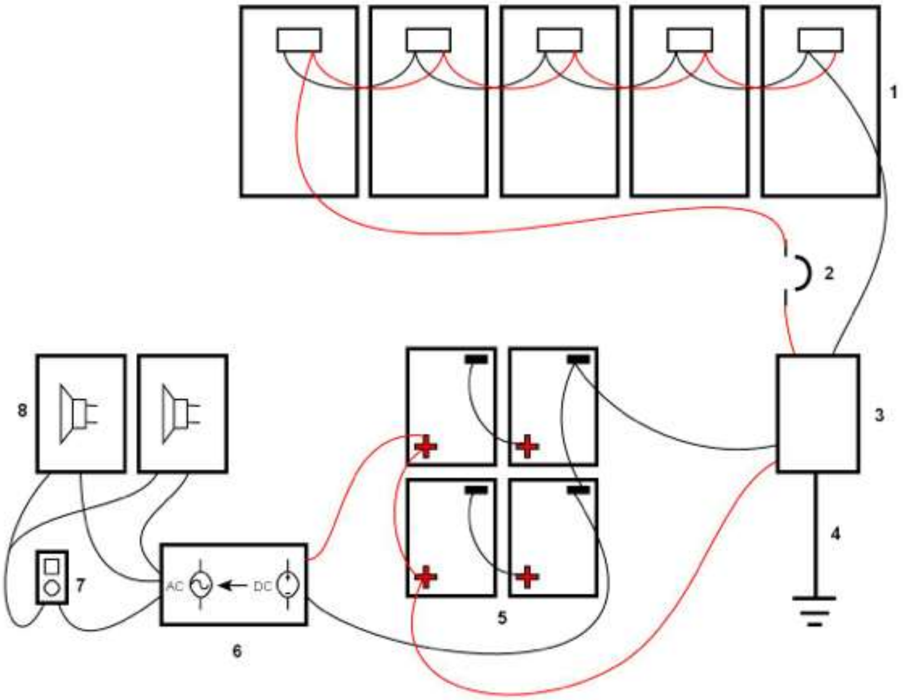


Figure 2.2 Solar-powered broadcasting systems used to record and broadcast noise of active pumpjacks at sites without oil infrastructure in southern Alberta, Canada, 2013, included (1) solar panels array, (2) kill switch, (3) charge controller, (4) grounding plate, (5) batteries, (6) inverter, (7) iPod, and (8) speakers.

Comparing sound characteristics of broadcast stimuli and real pumpjack noise

I tested the fidelity of the broadcasting system by comparing spatial attenuation trends and spectral composition (i.e., the distribution of component frequencies) to actual pumpjack noise. To measure the system's ability to accurately reproduce the noise from the original source, I compared sound pressure level (SPL) measurements between pumpjacks and broadcasting systems. Measurements of SPL are essential for characterising and comparing noise sources because SPL is the physical acoustic pressure in air, and hence translates directly into amplitude or loudness level (Huber and Runstein 2005). Sound pressure level can be measured across all frequencies (broadband) or for individual frequency bands to characterise spectral composition. I used a Brüel and Kjær 2250 SPL metre/frequency analyser (Brüel and Kjær, Nærum, Denmark) to take SPL measurements along transects radiating from four generator and four power-grid pumpjacks, including some that were previously used for recordings (one generator and three power-grid pumpjacks). I surveyed four transects/pumpjack, in cardinal directions. Measurements were taken at 5, 10, 15, 20, 25, 30, 40, 50, 60, 70, 80, 90, and 100 m from generator and power-grid pumpjacks. I recorded L_{eq}, a time-averaged value of SPL in decibels, along each transect, with both C weighting for broadband sound (LC_{eq}) and Z weighting for individual one-third-octave frequency bands (LZ_{eq}). The measurement period ranged from 10 seconds to 50 seconds depending on the time each pumpjack took to complete a cycle, and thus included the entire range of sounds produced by the pumpjack. I also took background SPL measurements immediately following transects, at a sufficient distance from the pumpjack that no infrastructure or playback noise could be heard. These measurements allowed me to control for variation in ambient noise due to wind, birdsong, and other factors. All SPL measurements were taken in wind <7 km/hour. I then used the average SPL at 10 m for generator and power-grid pumpjacks to calibrate the corresponding playback units. I conducted 100-m SPL transects at a playback unit broadcasting generator pumpjack noise, according to the methods described for transects at real pumpjacks. I then compared the attenuation of sound from real pumpjacks to the attenuation of sound from the broadcasting system.

I used a generalised nonlinear mixed model (PROC NLMIXED; SAS Institute, Inc. 2011) to determine whether attenuation measured using LC_{eq} (the time-averaged SPL value for broadband) differed between a real generator pumpjack and the playback unit broadcasting that pumpjack's noise. Mixed models enabled me to control for taking multiple observations per transect or site; I obtained similar results using transect or site as the random variable, and thus only show results for models including transect as the random variable. LC_{eq} values were continuously and normally distributed after log-transformation (PROC UNIVARIATE; SAS Institute, Inc. 2011); thus, after centring distance values to minimise collinearity with interaction terms, I log-transformed and modeled LC_{eq} with a Gaussian distribution as a quadratic function of distance from the noise source (km), and included an interaction term between distance, distance^2, and type of noise source (pumpjack or broadcast structure). If topography or other noise sources interrupted pumpjack noise further away from the pumpjack (e.g., 100 m), a portion of the transect was omitted from analyses (occurred for 9 of 32 transects), because this effect was location-specific.

In addition to overall broadband measurements, the adequate characterisation of a sound source also involves spectra that depict how amplitude varies with frequency (Pater et al. 2009). Thus, as another indicator of system fidelity, I compared the spectral composition of noise from real pumpjacks and playback systems, using power spectra generated by two different methods. First, I rerecorded the sound broadcasting from the playback system using a Zoom H4N handheld recorder, and then compared this recording to the recording of the original pumpjack. Power spectra of these recordings were created from WAV files by fast Fourier transformation and compared using Raven Pro 1.4 (Bioacoustics Research Program 2011). Next, I generated spectra from one-third-octave SPL data, taken with the Brüel and Kjær 2250 SPL metre/frequency analyser, for both real pumpjacks and playback units. I compared the spectra of four pumpjacks (one generator, three power-grid) to spectra of the broadcast structures playing noise from those pumpjacks, measured at 10 m from infrastructure. There were 2–4 measurements at 10 m from each structure and, hence, 2–4 spectra/structure. For each spectrum, I measured SPL values at 19 frequencies (specifically, LZ_{eq}, the time-averaged SPL values of the midpoint frequency for 19 one-third-octave frequency bands between 315 Hz and 20 kHz to encompass the range of hearing of birds (Dooling 1980, 1982, 1992). LZ_{eq} values were continuously and normally distributed. For the generator pumpjack, I had four measurements/frequency. I compared the difference in SPL values at each frequency band between real and projected sound using *t*-tests (PROC T-TEST; SAS Institute, Inc. 2011). For the three power-grid pumpjacks and their broadcast structures, there were 2–4 spectra/structure (n = 19 SPL measurements/frequency across all structures). I ran nonlinear mixed models separately by frequency (Gaussian distribution) to determine whether SPL measurements differed between pumpjack and broadcast sites (PROC NLMIXED; SAS Institute, Inc. 2011). I compared models with either pumpjack ID or SITE included as a random variable; results were similar, so I show only those results with random variable = SITE.

Modeling effects of environmental factors on playback unit performance

I used a generalised nonlinear mixed model (PROC NLMIXED; SAS Institute, Inc. 2011) to identify environmental factors that significantly influenced DC voltage, including the random variable SITE. Voltage values were continuously and normally distributed after log-transformation. I modelled log (DC voltage) with a Gaussian distribution as a function of time of day (with a quadratic term), time of season (no. of days since 31 May), cloud cover (percentage of sky from horizon to horizon), and fecal cover (number of fecal droppings) on the solar panel arrays, using a frequentist approach (Mundry 2011).

RESULTS

Comparing sound characteristics of broadcast stimuli and real pumpjack noise

Log-transformed LC_{eq} decreased with increasing distance (km) from noise sources ($\beta_{distance}$ = −3.08 ± 0.26 [SE], $P < 0.001$; $\beta_{distance^2}$ = 21.95 ± 10.08, $P = 0.070$), but did not differ between playback infrastructure and real pumpjacks (β_{type} = 0.00 ± 0.02, $P = 0.870$; $\beta_{type\times distance}$ = −0.00 ± 0.17, $P = 0.990$; $\beta_{type\times distance^2}$ = 12.32 ± 6.60, $P = 0.100$; Fig. 2.3).

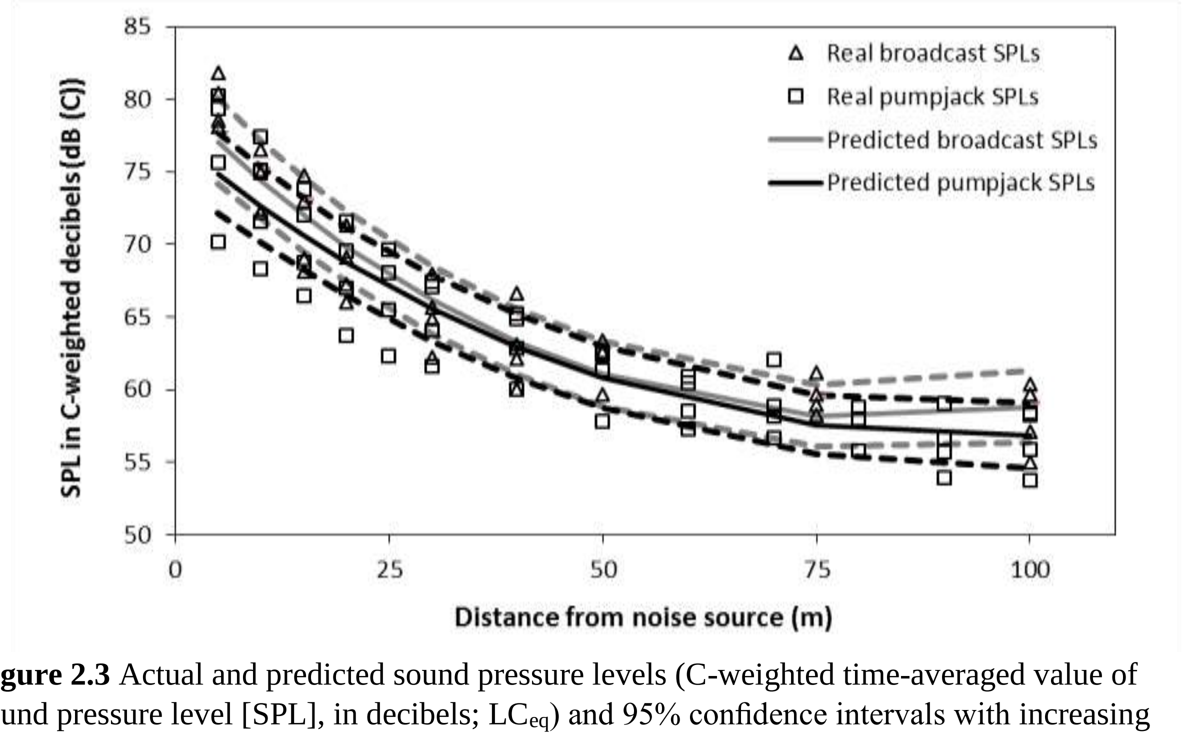


Figure 2.3 Actual and predicted sound pressure levels (C-weighted time-averaged value of sound pressure level [SPL], in decibels; LC_{eq}) and 95% confidence intervals with increasing distance (m) from a generator pumpjack and the corresponding playback unit (of recorded noise of active pumpjacks at sites without oil infrastructure) in southern Alberta, Canada, 2013.

Generator pumpjacks tended to emit low-frequency sound with more intensity than high-frequency sound (Fig. 2.4). The spectral composition was similar between the original and reproduced sound (Fig. 2.4A, B). There were few significant differences in SPLs of the one-third-octave frequency bands between the pumpjacks and their corresponding broadcast structures (Fig. 2.5A, B).

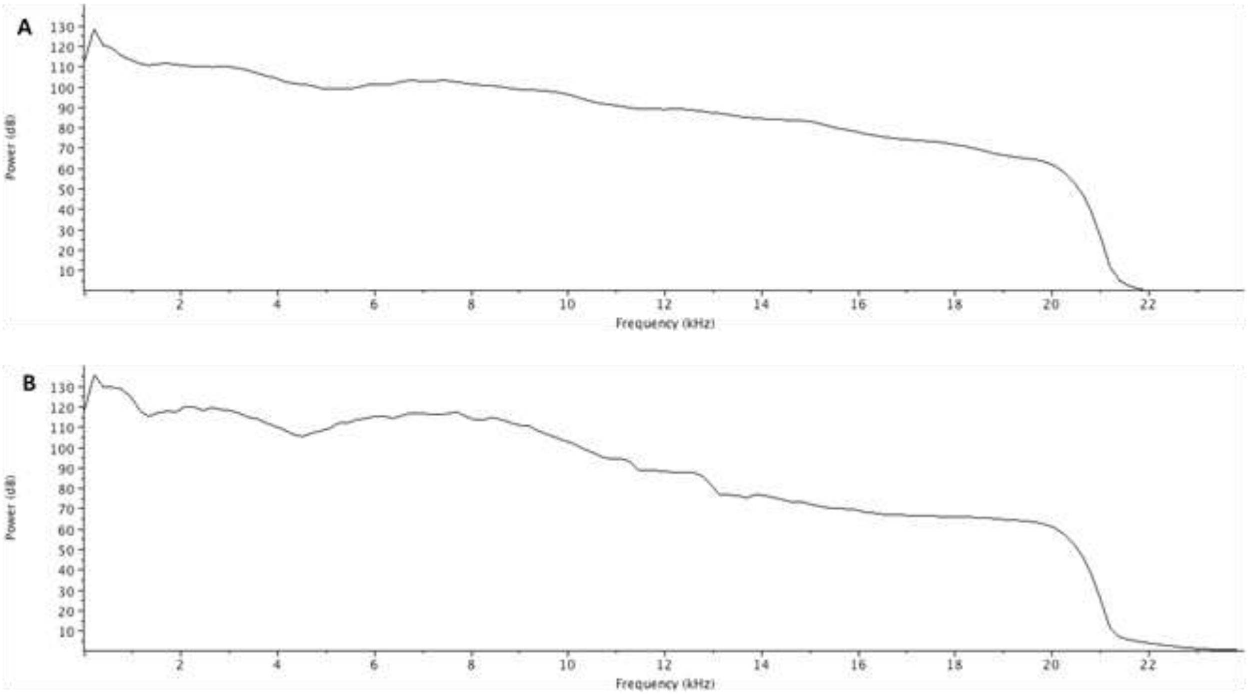


Figure 2.4 Power spectra illustrating spectral composition of (A) generator pumpjack noise and (B) rerecorded broadcasted pumpjack noise (recorded at active pumpjacks and broadcasted at sites without oil infrastructure) in southern Alberta, Canada, 2013. Relative power (dB) values were produced by fast Fourier transformation of WAV recordings and therefore are not analogous to absolute sound pressure level (SPL) values measured with an SPL metre/frequency analyser.

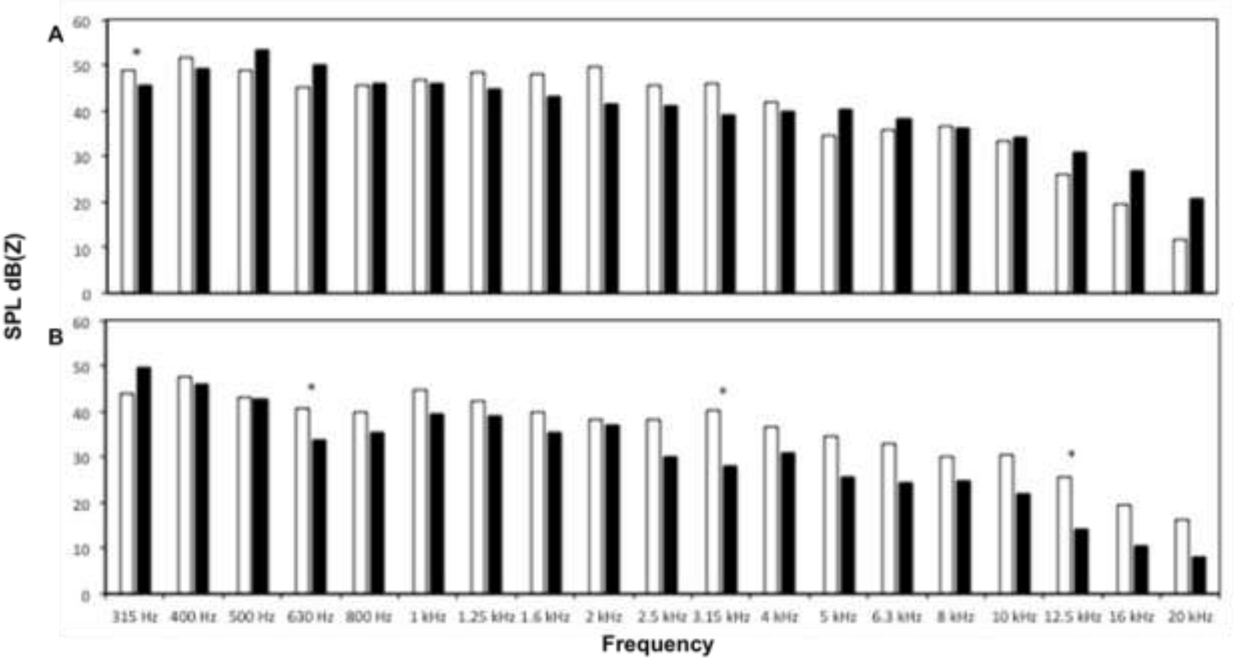


Figure 2.5 Predicted sound pressure levels (SPL; Z-weighted time-averaged value of SPL, in decibels; LZ_{eq}) of midpoint frequencies of one-third-octave frequency bands from 315 Hz to 20 kHz, measured at a generator pumpjack (black bars) and its corresponding broadcast system (white bars), as recorded in southern Alberta, Canada, 2013: (A), and at three power-grid pumpjacks (black bars) and their corresponding broadcast systems (white bars; B). Asterisks indicate statistically significant differences in SPLs: * = $P < 0.050$.

Effects of environmental factors

Direct-current voltage increased as a quadratic function of time of day ($\beta_{\text{hours(centered)}} = 0.20 \pm 0.02$, $P < 0.001$; $\beta_{\text{hours(centered)}}{}^2 = -0.04 \pm 0.01$, $P < 0.001$), and was predicted to peak at 14.2 V (actual) around 1300 hours (Fig. 2.6). Voltage declined slightly with increasing number of days since 1 May ($\beta_{\text{days since 1 May}} = -0.006 \pm 0.003$, $P = 0.049$), but not with cloud cover ($\beta_{\text{cloud cover}} = 0.01 \pm 0.01$, $P = 0.600$) or the number of fecal droppings on solar panels ($\beta_{\text{fecal pats}} = -0.002 \pm 0.002$, $P = 0.170$).

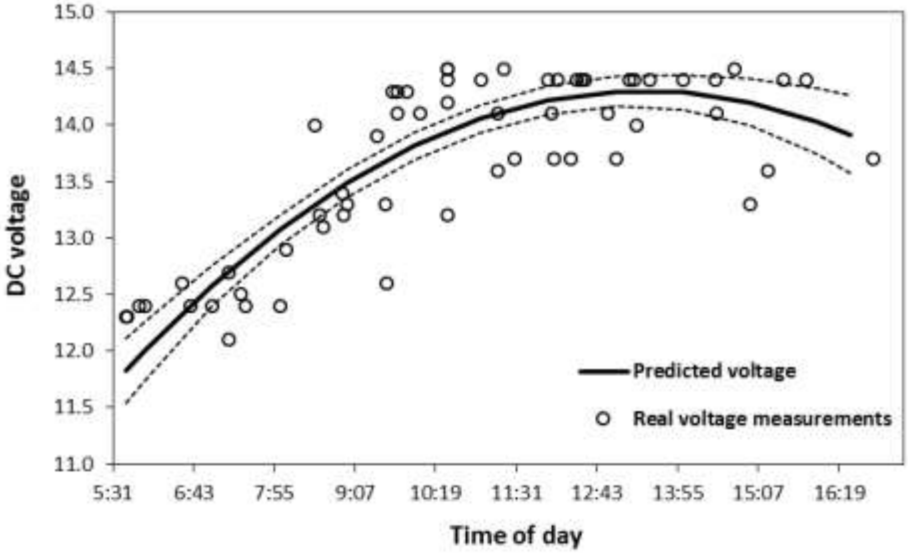


Figure 2.6 Real and predicted power output with 95% confidence limits of broadcast systems (*n* = 6; used to record) as a function of time of day in southern Alberta, Canada, 2013, after accounting for effects of time of season, cloud cover, and fecal droppings on solar panels.

DISCUSSION

The solar-powered broadcasting system I designed was effective at reproducing noise from the original source. To my knowledge, no previous studies have demonstrated that the recreated soundscape was comparable to the original soundscape. A recent study qualitatively compared the spectral composition of playback stimuli to typical traffic noise, although they did not evaluate fidelity of attenuation trends (McClure et al. 2013). Validating fidelity to the original source is essential, because not replicating the sound quality and amplitude accurately across the range of frequencies detectable by the focal species could lead to behavioural responses to projected noise that differ from behavioural responses to real noise.

The capacity of this system to reproduce anthropogenic noise with a high degree of fidelity can be attributed primarily to two factors: the quality of the audio files projected and the quality of the speakers used. Although 48-kHz sample rate, 24-bit WAV files are much larger than the lower quality or compressed audio files employed in most previous studies (e.g., MPEG Audio Layer III [MP3] or WAV files with lower sample rate and bit depth; e.g., Zanette et al. 2011, Blickley et al. 2012, Arroyo-Solís et al. 2013, McClure et al. 2013), they are advantageous because they retain more of the acoustic characteristics and resolution of the original recorded noise. Compressed file formats such as MP3 have data removed to achieve a small file size. This loss of data translates into a reduction in audio quality that can manifest itself in multiple ways, including reduced frequency and dynamic range and introduced noise artifacts (Huber and Runstein 2005, Sterne 2006).

Accurate reproduction of the original noise is also strongly influenced by speaker quality. Mackie SRM350v2 speakers were used because of their relatively flat frequency response (i.e., equal reproduction of sound across the entire frequency spectrum) and because they have low total harmonic distortion (i.e., negligible difference in harmonic content of the signal before and after the amplifier). These speakers are also loud, with a reported long-term SPL maximum of 118 dB at 1 m (LOUD Technologies, Inc. 2011). Their capacity allowed me to attain the SPLs necessary to reproduce real pumpjack noise, and can accommodate the levels required for the reproduction of other typical anthropogenic and natural noises, such as traffic or waves. The speakers' internal amplifiers are beneficial because they eliminate the need for another component to the system, which would further modify the sound, decreasing fidelity to the original sound source (Huber and Runstein 2005). These speakers are also durable and suitable for outside or field conditions if adequately protected. In this experiment, they endured three months of continuous play under variable weather conditions, with minimal protection from a wooden box, without overheating or succumbing to humidity or water damage. These characteristics of the speakers allowed the systems to broadcast sound continuously throughout the breeding season, recreating the long-term sound projected by real anthropogenic infrastructure. Most previous noise playback studies have used relatively low-fidelity outdoor (e.g., Blickley et al. 2012), marine (e.g., Cunnington and Fahrig 2012), or desktop computer (e.g., Zanette et al. 2011) speakers, which are unlikely to reproduce sound with high fidelity (Huber and Runstein 2005).

Appropriate acoustic metrics are necessary to characterise sound and thus demonstrate a broadcasting system's ability to accurately reproduce a source of anthropogenic noise (Francis and Barber 2013). I used L_{eq} because in the case of chronic anthropogenic noise, a time-averaged value is more informative than an instantaneous measurement (Francis and Barber 2013). I also characterised pumpjack and playback stimuli noise with both C- and Z-weighted L_{eq} values, for broadband and one-third-octave analyses respectively. The use of A-weighted measurements in bird studies is widespread because it is thought to adequately estimate avian ranges of hearing (Dooling and Popper 2007). However, because A-weighting puts more emphasis on frequencies detectable to humans, which can differ significantly from frequencies detected by other species (Pater et al. 2009), a flatter, less weighted frequency filter may be more generalizable among many species, and it also avoids difficulties with trying to quantify what frequencies are detectable by free-living individuals of a range of species. Hence, when comparing sounds produced by real noise sources and broadcasted stimuli, I suggest use of the flatter LC_{eq} or the unweighted LZ_{eq}.

The playback systems designed were also robust. The voltage produced by solar panels never dropped below 12.1 V, which is above the minimum voltage of 10.5 V required to maintain system function (Schumacher Electric 2012). Although I detected a significant drop in voltage levels from broadcasting nonstop both day and night, there was more than enough sunlight in prairie conditions for these systems to recharge themselves sufficiently. This robustness and consistency in power production is essential for the experimental study of chronic noise in an ecological field setting. However, because access to sunlight may be a limiting factor, the solar-powered component of this design may not be appropriate for studies conducted in densely forested areas. In habitats with adequate sunlight, self-powered systems such as the one I tested here are not only more sustainable, but decrease the frequency at which a site must be visited to change batteries, thus minimising disturbance to wildlife populations by the presence of humans and allowing its use in remote or relatively inaccessible areas.

Although this infrastructure was designed to assess effects of chronic noise, short-term studies that monitor impacts of acute noise disturbances would also benefit from the quality and robustness of the equipment, and its ability to reproduce noise accurately. This playback design presents opportunities for further ecologically important experimental designs, because effects of chronic noise may differ from effects of acute noise (e.g., Romero 2004, Wright and Kuczaj 2007, Lackey et al. 2012). Playback studies may be particularly useful for evaluating acute effects of noise under controlled conditions, because the sound emitted from playback units can be readily turned off and the amplitude can be adjusted along a continuum.

I recognise that there is a trade-off between the cost and portability of a playback system and its capability to reproduce noise accurately. However, when the purpose of a study is to determine whether the implementation of costly noise mitigation measures are appropriate and would help conservation efforts, broadcasting highly accurate sound stimuli may enable researchers to not only identify the more general behavioural response trends (i.e., site occupancy and abundance) but also more indirect costs to species inhabiting noisy areas, such as consequences on individual fitness and complex interspecific interactions. Despite its high monetary cost and lower portability, this type of experimental design can empowers researchers to investigate effects of noise at a finer scale than what previous studies have been able to achieve. Until now, it seemed unlikely that a sound broadcasting system would be capable of reproducing the whole suite of acoustic characteristics of an actual sound source, and it was anticipated that species would respond differently because of acoustical differences between original and broadcasted sound (Pater et al. 2009). However, the system design presented here, although more expensive, is a solution to the problems previously associated with the use of sound broadcasting systems.

I recommend that future playback studies implement certain key components and procedures. High-quality recordings and sound files coupled with high-fidelity playback equipment are essential to accurately reproduce sound. Speakers that are weather-resistant and have a flat frequency response, low total harmonic distortion, and preferably an internal amplifier can ensure a robust and high-fidelity system. Fidelity to the original noise source, and attenuation, should be verified by analyses of SPL attenuation trends and spectral composition. This can be accomplished by measuring appropriate sound metrics that cater to the type of noise source under investigation (e.g., time-averaged SPL values with a flatter [C] or unweighted [Z] frequency filter). If researchers opt for lower quality, less expensive playback systems, I recommend thoroughly characterising the playback stimulus with multiple appropriate sound metrics so that species' responses can be attributed to specific acoustic properties of the stimulus, particularly if those properties differ from those found in the original sound source. I also recommend exploiting self-powered and self-sustaining options to conduct playback studies in lieu of ineffective, high-maintenance, and wasteful power sources (e.g., disposable battery systems requiring frequent replacement). Although short-term and intermittent playback experiments have been the norm in noise impact studies, technology has advanced sufficiently such that long-term, continuous playbacks can now be conducted with robust, high-fidelity equipment.

LITERATURE CITED

Arroyo-Solís, A., J. M. Castillo, E. Figueroa, J. L. López-Sánchez, and H. Slabbekoorn. 2013. Experimental evidence for an impact of anthropogenic noise on dawn chorus timing in urban birds. Journal of Avian Biology 44:288–296.

Barber, J. R., K. R. Crooks, and K. M. Fristrup. 2010. The costs of chronic noise exposure for terrestrial organisms. Trends in Ecology and Evolution 25:180–189.

Bayne, E. M., L. Habib, and S. Boutin. 2008. Impacts of chronic anthropogenic noise from energy-sector activity on abundance of songbirds in the boreal forest. Conservation Biology 22:1186–1193.

Beason, C. R. 2004. What can birds hear? U.S. Department of Agriculture National Wildlife Research Center-Staff Publications 78:92-96.

Bioacoustics Research Program. 2011. Raven Pro: interactive sound analysis software. Version 1.4. The Cornell Lab of Ornithology, Ithaca, New York, USA.

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

Cunnington, G. M., and L. Fahrig. 2012. Mate attraction by male anurans in the presence of traffic noise. Animal Conservation 16:275–285.

Delaney, D. K., L. L. Pater, L. D. Carlile, E. W. Spadgenske, T. A. Beaty, and R. H. Melton. 2011. Response of red-cockaded woodpeckers to military training operations. Wildlife Monographs 177.

Dooling, R. J. 1980. Behavior and psychophysics of hearing in birds. Pages 261–288 *in* A. N. Popper and R. R. Fay, editors. Comparative studies of hearing in vertebrates. Springer-Verlag, New York, New York, USA.

Dooling, R. J. 1982. Auditory perception in birds. Pages 95–130 *in* D. E. Kroodsma and E. H. Miller, editors. Acoustic communication in birds. Volume 1. Academic Press, New York, New York, USA.

Dooling, R. J. 1992. Hearing in birds. Pages 545–559 *in* D. B. Webster, R. R. Fay, and A. N. Popper, editors. The evolutionary biology of hearing. Springer-Verlag, New York, New York, USA.

Dooling, R. J., and A. N. Popper. 2007. The effects of highway noise on birds. Environmental BioAcoustics LLC, Rockville, Maryland, USA.

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

Grubb, T. G., L. L. Pater, and D. K. Delaney. 1998. Logging truck noise near nesting northern goshawks. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.

Huber, D. M., and R. E. Runstein. 2005. Modern recording techniques. Sixth edition. Elsevier, Burlington, Massachusetts, USA.

Kight, C. R., and J. P. Swaddle. 2011. How and why environmental noise impacts animals: an integrative, mechanistic review. Ecology Letters 14:1052–1061.

Kight, C. R., M. S. Saha, and J. P. Swaddle. 2012. Anthropogenic noise is associated with reductions in the productivity of breeding eastern bluebirds (*Sialia sialis*). Ecological Applications 22:1989–1996.

Knopf, F. L. 1994. Avian assemblages on altered grasslands. Studies in Avian Biology 15:247–257.

Lackey, M. A., M. L. Morrison, Z. G. Loman, B. A. Collier, and R. N. Wilkins. 2012. Experimental determination of the response of golden-cheeked warblers (*Setophaga chrysoparia*) to road construction noise. Ornithological Monographs 74:91–100.

LOUD Technologies, Inc. 2011. SRM350v2 powered loudspeaker owner's manual. Loud Technologies, Woodinville, Washington, USA.

McClure, C. J. W., H. E. Ware, J. Carlisle, G. Kaltenecker, and J. R. Barber. 2013. An experimental investigation into the effects of traffic noise on distributions of birds: avoiding the phantom road. Proceedings of the Royal Society B 280:20132290.

Mundry, R. 2011. Issues in information theory-based statistical inference—a commentary from a frequentist's perspective. Behavioral Ecology and Sociobiology 65:57–68.

Necker, R. 2000. The avian ear and hearing. Pages 21–38 *in* G. C. Whinow, editor. Sturkie's avian physiology. Fifth edition. Academic Press, New York, New York, USA.

Pater, L. L., T. G. Grubb, and D. K. Delaney. 2009. Recommendations for improved assessment of noise impacts on wildlife. Journal of Wildlife Management 73:788–795.

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

Rabin, L. A., R. G. Coss, and D. H. Owings. 2006. The effects of wind turbines on antipredator behavior in California ground squirrels (*Spermophilus beecheyi*). Biological Conservation 131:410–420.

Reijnen, R., R. Foppen, C. ter Braak, and J. Thissen. 1995. The effects of car traffic on breeding bird populations in woodland. III. Reduction of density in relation to the proximity of main roads. Journal of Applied Ecology 32:187–202.

Robbins, M. B., and B. C. Dale. 1999. Sprague's pipit (*Anthus spragueii*). Account 439 *in* A. Poole and F. Gill, editors. The birds of North America. The Academy of Natural Sciences, Philadelphia, Pennsylvania, and The American Ornithologists' Union, Washington, D.C., USA.

Romero, L. M. 2004. Physiological stress in ecology: lessons from biomedical research. Trends in Ecology and Evolution 19:249–255.

SAS Institute, Inc. 2011. SAS statistical software. Version 9.3. SAS Institute, Cary, North Carolina, USA.

Sauer, J. R., W. A. Link, and W. L. Kendall. 2008. A hierarchical model for estimating change in American woodcock populations. Journal of Wildlife Management 72:204–214.

Schumacher Electric Corporation. 2012. Model PID-410 power inverter owner's manual. Schumacher Electric, Mount Prospect, Illinois, USA.

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

Slabbekoorn, H., and E. A. P. Ripmeester. 2008. Birdsong and anthropogenic noise: implications and applications for conservation. Molecular Ecology 17:72–83.

Sterne, J. 2006. The mp3 as a cultural artifact. New Media and Society 8:825–842.

Warren, P. S., M. Katti, M. Ermann, and A. Brazel. 2006. Urban bioacoustics: it’s not just noise. Animal Behaviour 71:491–502.

Wright, A. J., and S. Kuczaj. 2007. Noise-related stress and marine mammals: an introduction. International Journal of Comparative Psychology 20:iii–viii.

Zanette, L. Y., A. F. White, M. C. Allen, and M. Clinchy. 2011. Perceived predation risk reduces the number of offspring songbirds produce per year. Science 334:1398–1401.

CHAPTER 3. INTEGRATING MULTIPLE DISCIPLINES TO UNDERSTAND EFFECTS OF ANTHROPOGENIC NOISE ON ANIMAL COMMUNICATION

ABSTRACT

Anthropogenic noise is pervasive and may affect wildlife in many ways. Anthropogenic noise also adds to the acoustic environment's complexity, making it more difficult for animals to detect and discriminate among important signals. By integrating knowledge gained from research in experimental psychoacoustics, psychophysics, and neurophysiology into applied ecology, we can refine our understanding of the impacts of anthropogenic noise on wild populations. A multidisciplinary approach is particularly important for understanding signal perception, masking, auditory scene analysis, multimodal communication, and cross-modal interference. I demonstrate the benefits of using knowledge gained from a variety of different disciplines to understand masking effects of anthropogenic noise using my research on effects of petroleum infrastructure on grassland songbirds. Incorporating knowledge from diverse disciplines and involving several taxa, including humans, can help inform ecological conservation and management practices, and has the potential to help researchers generate novel and effective mitigation measures to counter negative effects of noise.

INTRODUCTION

Anthropogenic noise is becoming more prevalent across all habitats. It is typically characterised by higher amplitudes and occurs more frequently, compared to ambient noise found in natural environments (Patricelli and Blickley 2006, Slabbekoorn and Ripmeester 2007, Barber et al. 2010). Ecological soundscapes altered by human activity thus have the potential to provoke diverse responses from biological systems, and these responses by individuals to noise may dramatically aggravate effects of habitat loss, degradation, and fragmentation on populations (Barber et al. 2010).

Although assessing impacts of noise on wildlife is challenging, researchers have long been aware of the potential repercussions of noise disturbances on communication events and research on the subject has experienced a significant upsurge since 2010 (see Shannon et al. 2016a). Anthropogenic noise can impose constraints on animal communication by reducing the distance at which a signal can be detected (Slabbekoorn and Peet 2003), limiting the ability of the signal to reach its intended receiver, and decreasing the amount of information that can be extracted from a signal (Read et al. 2014). These effects can either reduce accuracy in communication among animals or result in an inaccurate assessment of the environment, leading to sub-optimal decisions (see Chan and Blumstein 2011). There have been several comprehensive reviews assessing effects of noise on wildlife (Dooling and Popper 2007, Barber et al. 2010, Shannon et al. 2016a) and proposed frameworks for understanding and evaluating species' responses to noise (Francis and Barber 2013, Swaddle et al. 2015). However, the underlying mechanisms that explain these behavioural responses are less well understood. In general, ecologists seem much more likely to attribute effects of noise to signal masking than to other mechanisms, as illustrated by Fig. 3.1, which shows that studies considered effects of energetic masking more than all other potential mechanisms (e.g., informational masking, auditory scene analysis, multimodal communication, and cross-modal effects; see Table 3.1 for concept descriptions) combined. Although other mechanisms have more recently been considered, an interdisciplinary overview of these concepts is necessary to understand how to better mitigate effects related to anthropogenic noise.

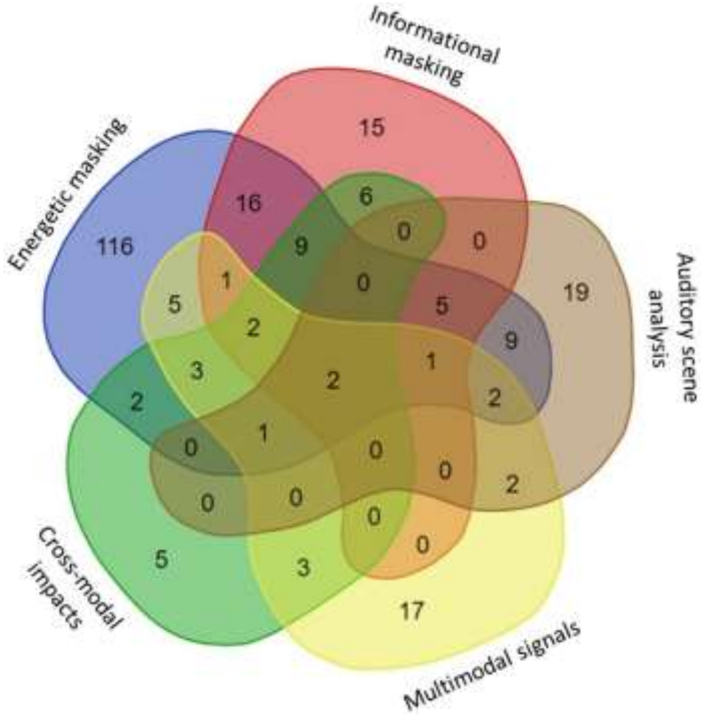


Figure 3.1 Publications including research studies, reviews, and perspectives focused on potential effects of noise on animal communication that reference energetic and informational masking, auditory scene analysis, multimodal communication, and cross-modal effects since 2010 (see Appendix S3.1). Most studies consider only one perspective on effects of noise on communication, with more ecologists considering effects of energetic masking than all other impacts combined.

Table 3.1 Key concepts pertaining to the understanding of noise impacts on communication.

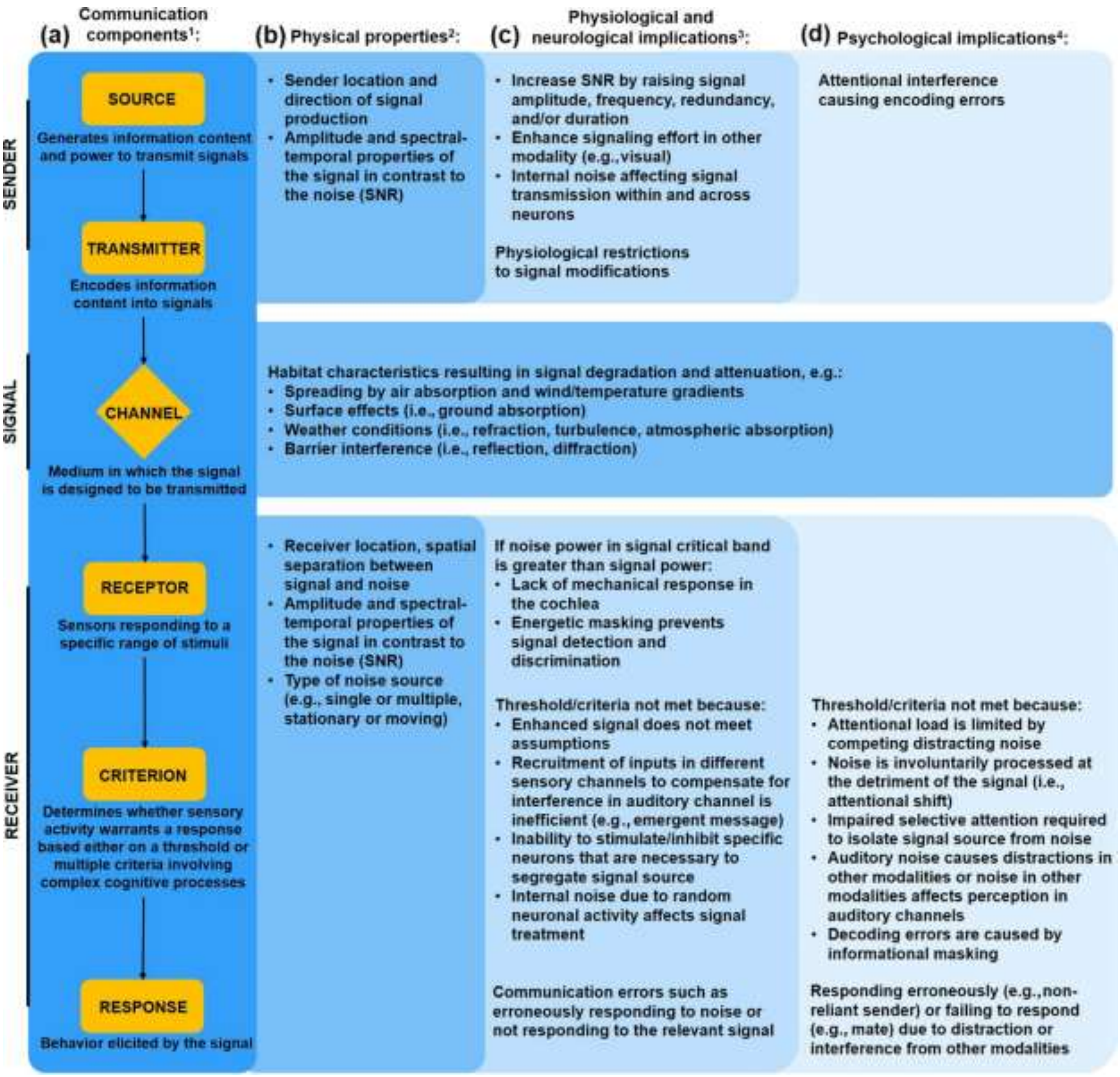
Concept	Description
Energetic masking	Noise overlap in frequency and timing prevents detection or discrimination of entire signal (i.e., frequency masking), part of the signal (i.e., partial masking), or noise interferes a few milliseconds before or after the signal (i.e., temporal masking), due to a lack of physiological response at the auditory periphery.
Informational masking	Despite the ability to physiologically detect the signal from the noise, signal detection, discrimination and/or identification does not occur due to a distracting stimulus. Thought to occur in any of the many cognitive processing stages and is interconnected with scene analysis, attention, memory, and other cognitive abilities.
Distraction	Redirected attention (i.e., attentional shift) and/or attentional overload where irrelevant stimuli outcompete for limited attentional resources. Consequence of informational masking. Occurs within and across sensory modalities.
Auditory scene analysis	Cognitive process by which organisms group and segregate acoustic cues into auditory streams. Consists of a perceptual organisation of the soundscape allowing for the isolation of relevant acoustic streams from multiple irrelevant ones.
Multimodal signals	Occurs simultaneously in more than one sensory modality (e.g., visual and auditory) to convey multiple, emergent, or redundant messages depending on employed communication strategy.
Cross-modal interference	Irrelevant stimulus in one sensory modality (e.g., acoustic) hampers perceptual sensitivity of signals occurring in another modality (e.g., visual) due to distraction across sensory modalities.

There is extensive knowledge in the experimental psychoacoustics, psychophysics, and neurophysiology literature about effects of ambient noise on the ability to process information and complete important tasks. Laboratory studies conducted in these fields have long been incorporated to assess effects of noise, particularly on birds (Dooling 1980, 1982, 1992, Dooling et al. 2000). In recent years, there has been a noticeable effort to integrate knowledge from these disciplines into ecological research to improve assessment of complex interactions affecting animal communication systems across several taxa (e.g., see Kight and Swaddle 2011, Blumstein and Berger-Tal 2015, Halfwerk and Slabbekoorn 2015, Bee and Miller 2016), and knowledge gained from these efforts has made it clear that most past assessments of noise impacts on animal behaviour have probably underestimated the true ecological costs (McGregor et al. 2013). In this paper, I emphasise the necessity and benefits of integrating theories from multiple disciplines to understand effects of anthropogenic noise to help us refine ecological knowledge, better estimate the biological consequences of anthropogenic noise, and increase the effectiveness of conservation and management efforts.

Here, I review selected literature from a range of disciplines to highlight theories and empirical studies that can help us understand the extent to which noise disturbances can affect wildlife by impeding communication. I primarily use birds as a biological model because they are highly dependent on complex acoustic communication (Rendall et al. 2009) and have been the subject of many psychoacoustic experiments (Dooling et al. 2000); however, I also demonstrate the benefits of this approach to understanding effects of noise on other taxa. I focus my discussion on five concepts in applied bioacoustics that can be better understood by considering relevant cognitive and physiological mechanisms, including energetic and informational masking, auditory scene analysis, multimodal communication, and cross-modal interference (Table 3.1). I discuss the progress realised by ecological research by incorporating these concepts to improve assessment efforts, and highlight areas where further research is needed. To illustrate how these efforts can help us interpret effects of noise on species in natural environments, I present an example of potential masking effects of energy development noise on grassland songbirds. Overall, this approach helps us understand underlying mechanisms regulating signal perception, which is now increasingly recognised as necessary for developing effective mitigation measures (Luo et al. 2015).

BACKGROUND

Characteristics of background noise can significantly reduce a signal's active space (i.e., the maximum distance where it can be perceived by the receiver; e.g., Klump 1996), thus affecting communication by interfering during signal transmission and reception (Fig. 3.2a). Active space can be influenced by many physical and environmental factors related to the spectra-temporal properties of the signal and interfering noise, the sender and receiver, and the environment in which the signal is being transmitted (Fig. 3.2b). Communicating in noisy environments can lead to physiological and neurological implications affecting the sender (i.e., source) and its ability to convert information into signals (i.e., transmitter), as well as the receiver's sensory receptors, sensory threshold or criteria to initiate a response (i.e., criterion), and consequently, the response itself (Fig. 3.2c). Although not as extensively studied, effective communication in noisy environments can also be hindered by psychological mechanisms that predominately affect the receiver's ability to determine whether the signal warrants a response, and the probability of committing responding errors, that is, missed opportunities or predation (Fig. 3.2d). Thus, incorporating findings from multiple and varied disciplines to assess noise impacts can highlight effects on specific communication components that may not be apparent when approached within the context of a single discipline.



	(a) Communication components[1]:	(b) Physical properties[2]:	(c) Physiological and neurological implications[3]:	(d) Psychological implications[4]:
SENDER	**SOURCE** Generates information content and power to transmit signals **TRANSMITTER** Encodes information content into signals	• Sender location and direction of signal production • Amplitude and spectral-temporal properties of the signal in contrast to the noise (SNR)	• Increase SNR by raising signal amplitude, frequency, redundancy, and/or duration • Enhance signaling effort in other modality (e.g.,visual) • Internal noise affecting signal transmission within and across neurons Physiological restrictions to signal modifications	Attentional interference causing encoding errors
SIGNAL	**CHANNEL** Medium in which the signal is designed to be transmitted	Habitat characteristics resulting in signal degradation and attenuation, e.g.: • Spreading by air absorption and wind/temperature gradients • Surface effects (i.e., ground absorption) • Weather conditions (i.e., refraction, turbulence, atmospheric absorption) • Barrier interference (i.e., reflection, diffraction)		
RECEIVER	**RECEPTOR** Sensors responding to a specific range of stimuli **CRITERION** Determines whether sensory activity warrants a response based either on a threshold or multiple criteria involving complex cognitive processes **RESPONSE** Behavior elicited by the signal	• Receiver location, spatial separation between signal and noise • Amplitude and spectral-temporal properties of the signal in contrast to the noise (SNR) • Type of noise source (e.g., single or multiple, stationary or moving)	If noise power in signal critical band is greater than signal power: • Lack of mechanical response in the cochlea • Energetic masking prevents signal detection and discrimination Threshold/criteria not met because: • Enhanced signal does not meet assumptions • Recruitment of inputs in different sensory channels to compensate for interference in auditory channel is inefficient (e.g., emergent message) • Inability to stimulate/inhibit specific neurons that are necessary to segregate signal source • Internal noise due to random neuronal activity affects signal treatment Communication errors such as erroneously responding to noise or not responding to the relevant signal	Threshold/criteria not met because: • Attentional load is limited by competing distracting noise • Noise is involuntarily processed at the detriment of the signal (i.e., attentional shift) • Impaired selective attention required to isolate signal source from noise • Auditory noise causes distractions in other modalities or noise in other modalities affects perception in auditory channels • Decoding errors are caused by informational masking Responding erroneously (e.g.,non-reliant sender) or failing to respond (e.g., mate) due to distraction or interference from other modalities

Figure 3.2 Effects of noise on animal communication from the perspective of multiple disciplines. Communication components (a) are based on Wiley's (2015) adaptation of communication in the presence of noise, where noise affects each component instead of only interfering during signal transmission as previously proposed (see Shannon 1948). Examples of physical and environmental properties affecting signal transmission in noise (b), and potential negative noise impacts at the physiological and neurological levels (c), and psychological level (d) are compared to highlight contributions from these different fields to ecological noise assessment studies. Physical and environmental properties (b) likely do not directly affect signal transmitter, receiver criterion, or response. Negative physiological and neurological consequences on communication in noisy environments (c) influence all components related to the sender and receiver, while psychological consequences (d) have a greater impact on the receiver compared to the sender and do not target signal receptors. [1](Shannon 1948, Shannon and

Weaver 1963, Wiley 2013, 2015). [2](e.g., Embleton 1996, Wiley 2015, Erbe et al. 2016). [3](e.g., Johnstone 1996, Kastner and Ungerleider 2000, Lentz and Leek 2001, Lohr et al. 2003, Moore 2007, Luther and Gentry 2013). [4](e.g., Dukas 2004, Appeltants et al. 2005, Beaman 2005, Kidd et al. 2008, Blumstein 2014, Halfwerk and Slabbekoorn 2015).

MASKING

Energetic masking

One of the ways that noise reduces animal's abilities to perceive signals is by masking. The concept of energetic masking has been embraced by many ecologists working in terrestrial (Barber et al. 2010, Luther and Gentry 2013) and marine (Popper and Hawkins 2012, 2016, Erbe et al. 2016) environments, and it has been applied to explain effects of noise in far more ecological studies than any other concept discussed in this paper (Fig. 3.1). It is, therefore, a useful concept with which to demonstrate the underlying physiological and psychoacoustic mechanisms that explain its ecological impacts. In its simplest description, energetic masking occurs when there is overlap between the frequency distribution of the background noise and the signal, such that the signal becomes undetectable or not discriminable to the receiver (Bradbury and Vehrencamp 2011). When the signal and noise of higher amplitude occur simultaneously (i.e., energetic masking in the frequency domain or frequency masking), the threshold at which a signal can be detected is increased (Moore 2007); that is, signals must be louder to be detected. As the ratio of signal power compared to the power of the irrelevant noise increases (i.e., signal-to-noise ratio, or SNR; Forrest 1994, Fig. 3.3a), individuals are more likely to detect and extract information from signals (Lohr et al. 2003, Freyaldenhoven et al. 2006, Fig. 3.3b). In birds, frequency masking can increase the detection threshold by 25 dB or more, decreasing the distance at which a signal can be detected and thus the likelihood of effective communication (Klump 1996, Lohr et al. 2003, Moore 2007). Further, the ability to discriminate among two or more relevant signals demands a higher SNR than signal detection (Lohr et al. 2003, Freyaldenhoven et al. 2006, Fig. 3.3b). In an experiment on budgerigars (*Melopsittacus undulatus*) and zebra finches (*Taeniopygia guttata*), discriminating between two signals required a threshold 3.29 dB(A) greater than necessary to merely detect a contact call (Lohr et al. 2003). Physiologically, frequency masking has been shown to originate in the mechanical response of the basilar membrane in mammals or papilla in birds and reptiles (Dooling et al. 2000), both located in the cochlea, which are responsible for the transduction of sound vibrations into nerve impulses (Lentz and Leek 2001, Lauer et al. 2006, Recio-Spinoso and Cooper 2013). Therefore, the signal, which acts as a mechanical stimulus, is unable to trigger the sequence of events necessary for detection: the opening of the ion channels, depolarisation of cells, and finally the conversion of the mechanical signal into a neural signal.

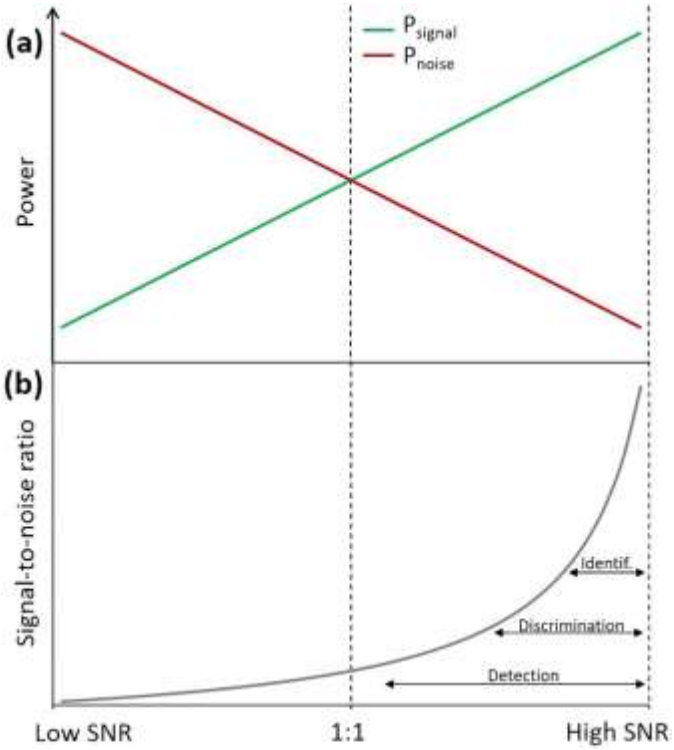


Figure 3.3 Relationship between the power of a signal (P_{signal}) and the power of background noise (P_{noise}; a). Corresponding signal-to-noise ratio (SNR = $P_{\text{signal}}/P_{\text{noise}}$; b). Area between dashed lines indicates active space of signal where it can be perceived by a receiver. Extent of signal perception (i.e., detection, discrimination, and identification) is highly reliant on SNR.

Understanding the physiological mechanisms responsible for masking has allowed researchers to find better indicators to predict the circumstances in which energetic masking is expected. At the auditory periphery, filters located on the basilar membrane or papilla of the cochlea act as sensors designed to enhance or diminish response to specific frequencies (i.e., critical bandwidth; Fletcher 1940, Dooling et al. 2000, Moore 2007). In the presence of noise, the receiver attends to the auditory filter with the greatest SNR, or the one that best represents the frequency of the signal (Fletcher 1940, Moore 2007). A response by the receiver can only occur if the SNR is above a certain threshold in the sensory receptor and the signal meets the criterion threshold (Fig. 3.2a). For example, vocal and best hearing capacity of birds ranges from approximately 2–5 kHz (Dooling and Popper 2016); hence, detection thresholds will be lower for signals within this frequency range and higher for signals of equal amplitude that fall outside of this range. Interestingly, in a laboratory study of bird detection and discrimination thresholds in noises with different spectral profiles (i.e., sound components' frequencies, amplitudes and phases), the SNR of the peak signal energy of the vocalisation (i.e., SNR within the frequency band with most signal power) was found to be more indicative of different masking effects in chronic noise conditions compared to the spectral profile of the noise (Lohr et al. 2003). Based on these findings, I present a field study of three grassland bird species with different song profiles exposed to noise emanating from two different oil well pumps (i.e., pumpjack and screwpump) powered by two different sources (i.e., generator or quieter power-grid; Appendix S3.2). For Baird's Sparrow (*Ammodramus bairdii*), Chestnut-collared Longspur (*Calcarius ornatus*), and Savannah Sparrow (*Passerculus sandwichensis*), I estimated energetic masking footprints of the different noise profiles by conducting spectral analyses to determine the distance at which SNR within peak song frequency band was greater than ambient noise for each focal species (Fig. 3.4). I found that the species with the lowest peak frequency (i.e., 3150 Hz), federally threatened Chestnut-collared Longspur (Government of Canada 2017), was confronted with a greater energetic masking footprint in most treatments when compared to other focal species (see Appendix S3.2: Tables S3.2.2, S3.2.3). Because anthropogenic noise typically has more energy in the lower frequencies, previous studies found that bird species with lower frequency songs tend to be less abundant in areas exposed to anthropogenic noise compared to species with higher frequency songs (Rheindt 2003, Francis et al. 2011a). Hence, psychoacoustic studies of bird hearing in noisy conditions and a more in-depth grasp of the physiological mechanisms responsible for energetic masking have led to better assessments of noise characteristics affecting animal communication.

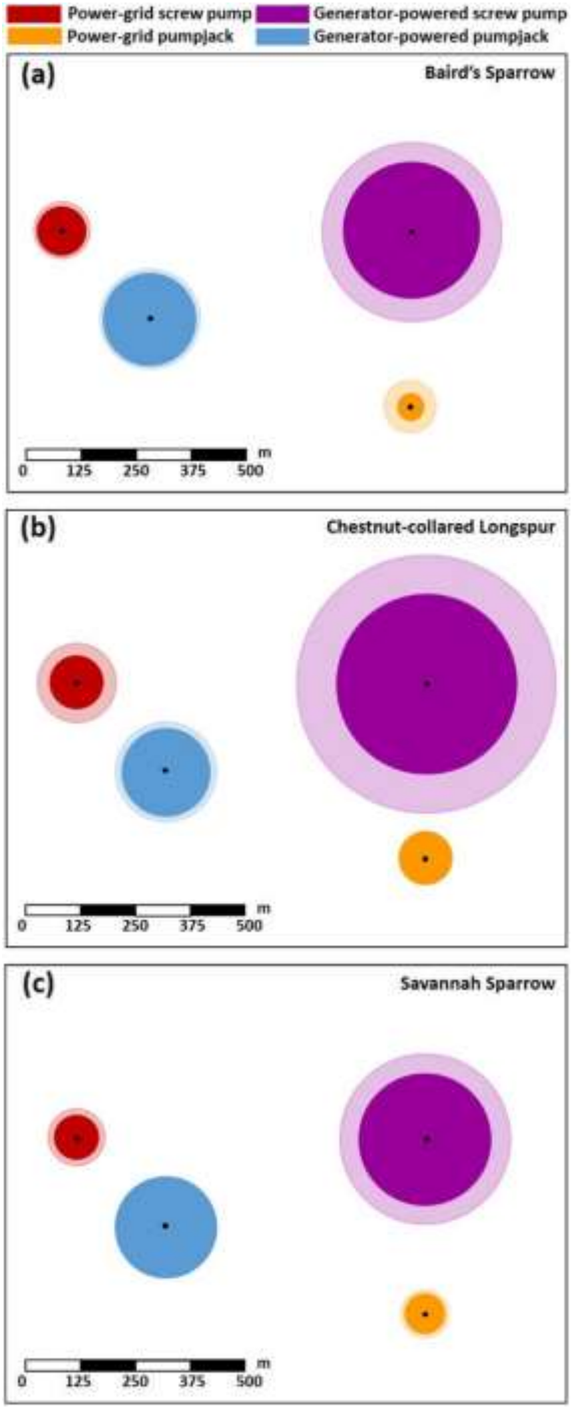


Figure 3.4 Spatial propagation of noise from four different oil infrastructure types and their estimated acoustic footprint for Baird's Sparrow (*Ammodramus bairdii*; a), Chestnut-collared Longspur (*Calcarius ornatus*; b), and Savannah Sparrow (*Passerculus sandwichensis*; c). Informational masking (i.e., lighter circles) generally covers a greater surface area than energetic masking (i.e., darker circles) and thus has the potential to result in greater functional habitat loss due to energy development. Masking threshold values were estimated by conducting spectral analyses of one-third octave bands using ISO standard calculation methods (Appendix S3.2).

As a result of these physiological characteristics, energetic masking can interfere with signal detection and discrimination to varying degrees at the species and community levels. Depending on the different acoustic components of the signals and the nature of the information being encoded, partial masking can result in different consequences based on the communication strategies employed. If each signal component encodes distinct information (i.e., multiple message) or grouping of components forms the content (i.e., emergent message; Johnstone 1996, Bro-Jørgensen 2010), partial energetic masking may lead to reduced information transfer. Conversely, if signal components convey redundant information to offset the risk of coding errors (Johnstone 1996, Bro-Jørgensen 2010), signal transmission will be much more resilient to anthropogenic noise interference. For example, a Tree Swallow (*Tachycineta bicolor*) nestling begging signal providing both hunger and thermal condition indices (Leonard and Horn 2001) may be disproportionally disadvantaged when compared to a Common Chaffinch's (*Fringilla coelebs*) serial redundancy of a specific song type (Brumm and Slater 2006) in noisy environments. Hence, partial masking by anthropogenic noise may act as a novel selection pressure with the potential of filtering communities not only based on vocalization frequencies (see Francis et al. 2011a), but also based on communication strategies. Understanding both the physiological basis for energetic masking and the differences in communication strategies can help us understand variable responses observed among species and among different types of anthropogenic noise (Francis and Blickley 2012).

Typically, ecologists studying masking consider only frequency masking (but see Chan and Blumstein 2011, Fig. 3.1), but other types of masking may also alter perception of sounds. For example, energetic masking can interfere with signal detection and discrimination when the noise and signal do not occur simultaneously (i.e., temporal masking; Moore 2007). Temporal masking occurs when a sudden or acute interfering acoustic stimulus conceals an acoustic signal occurring a few milliseconds before (i.e., backward masking) or after (i.e., forward masking) the masking sound (Moore 2007). The mechanisms responsible for the occurrence of non-simultaneous masking are still not well understood (Moore 2007, 2012). Several mechanisms have been proposed to account for forward masking (Moore 2007); for example, the presence of the masking noise prior to the signal may diminish the ability of the neurons to respond to the signal (Meddis and O'Mard 2005), resulting in the inability to detect a signal (Plomp 1964). With backward masking, the masking noise may obstruct the ability to detect the signal because the signal response is still accumulating when the masking noise occurs (Moore 1995, 2012). Hence, consideration of these neurological mechanisms can help understand observed effects that seem driven by noise, but not by frequency masking.

Informational masking

Compared to energetic masking, which is thought to be limited to the auditory periphery (but see Durlach et al. 2003), informational masking is a much more nuanced and complicated concept as it seems to result from reduced signal perception due to interference in cognitive processing leading to distraction (Kidd et al. 2008). Essentially, an individual's attention is limited by competing stimuli provoked by the presence of a distracting noise (Pollack 1976, Durlach et al. 2003, Kidd et al. 2008). Effects of informational masking can be even more extensive than effects of energetic masking, as it can occur well beyond the spatial extent at which noise amplitude is strong enough to energetically mask signal frequencies (Banbury et al. 2001). Nonetheless, this concept has been applied to understand effects of noise in far fewer ecological studies than has energetic masking (Fig. 3.1). Recent ecological studies have addressed the importance of informational masking on animal communication, particularly resulting from anthropogenic noise, leading to a series of studies attempting to isolate its effects from those driven by energetic masking (Chan et al. 2010a, b, Hubbard et al. 2015, Grade and Sieving 2016). However, our understanding of its potential impacts on ecological systems lags behind our understanding of effects of energetic masking, perhaps because the complexity of its psychological impacts results in greater variability among species in their responses to distraction.

Understanding the mechanisms that explain effects of informational and energetic masking is necessary to anticipate the different circumstances in which each type of masking might be influential. Informational masking in the auditory channel takes place when the signal and background noise are both energetically distinguishable, but the receiver is still unable to discern the acoustic signal from the irrelevant information (Brungart 2001, 2005). Similar to energetic masking, informational masking can provoke decreased detection and discrimination of signals (Leek et al. 1991); however, it is not due to frequency overlap or low SNR within the auditory filters (Neff 1995). Instead, informational masking interferes with a receiver's ability to recognise or identify a signal. In animal communication systems, identification increases efficiency by allowing the receiver to adjust their response in relation to sender (e.g., sex, age, species) and signal (e.g., alarm, mating) class, recognised individuals (Tibbetts and Dale 2007), previous interactions (Caldwell 1992), or sender reliability (Hare and Atkins 2001). Informational masking may occur because the brain's processing rate of information is limited compared to the amount of information the peripheral organs can perceive (i.e., reduced information processing; Dukas 2004), and/or because irrelevant stimuli are involuntarily processed to the detriment of stimuli relevant to the completion of a task (i.e., attentional shift; Beaman 2005). Therefore, a triage needs to occur to determine what information is relevant and what information is not (Hockey 1997, Beaman 2005), at which point the addition of anthropogenic noise can interfere with this process and lead to sub-optimal decisions affecting communication (Szalma and Hancock 2011).

The reallocation of limited attention to irrelevant stimuli has been considered in the distracted prey hypothesis (Chan et al. 2010a). According to this hypothesis, irrelevant stimuli within an animal's perceptual range have the potential to distract the individual, hindering the receiver's ability to respond appropriately to a potential predator (Chan et al. 2010a). This effect can occur across sensory modalities (Blumstein 2014) and in any animal with attentional capabilities (Chan and Blumstein 2011). Although increased amplitude and duration of white noise resulted in greater distraction in a study of Caribbean hermit crabs (*Coenobita clypeatus*; Chan et al. 2010b), informational masking can occur in low-amplitude noise conditions provided it is still detectable by the auditory periphery (Banbury et al. 2001, Beaman 2005, Chan et al. 2010a). Consistent with this, human psychological studies assessing effects of irrelevant sounds have demonstrated that reduced performance in short-term memory tasks caused by the involuntary attentional shift to a distracting stimuli is not directly dependent on noise amplitude (Jones et al. 1990, Jones 1993, Ellermeier and Hellbrück 1998). Instead, informational masking is context-dependent, varying with the characteristics of interfering background noise (i.e., intermittent noise more distracting than chronic; e.g., Loeb 1986, Leek et al. 1991) and vigilance demands of the task (i.e., low perceptual loads more prone to interruption from distractor; e.g., Beaman and Jones 1997, 1998, Lavie et al. 2014). Although exposure to a distracting noise prior to performing a task may lead to habituation in human listeners, these reported temporary reductions in masking were dependent on length of exposure period and number of repetitions, on the vigilance demands of the task, and were highly variable among studies (Cowan 1995, Röer et al. 2011, Bell et al. 2012). Hence, the extent to which anthropogenic noise might lead to informational masking in free-living animals is unclear.

The differences among the mechanisms that result in energetic and informational masking explain why informational masking may have a more extensive ecological impact than energetic masking (Table 3.2). To demonstrate the extent to which informational masking can influence communication, I compared energetic and informational masking acoustic footprints of noise produced by the different oil well pumps on three grassland songbird species (Appendix S3.2). Since informational masking can occur in conditions where noise is just perceivable (Dooling and Blumenrath 2013), its acoustic footprint was estimated by conducting spectral analyses of the different noise profiles and determining the distance at which SNR across the song frequency range was greater than ambient noise for each focal species. I found that informational masking had the potential to interfere with communication events across a greater spatial area than energetic masking (Fig. 3.4; see Appendix S3.2: Table S3.2.3). For Baird's Sparrow, there was a 20–266.7% increase in acoustic footprint due to informational masking (Fig. 3.4a; see Appendix S3.2: Table S3.2.3a). Chestnut-collared Longspur was equally influenced by informational and energetic masking in power-grid pumpjack sites, but informational masking had a 106.8–127.3% greater acoustic footprint than energetic masking for both generator and power-grid powered screwpumps (Fig. 3.4b; see Appendix S3.2: Table S3.2.3b). Savannah Sparrows were also more exposed to informational than energetic masking by most types of infrastructure (Fig. 3.4c; Appendix S3.2: Table S3.2.3c). Because sound amplitude drops off quickly and exponentially as distance to the source increases, only animals within a relatively small radius of the noise source are affected by energetic masking. However, informational masking occurs well beyond the point at which noise power is no longer strong enough to physiologically mask a signal. Integrating this background on psychoacoustic mechanisms into noise impact studies of wild populations can enable ecologists to better estimate potential acoustic footprint of different noise sources for different species.

Table 3.2 Comparison of attributes between energetic and informational masking.

Attribute	Energetic masking	Informational masking
Point of origin	auditory periphery	central cognitive processes
Cause	lack of mechanical response of the basilar membrane in the cochlea	irrelevant stimuli causing involuntary redistribution of attention due to reduced information processing or attentional shift
Circumstance	spectra-temporal overlap between signal and background noise frequencies of noise falling within auditory filters’ critical bandwidth contribute most to signal masking	content and properties of stimuli leading signal to be undiscernible from noise although energetically distinguishable due to uncertainty or similarity
Outcome	receiver unable to detect a signal or discriminate among signals	distraction impedes signal detection, discrimination and/or identification reduced working memory or increased mental work load, and reduced performance accuracy
Consequences of reducing noise at the source	reduced probability of masking	difficult to assess due to dependency on context but will reduce acoustic footprint
	reduced probability of communication errors	potentially little to no effect on communication error since distraction can occur at low noise amplitudes and can result from attentional shifts not directly amplitude-dependent

Although implementing noise reduction measures would reduce the footprint of both energetic and informational masking, effects of informational masking will still cover a greater area. As distractions interfere with the ability to recognise subtle differences among signals necessary for identification (Wiley 2015), anthropogenic noise may have widespread effects on communication events that require, for example, offspring, mate, or neighbour recognition. Further, informational masking may help explain the effects of noise that are not a direct function of noise amplitude, namely effects that do not decline as distance to the noise source increases and cannot be explained by the conventional signal detection theory model (Akre and Johnsen 2016). Hence, if informational masking is occurring, reducing the amplitude of the noise without manipulating its content may not decrease the intensity of the distraction (Jones et al. 1990, Ellermeier and Hellbrück 1998). Therefore, I argue that effects of informational masking should be considered when evaluating effects of anthropogenic noise, and that consequences of noise exposure on animal communication may be undetected if knowledge from a range of disciplines is not integrated.

Release from masking

Despite the prevalence of noise in natural environments, animals exposed to anthropogenic noise can experience release from energetic and informational masking. The potential for and effectiveness of this strategy depends on spatial location, properties of interfering noise, and behavioural plasticity of the organism, and offers a partial release from masking (Langemann and Klump 2005). Psychoacoustic studies have found that signal perception can be improved by changing the orientation of the head to increase differences in amplitude and phase of frequency components arriving to each ear (e.g., binaural cues), or if the signal is spatially separated from the masking noise (e.g., humans, Ebata et al. 1968, anurans, Schwartz and Gerhardt 1989, birds, Klump 2000). For example, in a laboratory study of budgerigars, signal detection thresholds were lower when binaural listening was possible and when the signal was separated by 90° from the noise source (Dent et al. 1997). Further, anthropogenic noise sources are often amplitude-modulated (Richards and Wiley 1980, Singh and Theunissen 2003), meaning they fluctuate in amplitude over time and across different frequency ranges (Klump 1996, Nelken et al. 1999, Schnupp et al. 2011). When a broadband noise has a predictable pattern of amplitude modulation (i.e., coherently modulated), signal perception is improved compared to detection in the presence of a noise with constant amplitude (i.e., comodulation masking release; humans, Hall et al. 1984, anurans, see Vélez et al. 2013, birds, see Dooling and Blumenrath 2013, non-human mammals, e.g., Pressnitzer et al. 2001). In female Cope's gray tree frog (*Hyla chrysoscelis*), detection thresholds of a signal decreased approximately 3–5 dB in the amplitude-modulated treatment compared to noise with constant amplitude (Bee and Vélez 2008). Finally, since spatially mediated and comodulation masking release allows for better sound segregation between signal and noise, these mechanisms are also expected to provide release from informational masking in humans and potentially to a greater degree than when confronted with energetic masking (Best et al. 2005, Kidd et al. 2005, Watson 2005). Although ecological studies have addressed how these masking release processes of receivers can reduce effects of energetic masking (Parris and McCarthy 2013), integrating knowledge from psychoacoustics and a more in-depth understanding of sound physics allows for a better assessment of informational masking impacts on wild populations.

Because informational masking is regulated by cognitive mechanisms rather than physical ones, strategies that animals adopt to enhance signals or decrease noise when faced with energetic masking may not resolve the problem of informational masking. For example, increasing SNR can reduce the risk of energetic masking, and animals can achieve this by changing their location (Bayne et al. 2008) or the timing of signal production (Fuller et al. 2007, Brumm and Zollinger 2013). However, increasing SNR may not reduce effects of informational masking, in which the signal and background noise are already energetically distinguishable (Brungart 2001, 2005). Similarly, signal enhancement strategies used to counter energetic masking such as increasing amplitude (Brumm and Zollinger 2011), redundancy (Brumm and Slater 2006), or modifying duration (Pohl et al. 2013) and frequency of the signal (Slabbekoorn and Peet 2003) may be inefficient in resolving communication issues caused by informational masking. Hence, applying neuropsychological and psychoacoustical concepts to behavioural ecology may help to properly understand effects of and differences between informational and energetic masking.

AUDITORY SCENE ANALYSIS

Anthropogenic noise may also add to the complexity of the acoustic environment, and noise contributions from multiple sources may make it more difficult for animals to detect and discriminate among important signals. The attentional process involved in isolating one acoustic stimulus from an acoustic background composed of multiple acoustic stimuli is called auditory scene analysis. Auditory scene analysis is the process of assembling and isolating different auditory streams to interpret them as a whole or independently, and is dependent on selective attention (Bregman 1990). From a neurophysiological perspective, selective attention is when the affinity for one stimulus is heightened by means of the stimulation of some neurons and the inhibition of other neurons (Kastner and Ungerleider 2000, Treue 2001). To segregate irrelevant acoustic stimuli from relevant ones into different auditory streams (i.e., auditory stream segregation; Bregman 1990), neurons tuned to a set of physical acoustic properties of the relevant signal are thought to be favoured at the detriment of the neurons associated with features of irrelevant stimuli (see Klump 2016, Itatani and Klump 2017). When acoustic scene analysis is not possible, individuals may not be able to react appropriately to environmental stimuli, consequently leading to fitness-related costs (Fay 2008).

In humans, this phenomenon has been extensively explored, especially in the context of the "cocktail party problem", which implies that an individual in a cocktail party setting is challenged to isolate the voice of one individual from an assortment of other voices (Cherry 1953, Wood and Cowan 1995, Conway et al. 2001). Since many animals communicate in groups and are subject to interfering noise, evidence of acoustic scene analyses has been found in many taxa such as non-human mammals, birds, frogs, and fish (reviewed in Lewicki et al. 2014, Itatani and Klump 2017). For example, tree frogs in the genus *Hyla* are able to discriminate among conspecifics and heterospecifics in choruses (see Bee 2015) and European Starlings (*Sturnus vulgaris*) can identify songs of known individuals among a chorus of multiple conspecifics (Wisniewski and Hulse 1997). In a playback experiment where conspecific songs and white noise was broadcasted, male canaries (*Serinus canaria*) were able to isolate and appropriately respond to a song, but performance decreased with increasing amplitude of white noise and with number of added distracting stimuli (Appeltants et al. 2005), suggesting negative effects of ambient noise on accuracy in auditory scene analysis. Hence, it is clear that discrimination and identification capacities are dependent on the ability to analyse the acoustic scene in complex natural environments (Bregman 1990, Griffiths and Warren 2004), and this process is influenced by attention (Bregman 2007), which is susceptible to informational masking. Auditory scene analysis is influenced by both neurophysiological processes of the individual and the acoustic environment created by the surrounding population and community, as well as the presence of anthropogenic noise sources.

Auditory scene analysis varies significantly among species and across the anthropogenic landscape, depending on distribution and density of industrial and urban developments. For example, certain species need to isolate the signal of a specific individual from a chorus of conspecific and heterospecific signals (e.g., birds, frogs). If several anthropogenic noise sources result in multiple auditory inputs coming from different locations, this could increase the potential for distraction compared with a single noise source (Jones and Macken 1995). This problem could be reduced by centralising noise sources (e.g., multiple horizontal oil wells from centralised well pads), ensuring that noise is emitted from a single location instead of multiple locations distributed across the landscape. A study modelling the acoustic footprint of gas well compressors in a 16 km^2 investigated various noise reduction scenario and their potential influence on surrounding bird habitat (Francis et al. 2011b). They found that installing sound barrier walls around the present infrastructure distribution or around a centralised noise source composed of multiple compressors resulted in a 70% decrease in acoustic footprint (Francis et al. 2011b).

Properties of background noise strongly influence whether irrelevant sound is likely to impact communication. Different types of anthropogenic noise are expected to have different ecological effects; however, predicting these differences is not always straightforward, as effects of some features of background noise are not intuitive. In experimental psychological studies, background noise characterised by multiple relatively similar proximate sound sources was found to mask each other (Jones and Macken 1995). Conversely, in the case of less predictable intermittent noise sources, if the amplitude of an acoustic distraction causing involuntary attention shifts is decreased, this will decrease the probability of energetic masking, but may not decrease the intensity of informational masking (Jones et al. 1990, Ellermeier and Hellbrück 1998). Auditory scene analysis, and the differences between mechanisms that result in energetic vs. informational masking, suggests that mitigation measures for wild populations that simply reduce the amplitude of anthropogenic noise without manipulating its content (i.e., frequency range and variations) may not be successful in reducing acoustic distractions in exposed animal populations. As a greater spatial extent is subject to informational masking than frequency masking, this has wide-ranging conservation implications.

MULTIMODAL COMMUNICATION

While acoustic masking prevents the detection of auditory signals, animal communication often occurs in more than one sensory modality (see Halfwerk and Slabbekoorn 2015), and thus, impacts of anthropogenic noise on behaviour can be complex. The presence of added noise in one sensory channel (e.g., acoustic) can result in the recruitment of inputs in different sensory channels by the sensory system (Gazzaniga et al. 2009). This "integration effect" occurs when an input in one modality is not strong enough to elicit a behavioural response; thus, other sensory inputs need to be engaged for an individual to perceive a multimodal signal and extract the essential information that is likely to influence the decision-making process (Gazzaniga et al. 2009). Multimodal signals allow receivers to rely on other modalities less prone to masking to interpret a signal, and allow senders to enhance other signal components (e.g., visual) when the primary sensory channel is compromised (i.e., redundant signalling), and thus could potentially reduce the impacts of acoustic masking (Møller and Pomiankowski 1993, Brumm and Slabbekoorn 2005, Hebets and Papaj 2005).

Although multimodal signals may increase signal detectability and help counter some of the risks associated with communicating in anthropogenic noise (Wiley 2013), they can also increase the probability of detection by a predator or parasite, or eavesdropping by competing conspecifics (Partan and Marler 2005). A recent review of multimodal shifts due to anthropogenic interference across several taxa (i.e., mammals, birds, amphibians, fish, insects, arachnids) showed that most multimodal signals investigated communicated non-redundant messages (Partan 2017), where the grouping of signals in different modalities forms the content, or the distinct components provide separate indices (Narins et al. 2003), and thus, obstruction in one modality can lead to a lack of response from the receiver. In male túngara frogs (*Physalaemus pustulosus*), the difference in arrival time between signals from different modalities (e.g., sound and odour) serves as an estimate of distance from the source of the signal (e.g., sender; Halfwerk et al. 2014). In Red-winged Blackbirds (*Agelaius phoeniceus*), the vocal components of nestling begging signals influenced feeding rate, while the visual signals were associated with gaining access to food while competing with siblings (Glassey and Forbes 2002). Hence, signals may be particularly sensitive to environmental noise when the appropriate response is dependent on multiple modalities (Halfwerk and Slabbekoorn 2015). Neurophysiological studies and physiological evidence help us understand why communication may be disrupted in noisy habitats even when signals are multimodal.

CROSS-MODAL INTERFERENCE

Although historically considered to be modality-specific, it is now widely accepted that informational masking can occur not just within one sensory modality (e.g., distraction from sound stimulus by another sound source) but also among different sensory modalities (e.g., distraction from visual stimulus by sound source; Driver and Spence 1998a, b). During the processing of signals, attention requires prioritisation of certain information at the detriment of less relevant information (Smith et al. 2007). Therefore, attentional processing of a primary signal can be affected by signals presented in other sensory modalities (Driver and Spence 1998a, Chan and Blumstein 2011). Studies in brain imaging have demonstrated that the areas historically assumed responsible for the treatment of information coming from a single sensory modality may also be stimulated or controlled by stimuli originating from other sensory modalities (Calvert et al. 1997, Macaluso et al. 2000). Therefore, signal processing in these modality-specific areas of the brain is also influenced by signals, or noise, presented in other sensory modalities (Driver and Spence 2000, Klemen et al. 2009).

Distractions occurring across sensory modalities have been studied extensively in humans in the fields of cognitive psychology and neuroscience, particularly in the completion of auditory-visual tasks (Parmentier et al. 2008, SanMiguel et al. 2010, Ljungberg et al. 2012) and in the execution of tactile-visual tasks (Parmentier et al. 2011, Ljungberg and Parmentier 2012). For example, detecting the location of an acoustic stimulus can be affected and falsely altered by means of a distracting visual stimulus (i.e., ventriloquist effect; Howard and Templeton 1966, Jack and Thurlow 1973, Bertelson and Radeau 1981). Acoustic distractions have also been shown to alter perception of duration (Walker and Scott 1981), rate (Welch et al. 1986), and intensity (Stein et al. 1996) of a visual signal, and to affect temporal visual acuity (i.e., enhanced or impaired; Scheier et al. 1999) in humans. In a psychological experiment, acoustic stimuli proved to be a powerful distraction, causing an increased reaction time in the detection of both visual and acoustic signals (Leiva et al. 2015). Effects of cross-modal distractions may also be pervasive across free-living animal populations. For example, different oil pumps produce different multimodal stimuli and some structures may be more conducive to cross-modal interference than others. Screwpumps have a low vertical profile (typically 2.7 m tall) and their only observable movement is the continuous rapid rotation of the screw's axis atop the well head, while pumpjacks are taller (approximately 4.5 m) and comprise many moving parts (i.e., vertical nodding and simultaneously circular motions) which may lead to greater cross-modal interference to acoustic communication. Hence, knowledge of these cross-modal impacts found in psychological studies can aid ecological studies in interpreting patterns in response to anthropogenic noise that may have previously been considered spurious or irrelevant.

Distractions clearly influence communication; however, the extent to which distractions in another modality interfere with communication processes is much less well known in non-human animals. Norway rats (*Rattus norvegicus*) completing a visual discrimination task performed significantly worse when background noise was being broadcasted compared to the control condition (Maes and de Groot 2003). In a playback experiment of anthropogenic noise, researchers proposed that the decrease in predator vigilance behaviour in Caribbean hermit crabs was induced by the reallocation of attentional efforts to the noise disturbance (Chan et al. 2010b). This hypothesis was reinforced by the fact that adding a flashing light, or visual distraction, further decreased their response time to the presence of an apparent predator (Chan et al. 2010b). Kunc et al. (2014) examined the impacts of anthropogenic noise on the common cuttlefish (*Sepia officinalis*), a species that does not primarily use acoustic cues as a means of communication. Following exposure to an anthropogenic sound stimulus, cuttlefish modified behaviours in the visual channel and the tactile channel, suggesting increased vigilance (Kunc et al. 2014). In a recent playback study of road noise, dwarf mongoose (*Helogale parvula*) took longer to detect the presence of predators in noise treatments compared to ambient treatments (Morris-Drake et al. 2016).

Although cross-modal distractions due to noise provoke decreased efficiency in the performance of anti-predator behaviours in several species (Chan et al. 2010b, Kunc et al. 2014, Morris-Drake et al. 2016), exposure to unfamiliar noise can also result in the opposite effect; exposed animals can benefit from greater vigilance and better predator detection (i.e., risk disturbance hypothesis; Frid and Dill 2002). For example, in noisy conditions black-tailed prairie dogs (*Cynomys ludovicianus*) exhibited anti-predator behaviours in response to the presence of humans sooner than under control conditions (Shannon et al. 2016b). In the psychology literature, the potential for distraction is thought to be related to vigilance demands (i.e., perceptual load) of the task (Jones 1993, Beaman and Jones 1997, 1998) which may be sufficiently great enough in this context (i.e., predator detection by a prey species) to prevent interference from a distracting noise (Lavie et al. 2014). However, since response to an approaching human was greater in noisy conditions, these results may be better explained by impaired selective attention in noisy conditions resulting in hyper-arousal and reduced selectivity (Belmonte and Yurgelun-Todd 2003). Although noise may seem to increase alertness for this species, the integration of mechanisms from another discipline offers an alternative explanation revealing potential negative noise impacts. I suggest that approaching behavioural ecology studies with a psychological perspective, such as those shown here, can allow for the exploration of alternative explanations for effects of noise.

CONCLUSIONS AND FUTURE DIRECTIONS

An approach to signal perception that integrates psychology, physiology, and neurophysiology with ecological knowledge can significantly increase our ability to understand the complexities involved in perception. Our understanding of the perception of sound (i.e., psychoacoustics), and how it is treated by central cognitive processes (i.e., cognitive psychology) and regulated by the nervous system (i.e., neurophysiology), ideally leading to a fitness-enhancing behavioural response (i.e., behavioural ecology and psychology), all enhance our understanding of how different species might respond to anthropogenic noise. Interpreting ecological impacts in light of these disciplines gives rise to a wealth of additional applicable and relevant information, and can contribute to a much deeper understanding of the underlying mechanisms regulating ecological processes.

Despite this tremendous amount of knowledge available in other disciplines, it is not currently being efficiently applied to ecological studies. Researchers should attempt to incorporate multiple concepts discussed in this paper instead of only presenting one of these mechanisms as a potential explanation for detrimental effects of noise on animal communication. Since anthropogenic noise has the potential to negatively affect a greater amount of species than can be estimated by effects of energetic masking alone (Luo et al. 2015), future ecological studies should aim to apply this knowledge from other disciplines to develop hypotheses, and subsequently, investigate them in wild populations. Further, retroactively interpreting existing ecological literature through the lens of hypotheses and frameworks developed by these disciplines would also benefit environmental impact assessments. Overall, I argue that an approach that integrates knowledge gained from research across many taxa can help direct ecological research efforts, enable a more refined analysis of effects of anthropogenic activities, and lead to novel alternative solutions to mitigate noise impacts on wild populations.

LITERATURE CITED

Akre, K. L. and S. Johnsen. 2016. Communication through a window of error: proportional processing and signal categorization. Pages 137–167 *in* M. A. Bee, and C. T. Miller, editors. Psychological mechanisms in animal communication (Vol. 5). Springer International Publishing, Cham, Switzerland.

Appeltants, D., T. Q. Gentner, S. H. Hulse, J. Balthazart, and G. F. Ball. 2005. The effect of auditory distractors on song discrimination in male canaries (*Serinus canaria*). Behavioural Processes 69:331–341.

Banbury, S. P., W. J. Macken, S. Tremblay, and D. M. Jones. 2001. Auditory distraction and short-term memory: phenomena and practical implications. Human Factors 43:12–29.

Barber, J. R., K. R. Crooks, and K. M. Fristrup. 2010. The costs of chronic noise exposure for terrestrial organisms. Trends in Ecology & Evolution 25:180–189.

Bayne, E. M., L. Habib, and S. Boutin. 2008. Impacts of chronic anthropogenic noise from energy-sector activity on abundance of songbirds in the boreal forest. Conservation Biology 22:1186–1193.

Beaman, C. P. 2005. Auditory distraction from low-intensity noise: a review of the consequences for learning and workplace environments. Applied Cognitive Psychology 19:1041–1064.

Beaman, C. P., and D. M. Jones. 1997. Role of serial order in the irrelevant speech effect: tests of the changing-state hypothesis. Journal of Experimental Psychology: Learning, Memory, and Cognition 23:459–471.

Beaman, C. P., and D. M. Jones. 1998. Irrelevant sound disrupts order information in free recall as in serial recall. The Quarterly Journal of Experimental Psychology: Section A 51:615–636.

Bee, M. A. 2015. Treefrogs as animal models for research on auditory scene analysis and the cocktail party problem. International Journal of Psychophysiology, 95:216–237.

Bee, M. A., and C. T. Miller. 2016. Psychological mechanisms in animal communication (Vol. 5). Springer International Publishing, Cham, Switzerland.

Bee, M. A., and A. Vélez. 2008. Comodulation masking release in the perception of vocalizations by gray treefrogs. Abstract Archives – Association for Research in Otolaryngology 31:#812.

Bell, R., J. P. Röer, S. Dentale, and A. Buchner. 2012. Habituation of the irrelevant sound effect: evidence for an attentional theory of short-term memory disruption. Journal of Experimental Psychology: Learning, Memory, and Cognition 38:1542–1557.

Belmonte, M. K., and D. A. Yurgelun-Todd. 2003. Functional anatomy of impaired selective attention and compensatory processing in autism. Cognitive Brain Research 17:651–664.

Bertelson, P., and M. Radeau. 1981. Cross-modal bias and perceptual fusion with auditory-visual spatial discordance. Attention, Perception, & Psychophysics 29:578–584.

Best, V., E. Ozmeral, F. J. Gallun, K. Sen, and B. G. Shinn-Cunningham. 2005. Spatial unmasking of birdsong in human listeners: energetic and informational factors. The Journal of the Acoustical Society of America 118:3766–3773.

Blumstein, D. T. 2014. Attention, habituation, and antipredator behaviour: implications for urban birds. Pages 41–53 *in* D. Gil, and H. Brumm, editors. Avian urban ecology. Oxford University Press, Oxford, UK.

Blumstein, D. T., and O. Berger-Tal. 2015. Understanding sensory mechanisms to develop effective conservation and management tools. Current Opinion in Behavioral Sciences 6:13–18.

Bradbury, J. W., and S. L. Vehrencamp. 2011. Principles of animal communication. Second edition. Sinauer Associates, Sunderland, Massachusetts, USA.

Bregman, A. S. 1990. Auditory scene analysis: the perceptual organization of sound. The MIT Press, Cambridge, Massachusetts, USA.

Bregman, A. S. 2007. Progress in the study of auditory scene analysis. IEEE Workshop on Applications of Signal Processing to Audio and Acoustics, 2007:122–126.

Bro-Jørgensen, J. 2010. Dynamics of multiple signalling systems: animal communication in a world in flux. Trends in Ecology & Evolution 25:292–300.

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

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

Brumm, H., and S. A. Zollinger. 2011. The evolution of the Lombard effect: 100 years of psychoacoustic research. Behaviour 148:1173–1198.

Brumm, H., and S. A. Zollinger. 2013. Avian vocal production in noise. Pages 187–227 *in* H. Brumm, editor. Animal communication and noise (Vol. 2). Springer Science & Business Media, Berlin.

Brungart, D. S. 2001. Informational and energetic masking effects in the perception of two simultaneous talkers. The Journal of the Acoustical Society of America 109:1101–1109.

Brungart, D. S. 2005. Informational and energetic masking effects in multitalker speech perception. Pages 261–267 *in* P. Divenyi. Speech separation by humans and machines. Kluwer Academic, Dordrecht.

Caldwell, R. L. 1992. Recognition, signalling and reduced aggression between former mates in a stomatopod. Animal Behaviour 44:11–19.

Calvert, G. A., E. T. Bullmore, M. J. Brammer, R. Campbell, S. C. Williams, P. K. McGuire, et al. 1997. Activation of auditory cortex during silent lipreading. Science 276:593–596.

Chan, A. A. Y. H., and D. T. Blumstein. 2011. Attention, noise, and implications for wildlife conservation and management. Applied Animal Behaviour Science 131:1–7.

Chan, A. A. Y. H., P. Giraldo-Perez, S. Smith, and D. T. Blumstein. (2010a). Anthropogenic noise affects risk assessment and attention: the distracted prey hypothesis. Biology Letters 6:458–461.

Chan, A. A. Y. H., W. D. Stahlman, D. Garlick, C. D. Fast, D. T. Blumstein, and A. P. Blaisdell. (2010b). Increased amplitude and duration of acoustic stimuli enhance distraction. Animal Behaviour 80:1075–1079.

Cherry, E. C. 1953. Some experiments on the recognition of speech, with one and with two ears. The Journal of the Acoustical Society of America 25:975–979.

Conway, A. R., N. Cowan, and M. F. Bunting. 2001. The cocktail party phenomenon revisited: The importance of working memory capacity. Psychonomic Bulletin & Review 8:331–335.

Cowan, N. 1995. Attention and memory: an integrated framework. Oxford University Press, London, UK.

Dent, M. L., O. N. Larsen, and R. J. Dooling. 1997. Free-field binaural unmasking in budgerigars (*Melopsittacus undulatus*). Behavioral Neuroscience 111:590–598.

Dooling, R. J. 1980. Behavior and psychophysics of hearing in birds. Pages 261–288 *in* A. N. Popper, and R. R. Fay, editors. Comparative studies of hearing in vertebrate. Springer-Verlag, New York, New York, USA.

Dooling, R. J. 1982. Auditory perception in birds. Pages 95–130 *in* D. H. Kroodsma, and E. H. Miller, editors. Acoustic communication in birds (Vol. 1). Academic Press, New York, New York, USA.

Dooling, R. J. 1992. Hearing in birds. Pages 545–559 *in* D. B. Webster, R. R. Fay, and A. N. Popper. The evolutionary biology of hearing. Springer-Verlag, New York, New York, USA,

Dooling, R. J., and S. H. Blumenrath. 2013. Avian sound perception in noise. Pages 229-250 *in* H. Brumm, editor. Animal communication and noise (Vol. 2). Springer Science & Business Media, Berlin.

Dooling, R. J., B. Lohr, and M. L. Dent. 2000. Hearing in birds and reptiles. Pages 308–359 *in* R. J. Dooling and R. R. Fay, editors. Comparative hearing: birds and reptiles. Springer-Verlag, New York, New York, USA.

Dooling, R. J., and A. N. Popper. 2007. The effects of highway noise on birds. The California Department of Transportation, Division of Environmental Analysis, Sacramento, California, USA.

Dooling, R. J., and A. N. Popper. 2016. Technical guidance for assessment and mitigation of the effects of highway and road construction noise on birds. The California Department of Transportation, Division of Environmental Analysis, Sacramento, California, USA.

Driver, J., and C. Spence. 1998a. Attention and the crossmodal construction of space. Trends in Cognitive Sciences 2:254–262.

Driver, J., and C. Spence. 1998b. Crossmodal attention. Current Opinion in Neurobiology 8:245–253.

Driver, J., and C. Spence. 2000. Multisensory perception: beyond modularity and convergence. Current Biology 10:R731–R735.

Dukas, R. 2004. Causes and consequences of limited attention. Brain, Behavior and Evolution 63:197–210.

Durlach, N. I., C. R. Mason, G. Kidd Jr, T. L. Arbogast, H. S. Colburn, and B. G. Shinn-Cunningham. 2003. Note on informational masking (L). The Journal of the Acoustical Society of America 113:2984–2987.

Ebata, M., T. Sone, and T. Nimura. 1968. Improvement of hearing ability by directional information. The Journal of the Acoustical Society of America 43:289–297.

Ellermeier, W., and J. Hellbrück. 1998. Is level irrelevant in" irrelevant speech"? Effects of loudness, signal-to-noise ratio, and binaural unmasking. Journal of Experimental Psychology: Human Perception and Performance 24:1406–1414.

Erbe, C., C. Reichmuth, K. Cunningham, K. Lucke, and R. Dooling. 2016. Communication masking in marine mammals: A review and research strategy. Marine Pollution Bulletin 103:15–38.

Fay, R. R. 2008. Auditory scene analysis. Bioacoustics 17:106–109.

Fletcher, H. 1940. Auditory patterns. Reviews of Modern Physics 12:47–65.

Forrest, T. G. 1994. From sender to receiver: propagation and environmental effects on acoustic signals. American Zoologist 34:644–654.

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

Francis, C. D., and J. L. Blickley. 2012. Introduction: research and perspectives on the study of anthropogenic noise and birds. Ornithological Monographs 74:1–5.

Francis, C. D., C. P. Ortega, and A. Cruz. 2011a. Noise pollution filters bird communities based on vocal frequency. PLoS ONE 6:e27052.

Francis, C. D., J. Paritsis, C. P. Ortega, and A. Cruz. 2011b. Landscape patterns of avian habitat use and nest success are affected by chronic gas well compressor noise. Landscape Ecology 26:1269–1280.

Freyaldenhoven, M. C., D. Fisher Smiley, R. A. Muenchen, and T. N. Konrad. 2006. Acceptable noise level: reliability measures and comparison to preference for background sounds. Journal of the American Academy of Audiology 17: 640–648.

Frid, A., and L. Dill. 2002. Human-caused disturbance stimuli as a form of predation risk. Conservation Ecology 6:11.

Fuller, R. A., P. H. Warren, and K. J. Gaston. 2007. Daytime noise predicts nocturnal singing in urban robins. Biology Letters 3:368–370.

Gazzaniga, M. S., R. B. Ivry, and G. R. Mangun. 2009. Cognitive neuroscience: the biology of the mind. Third edition. W.W. Norton and Company, New York, New York, USA.

Glassey, B., and S. Forbes. 2002. Muting individual nestlings reduces parental foraging for the brood. Animal Behaviour 63:779–786.

Government of Canada. 2017. Species at Risk Public Registry, https://www.sararegistry.gc.ca. Accessed November 7, 2017.

Grade, A. M., and K. E. Sieving. 2016. When the birds go unheard: highway noise disrupts information transfer between bird species. Biology Letters 12:20160113.

Griffiths, T. D., and J. D. Warren. 2004. What is an auditory object? Nature Reviews Neuroscience 5:887–892.

Halfwerk, W., R. A. Page, R. C. Taylor, P. S. Wilson, and M. J. Ryan. 2014. Crossmodal comparisons of signal components allow for relative distance assessment. Current Biology 24:1751–1755.

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

Hall, J. W., M. P. Haggard, and M. A. Fernandes. 1984. Detection in noise by spectro-temporal pattern analysis. The Journal of the Acoustical Society of America 76:50–56.

Hare, J. F., and B. A. Atkins. 2001. The squirrel that cried wolf: reliability detection by juvenile Richardson's ground squirrels (*Spermophilus richardsonii*). Behavioral Ecology and Sociobiology 51:108–112.

Hebets, E. A., and D. R. Papaj. 2005. Complex signal function: developing a framework of testable hypotheses. Behavioral Ecology and Sociobiology 57:197–214.

Hockey, G. R. J. 1997. Compensatory control in the regulation of human performance under stress and high workload: A cognitive-energetical framework. Biological Psychology 45:73–93.

Howard, I. P., and W. B. Templeton. 1966. Human spatial orientation. John Wiley & Sons, Oxford, UK.

Hubbard, L., W. King, A. Vu, and D. T. Blumstein. 2015. Heterospecific nonalarm vocalizations enhance risk assessment in common mynas. Behavioral Ecology 26:632–638.

Itatani, N., and G. M. Klump. 2017. Animal models for auditory streaming. Philosophical Transactions of the Royal Society B 372:20160112.

Jack, C. E., and W. R. Thurlow. 1973. Effects of degree of visual association and angle of displacement on the "ventriloquism" effect. Perceptual and Motor Skills 37:967–979.

Johnstone, R. A. 1996. Multiple displays in animal communication: ‘backup signals’ and ‘multiple messages’. Philosophical Transactions of the Royal Society B 351:329–338.

Jones, D. M. 1993. Objects, streams, and threads of auditory attention. Pages 167–198 *in* A. D. Baddeley, and L. Weiskrantz. Attention: selection, awareness and control. Clarendon Press, Oxford, UK,

Jones, D. M., and W. J. Macken. 1995. Auditory babble and cognitive efficiency: role of number of voices and their location. Journal of Experimental Psychology: Applied 1:216–226.

Jones, D. M., C. Miles, and J. Page. 1990. Disruption of proofreading by irrelevant speech: effects of attention, arousal or memory? Applied Cognitive Psychology 4:89–108.

Kastner, S., and L.G. Ungerleider. 2000. Mechanisms of visual attention in the human cortex. Annual Review of Neuroscience 23:315–341.

Kidd Jr, G., C. R. Mason, and F. J. Gallun. 2005. Combining energetic and informational masking for speech identification. The Journal of the Acoustical Society of America 118:982–992.

Kidd Jr, G., C. R. Mason, V. M. Richards, F. J. Gallun, and N. I. Durlach. 2008. Informational masking. Pages 143–189 *in* W. A Yost, A. N. Popper, and R. R. Fay, editors. Auditory perception of sound sources. Springer Science & Business Media, New York, New York, USA.

Kight, C. R., and J. P. Swaddle. 2011. How and why environmental noise impacts animals: an integrative, mechanistic review. Ecology Letters 14:1052–1061.

Klemen, J., C. Büchel, and M. Rose. 2009. Perceptual load interacts with stimulus processing across sensory modalities. European Journal of Neuroscience 29:2426–2434.

Klump, G. M. 1996. Bird communication in the noisy world. Pages 321–338 *in* D. E Kroodsma, and E. H. Miller, editors. Ecology and evolution of acoustic communication in birds. Cornell University Press, Ithaca, New York, USA,

Klump, G. M. 2000. Sound localization in birds. Pages 249–307 *in* R. R. Fay, and A. N. Popper, editors. Comparative hearing: birds and reptiles. Springer Science & Business Media, New York, New York, USA.

Klump, G.M. 2016. Hearing and communication. Pages 25-48 in J. Call, G. M. Burghardt, I. M. Pepperberg, C. T. Snowdon, and T. Zentall, editors. APA Handbook of comparative psychology, vol 2: perception, learning, and cognition. American Psychological Association, Washington DC, USA.

Kunc, H. P., G. N. Lyons, J. D. Sigwart, K. E. McLaughlin, and J. D. Houghton. 2014. Anthropogenic noise affects behavior across sensory modalities. The American Naturalist 184:E93–E100.

Langemann, U., and G. M. Klump. 2005. Perception and acoustic communication networks. Pages 451–480 *in* P. K. McGregor, editor. Animal communication networks, 451-480. Cambridge University Press, Cambridge, UK.

Lauer, A. M., R. J. Dooling, M. R. Leek, and J. J. Lentz. 2006. Phase effects in masking by harmonic complexes in birds. The Journal of the Acoustical Society of America 119:1251–1259.

Lavie, N., D. M. Beck, and N. Konstantinou. 2014. Blinded by the load: attention, awareness and the role of perceptual load. Philosophical Transactions of the Royal Society B 369:20130205.

Leek, M. R., M. E. Brown, and M. F. Dorman. 1991. Informational masking and auditory attention. Attention, Perception, & Psychophysics 50:205–214.

Leiva, A., F. B. R. Parmentier, and P. Andrés. 2015. Distraction by deviance: comparing the effects of auditory and visual deviant stimuli on auditory and visual target processing. Experimental Psychology 62:54–65.

Lentz, J. J., and M. R. Leek. 2001. Psychophysical estimates of cochlear phase response: Masking by harmonic complexes. Journal of the Association for Research in Otolaryngology 2:408–422.

Leonard, M. L., and A. G. Horn. 2001. Acoustic signalling of hunger and thermal state by nestling tree swallows. Animal Behaviour 61:87–93.

Lewicki, M. S., B. A. Olshausen, A. Surlykke, and C. F. Moss. 2014. Scene analysis in the natural environment. Frontiers in Psychology 5:199.

Ljungberg, J. K., and F. B. R. Parmentier. 2012. Cross-modal distraction by deviance: functional similarities between the auditory and tactile modalities. Experimental Psychology 59:355–363.

Ljungberg, J. K., F. B. Parmentier, A. Leiva, and N. Vega. 2012. The informational constraints of behavioral distraction by unexpected sounds: the role of event information. Journal of Experimental Psychology: Learning, Memory, and Cognition 38:1461–1468.

Loeb, M. 1986. Noise and human efficiency. John Wiley & Sons, Chichester, UK.

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

Luo, J., B. M. Siemers, and K. Koselj. 2015. How anthropogenic noise affects foraging. Global Change Biology 21:3278–3289.

Luther, D., and K. Gentry. 2013. Sources of background noise and their influence on vertebrate acoustic communication. Behaviour 150:1045–1068.

Macaluso, E., C. D. Frith, and J. Driver. 2000. Modulation of human visual cortex by crossmodal spatial attention. Science 289:1206–1208.

Maes, J. H. R., and G. de Groot. 2003. Effects of noise on the performance of rats in an operant discrimination task. Behavioural Processes 61:57–68.

McGregor, P. K., A. G. Horn, M. L. Leonard, and F. Thomsen. 2013. Anthropogenic noise and conservation. Pages 409–444 *in* H. Brumm, editor. Animal communication and noise (Vol. 2). Springer Science & Business Media, Berlin.

Meddis, R., and L. P. O’Mard. 2005. A computer model of the auditory-nerve response to forward-masking stimuli. The Journal of the Acoustical Society of America 117:3787–3798.

Møller, A. P., and A. Pomiankowski. 1993. Why have birds got multiple sexual ornaments? Behavioral Ecology and Sociobiology 32:167–176.

Moore, B. C. J. 1995. Frequency analysis and masking. Pages 161–205 in B. C. J. Moore. Hearing. Academic Press, New York, New York, USA.

Moore, B. C. J. 2007. Cochlear hearing loss: physiological, psychological and technical issues. John Wiley & Sons, West Sussex, UK.

Moore, B. C. J. 2012. An introduction to the psychology of hearing. Sixth edition. Emerald Group Publishing Limited, Bingley, UK.

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

Narins, P. M., W. Hödl, and D. S. Grabul. 2003. Bimodal signal requisite for agonistic behavior in a dart-poison frog, *Epipedobates femoralis*. Proceedings of the National Academy of Sciences 100:577–580.

Neff, D. L. 1995. Signal properties that reduce masking by simultaneous, random-frequency maskers. The Journal of the Acoustical Society of America 98:1909–1920.

Nelken, I., Y. Rotman, and O. B. Yosef. 1999. Responses of auditory-cortex neurons to structural features of natural sounds. Nature 397:154–157.

Parmentier, F. B. R., G. Elford, C. Escera, P. Andrés, and I. San Miguel. 2008. The cognitive locus of distraction by acoustic novelty in the cross-modal oddball task. Cognition 106:408–432.

Parmentier, F. B. R., J. K. Ljungberg, J. V. Elsley, and M. Lindkvist. 2011. A behavioral study of distraction by vibrotactile novelty. Journal of Experimental Psychology: Human Perception and Performance 37:1134–1139.

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

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

Partan, S. R., and P. Marler. 2005. Issues in the classification of multimodal communication signals. The American Naturalist 166:231–245.

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

Plomp, R. 1964. Rate of decay of auditory sensation. The Journal of the Acoustical Society of America 36:277–282.

Pohl, N. U., H. Slabbekoorn, H. Neubauer, P. Heil, G. M. Klump, and U. Langemann. 2013. Why longer song elements are easier to detect: threshold level-duration functions in the great tit and comparison with human data. Journal of Comparative Physiology A 199:239–252.

Pollack I. 1976. Identification of random auditory waveforms. III. Effect of interference. The Journal of the Acoustical Society of America 60:680–686.

Popper, A. N., and A. D. Hawkins. 2012. The effects of noise on aquatic life (Vol .730). Springer Science & Business Media, New York, New York, USA.

Popper, A. N., and A. Hawkins. 2016. The effects of noise on aquatic life II (Vol. 875). Springer Science & Business Media, New York, New York, USA.

Pressnitzer, D., R. Meddis, and I. M. Winter. 2001. Physiological correlates of comodulation masking release in the mammalian ventral cochlear nucleus. The Journal of Neuroscience 21:6377–6386

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

Recio-Spinoso, A., and N. P. Cooper. 2013. Masking of sounds by a background noise–cochlear mechanical correlates. The Journal of Physiology 591:2705–2721.

Rendall, D., M. J. Owren, and M. J. Ryan. 2009. What do animal signals mean? Animal Behaviour 78:233–240.

Rheindt, F. E. 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.

Richards, D. G., and R. H. Wiley. 1980. Reverberations and amplitude fluctuations in the propagation of sound in a forest: implications for animal communication. The American Naturalist 115:381–399.

Röer, J. P., R. Bell, S. Dentale, and A. Buchner. 2011. The role of habituation and attentional orienting in the disruption of short-term memory performance. Memory & Cognition 39:839–850.

SanMiguel, I., D. Linden, and C. Escera. 2010. Attention capture by novel sounds: Distraction versus facilitation. European Journal of Cognitive Psychology 22:481–515.

Scheier, C. R., R. Nijhawan, and S. Shimojo. 1999. Sound alters visual temporal resolution. Investigative Ophthalmology & Visual Science 40:4169.

Schnupp, J., I. Nelken, and A. King. 2011. Auditory neuroscience: making sense of sound. The MIT press, Cambridge, Massachusetts, USA.

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

Shannon, C. E. 1948. The mathematical theory of communication, I and II. Bell System Technical Journal 27:379–423, 623–656.

Shannon, C. E., and W. Weaver. 1963. The measurement theory of communication. University of Illinois Press, Urbana, Illinois, USA.

Shannon, G., K. R. Crooks, G. Wittemyer, K. M. Fristrup, and L. M. Angeloni. 2016b. Road noise causes earlier predator detection and flight response in a free-ranging mammal. Behavioral Ecology 27:1370–1375.

Shannon, G., M. F. McKenna, L. M. Angeloni, K. R. Crooks, K. M. Fristrup, E. Brown, et al. 2016a. A synthesis of two decades of research documenting the effects of noise on wildlife. Biological Reviews 91:982–1005.

Singh, N. C., and F. E. Theunissen. 2003. Modulation spectra of natural sounds and ethological theories of auditory processing. The Journal of the Acoustical Society of America 114:3394–3411.

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

Slabbekoorn, H., and E. A. Ripmeester. 2007. Birdsong and anthropogenic noise: implications and applications for conservation. Molecular Ecology 17:72–83.

Smith, E. E., S. M. Kosslyn, and L. W. Barsalou. 2007. Cognitive psychology: mind and brain. Pearson Prentice Hall, Upper Saddle River, New Jersey, USA.

Stein, B. E., N. London, L. K. Wilkinson, and D. D. Price. 1996. Enhancement of perceived visual intensity by auditory stimuli: a psychophysical analysis. Journal of Cognitive Neuroscience 8:497–506.

Swaddle, J. P., C. D. Francis, J. R. Barber, C. B. Cooper, C. C. Kyba, D. M. Dominoni, et al. 2015. A framework to assess evolutionary responses to anthropogenic light and sound. Trends in Ecology & Evolution 30:550–560.

Szalma, J. L., and P. A. Hancock. 2011. Noise effects on human performance: a meta-analytic synthesis. Psychological Bulletin 137:682–707.

Tibbetts, E. A., and J. Dale. 2007. Individual recognition: it is good to be different. Trends in Ecology & Evolution 22:529–537.

Treue, S. 2001. Neural correlates of attention in primate visual cortex. Trends in Neuroscience 24:295–300.

Vélez, A., J. J. Schwartz, and M. A. Bee. 2013. Anuran acoustic signal perception in noisy environments. Pages 133–185 *in* H. Brumm, editor. Animal communication and noise (Vol. 2). Springer Science & Business Media, Berlin.

Walker, J. T., and K. J. Scott. 1981. Auditory–visual conflicts in the perceived duration of lights, tones, and gaps. Journal of Experimental Psychology: Human Perception and Performance 7:1327–1339.

Watson, C. S. 2005. Some comments on informational masking. Acta Acustica united with Acustica 91:502–512.

Welch, R. B., L. D. DutionHurt, and D. H. Warren. 1986. Contributions of audition and vision to temporal rate perception. Attention, Perception, & Psychophysics 39:294–300.

Wiley, R. H. 2013. Signal detection, noise, and the evolution of communication. Pages 7–30 *in* H. Brumm, editor. Animal communication and noise (Vol. 2). Springer Science & Business Media, Berlin.

Wiley, R. H. 2015. Noise matters: The evolution of communication. Harvard University Press, Cambridge, Massachusetts, USA.

Wisniewski, A. B., and S. H. Hulse. 1997. Auditory scene analysis in European Starlings (*Sturnus vulgaris*): discrimination of song segments, their segregation from multiple and reversed conspecific songs, and evidence for conspecific song categorization. Journal of Comparative Psychology 111:337–350.

Wood, N., and N. Cowan. 1995. The cocktail party phenomenon revisited: how frequent are attention shifts to one's name in an irrelevant auditory channel? Journal of Experimental Psychology: Learning, Memory, and Cognition 21:255–260.

CHAPTER 4. ANTHROPOGENIC NOISE AND INFRASTRUCTURE DECOUPLE HABITAT USE FROM HABITAT QUALITY IN GRASSLAND SONGBIRDS

ABSTRACT

Anthropogenic disturbances can hinder the ability of birds to assess and choose habitats that allow them to optimise their reproductive output. To estimate habitat quality, birds rely on environmental cues historically associated with greater productivity, but these cues may no longer be reliable in human-altered habitats. To test whether both noise and above-ground infrastructure could decouple apparent from realised habitat quality in grassland songbirds, I designed and implemented a novel large-scale, spatially and temporally replicated playback experiment that recreated soundscapes produced by acute (drilling) and chronic (active well) oil infrastructure noise, and compared impacts of noise-producing and quiet playback infrastructure. Three out of four focal species showed a mismatch between relative habitat use and habitat quality. Noise resulted in a perceptual trap for Chestnut-collared Longspurs (i.e., avoided noisy yet otherwise suitable habitats for reproduction) and infrastructure resulted in an ecological traps for Vesper Sparrows (i.e., select habitats that are detrimental for reproduction). Unpredictable, acute drilling noise had a greater impact on habitat use and quality than rhythmic, chronic oil-well noise, although both types of noise resulted in some ecological impacts. While this study demonstrates that noise alone can negatively impact habitat use, nesting success, and nestling quality, it is also clear that effective mitigation strategies depend on determining whether noise or infrastructure leads to negative ecological impacts, and that both must be managed to mitigate impacts on wildlife.

INTRODUCTION

The steady encroachment of anthropogenic noise into natural environments is a source of significant concern for wildlife conservation (Shannon et al. 2016a). Increased levels of anthropogenic noise may reduce the abundance of certain species (Francis et al. 2011), affect predator-prey dynamics (Francis et al. 2009, Shannon et al. 2016b), interfere with acoustic communication (Warren et al. 2006), and act as a physiological stressor (Blickley et al. 2012a, b), all of which can lead to fitness consequences at impacted sites (Barber et al. 2010). Hence, noise pollution results in functional habitat loss and degradation (Francis 2015), and has a particularly large footprint due to the propogation of noise far beyond the perimeter of the built environment. The remarkable rise in noise associated with oil and gas extraction (Bayne et al. 2008) is likely to worsen conditions for species reliant on acoustic communication that are already experiencing extensive and abrupt population declines (Barber et al. 2010), such as North American grassland birds (Sauer et al. 2017).

Anthropogenic disturbances, including noise, might also hinder the ability of birds to assess and choose habitats in which they can optimise their fitness (Bock and Jones 2004). To estimate the relative quality of different breeding sites, birds rely on environmental cues that were historically associated with greater reproductive output (Martin 1995). However, in environments altered by human disturbances, these cues may no longer be effective in predicting habitat quality (e.g., Robertson and Hutto 2006). Hence, noise could potentially decouple proximate (i.e., attractive habitat features) from ultimate (i.e., fitness optimization) factors (Block and Brennan 1993), resulting in species avoiding noisy yet otherwise suitable habitats for reproduction (i.e., perceptual trap or undervalued resource; Patten and Kelly 2010, Robertson and Chalfoun 2016) or selecting impacted habitats that are detrimental to reproduction (i.e., ecological trap; Schlaepfer et al. 2002). Perceptual and ecological traps occur when abundance or occurrence of species are no longer indicative of reproductive probabilities (e.g., Gillespie and Dinsmore 2014). For example, noise may alter the behaviour of nest predators, and thus nest predation rates, but not modify the physical habitat features birds use as cues to assess habitat quality (e.g., Kokko and Sutherland 2001). Therefore, it is necessary to compare both relative abundance and reproductive output between noisy and quiet habitats to determine whether noise results in maladaptive habitat selection behaviours that can accelerate population declines (e.g., Schlaepfer et al. 2002, Gillespie and Dinsmore 2014, Robertson and Chalfoun 2016).

To date, studies on wild populations have found variable responses to noise, and concluded that noise may have negative, positive, or neutral ecological effects (reviewed in Shannon et al. 2016a). This inconsistency might result in part from difficulties in isolating effects of noise from effects driven by other factors associated with the presence of the anthropogenic source (e.g., physical infrastructure, roads and other linear features, chemical pollution; see Shannon et al. 2016a). Surprisingly, even noiseless and diminutive (1 m in height) shallow-gas wells impact abundances of grassland songbirds (Fig. 4.1a; Rodgers and Koper 2017), demonstrating that even minimal structural disturbances might explain some effects of energy infrastructure that have previously been attributed to noise. Controlled playback experiments that isolate the effects of noise and physical infrastructure from one another and from other confounding factors are thus pivotal to understand responses to anthropogenic noise, and underlying behavioural and ecological mechanisms that explain these patterns (Shannon et al. 2016a). Recent playback studies simulating traffic noise at migratory stopover sites demonstrate that noise alone can affect abundance and weight gain (McClure et al. 2013, 2017; Ware et al. 2015), and noise *per se* also negatively impacts lek attendance by Greater Sage-Grouse

(*Centrocercus urophasianus*, Blickley et al. 2012a). However, no studies have used a landscape-scale noise playback experiment to assess effects of noise on productivity, or determine whether environmental cues that birds use to assess habitat quality are consistent with high reproductive output in landscapes impacted by anthropogenic noise.

Figure 4.1 Shallow gas well pads (a), which are abundant across this region, have a very similar footprint (average 23.1 m^2) and height (1.44 m; Rodger and Koper 2017) to playback units (b) designed for the present study (footprint: 35.8 m^2, height: 1.25 m; Rosa et al. 2015), and are composed of some of the same materials (i.e., identical technical fencing). Both are diminutive in comparison with oil well drilling rigs (height: 24 m; c) and pumpjacks (height: 4.5 m; d).

One reason that noise may decouple perceived from actual habitat quality is that noise may impact songbirds and their predators at different spatial scales (e.g., Chalfoun et al. 2002, Stephens et al. 2003). At a local scale, territorial male songbirds may avoid selecting noisy sites because it hinders their ability to hear neighbours' songs, resulting in more aggressive encounters, increased susceptibility to intrusion, and greater energetic costs associated with territory defence (e.g., Molle and Vehrencamp 2001, Mazerolle and Hobson 2002, Mockford and Marshall 2009, Curry et al. 2018). Studies on territorial songbirds showed that energy development noise could hinder territorial defence, potentially due to masking of communication events (Zwart et al. 2015, Kleist et al. 2016). However, physical habitat fragmentation caused by energy development influences nest predators at broader spatial extents than songbirds (Chalfoun et al. 2002), suggesting that other anthropogenic disturbances, such as noise, might also affect songbirds and their predators at different spatial scales. Hence, if grassland songbirds, which are subject to high nest predation rates (Martin 1993, 1995; Davis 2003), select breeding habitats based on local characteristics, but their nest predators are affected by anthropogenic disturbances at a broader scale, this may further disrupt the ability of songbirds to rely on habitat cues that have historically helped them to predict habitat quality for nesting.

Compared to adults, altricial grassland songbird nestlings may be more vulnerable to noise disturbances since they are restricted to the nest and less likely to habituate during their short exposure period (e.g., Crino et al. 2011). If exposure to anthropogenic noise occurs during early developmental stages, nestlings may endure effects on survival and future reproductive success (e.g., Crino et al. 2011, Injaian et al. 2018). Noise can interefere with nestling feeding efficiency (e.g., fail to detect arrival of parents at nest more often; Leonard and Horn 2012), and with anti-predator behaviours in nestlings (e.g., fail to cease vocalising and crouch down in nest following alarm call; McIntyre et al. 2014) and parents (e.g., fail to delay nest visit in response to conspecific alarm call; Antze and Koper 2018). Further, anthropogenic noise has been linked to changes in parent foraging-vigilance time budgets (Frid and Dill 2002, Shannon et al. 2014, Ware et al. 2015). This might result in a decrease in nestling body condition in noisy sites. Further, parents of greater quality typically produce more offspring and increase parental investment in current broods (Huet des Aunay et al. 2017). In presence of urban and traffic noises, female decrease investment by producing smaller clutches compared to quieter environments, potentially due to noise hindering their ability to assess and choose a high-quality mate (Halfwerk et al. 2011, Huet des Aunay et al. 2017). Therefore, clutch size might also be affected by anthropogenic noise.

Despite increasing restrictions and consumption efficiency, the oil industry accounts for approximately 2.5% of the global gross domestic product (GDP; Arezki et al. 2017) with world oil demand estimated at nearly 100 million barrels per day (International Energy Agency 2018). Noise produced by oil development in natural areas has a much greater ecological footprint when compared to loss of habitat (Rosa and Koper 2018). Oil extraction activities also produce noise stimuli that vary widely in amplitude, frequency, and predictability, and thus different types of oil infrastructure are expected to have different impacts (Francis and Barber 2013). Oil development thus provides the opportunity for an experimental design of both practical and theoretical interest. From a theoretical perspective, different oil infrastructure activities produce noise with different intensities, frequencies and patterns, and thus the effects of different types of oil infrastructure noise can be compared across otherwise similar ecosystems. For example, noise produced by drilling rigs (Fig. 4.1c) is intermittent and inconsistent, with frequent and irregular changes in frequency, amplitude and content, which may be perceived by wildlife as an immediate threat resulting in avoidance (Francis and Barber 2013). In contrast, active oil wells produce chronic, predictable noise (i.e., pumpjacks, Fig. 4.1d; Koper et al. 2016), which may interfere with detection (i.e., energetic masking) of signals and cues crucial to communication and predator detection (Wright et al. 2007). The mechanisms that explain effects of acute and chronic noises, therefore, differ (Francis and Barber 2013), and thus we might predict different effects of drilling noise compared with noise of active oil wells. Further, if noise is found to be problematic for breeding birds, then more specific recommendations can be proposed to mitigate these negative effects. For example, if impacts of noise are a function of amplitude, we would expect that quieter wells would have a smaller ecological footprint. From a management perspective, determining whether oil infrastructure influences wildlife because of the noise it emits or because of the presence of its above-ground infrastructure, and to determine which noise sources are most problematic, is essential to developing effective mitigation strategies.

There is also a gap between industry and legislation regarding our understanding of the impacts of anthropogenic noise on birds. While most oil activities produce noise that constitutes a high-risk sensory disturbance according to political regulations (e.g., 10 dB above ambient levels or noise levels higher than 50 dB; Environment and Climate Change Canada 2017), energy associations generally consider that migratory birds inhabiting these areas are likely habituated to the noise (e.g., Canadian Energy Pipeline Association 2013), and thus are at little risk from it. However, if noise influences relative abundance differently from its impacts on reproductive output, this may not be true. Investigating effects of oil development noise on these migratory grassland species is necessary to develop effective mitigation strategies and refine and reconcile existing policies (Dooling and Popper 2007).

To determine whether noise alone could decouple relative habitat use from habitat quality (indicated by increased reproductive outcome and higher reproductive output per nest), I conducted a large-scale, multi-year field playback experiment where I recreated the soundscape produced by energy infrastructure by making high-fidelity recordings of oil activities and playing these recordings in sites without oil infrastructure (Fig. 4.1b; Rosa et al. 2015). This study design allowed me to effectively disentangle effects of noise from effects driven by the presence of infrastructure, and determine whether acute and chronic noise sources had different ecological impacts. Treatments consisted of replicates of (1) acute intermittent drilling playbacks, (2) chronic generator pumpjack and (3) quieter, but still chronic, power-grid pumpjack playbacks, (4) infrastructure-only playbacks units, which replicated the structure of the broadcasting unit to control for effects caused by the presence of the equipment, and (5) control sites, with no playback or oil well infrastructure (Table 4.1). Focal species consisted of four grassland songbird species experiencing population declines across their North American range over the last 5 decades (Sauer et al. 2017), and included two federally Threatened species (Government of Canada 2018): Chestnut-collared Longspur (*Calcarius ornatus*) and Sprague's Pipit (*Anthus spragueii*); and two non-listed species: Savannah Sparrow (*Passerculus sandwichensis*) and Vesper Sparrow (*Pooecetes gramineus*). The acoustic footprint of each noise source differed among species due to differences in peak vocalisation frequency and frequency range of each species (Fig. 4.2; see Appendix S4.1). I compared relative abundance and nesting success of each species among the different treatments to determine whether noise or the presence of above-ground infrastructure interfered with birds' abilities to assess habitat quality. I also assessed reproductive output (i.e., nestling condition and clutch size) of one listed species (i.e., Chestnut-collared Longspur) and one non-listed species (i.e., Savannah Sparrow), for which I had more nests. I measured habitat use and quality at two spatial scales. Local-scale analyses, which evaluated effects of distance to infrastructure from 0–400 m, allowed me to determine whether impacts of noise and infrastructure were greatest closer to the disturbance, and whether effects of noise were amplitude-dependant. Site-scale analyses were conducted at the scale of quarter sections (64.7-ha sites), at which management actions are typically implemented in this region.

METHODS

Study sites and treatments

I monitored bird abundance and nests in 29, 64.7-ha (i.e., quarter section) mixed-grass prairie sites during three breeding seasons from early May to early August, 2013 to 2015, within 100 km of Brooks, County of Newell, Alberta (50°33’51” N 111°53’56” W), an area with one of the highest densities of oil development in Canada (Government of Alberta 2014). With over 30 000 oil and gas wells, this county operates 50% of all wells in Alberta and 37% of wells in Canada (County of Newell 2018). I recorded real energy infrastructure and then broadcasted high-fidelity recordings by means of solar-powered playback systems that I designed and built, and then placed at the centre of native prairie quarter-section sites that did not contain oil development or associated infrastructure (Rosa et al. 2015; see Appendix S4.1). Recordings of different pumpjacks or drilling rigs were emitted from each of the playback broadcasting units (Curry et al. 2018). Chronic pumpjack noise was broadcasted 24 hours/day for approximately 90 days each year, corresponding with the duration of the breeding season. Pumpjacks are a common type of oil pumping system, which adopts a nodding motion that facilitates liquid to rise from the bottom of the well at each stroke (or cycle) with a mechanism similar to a plunger. This type of pumping system can be either connected to the power-grid or powered by generators (which adds more noise). Pumpjacks produce chronic noise across a wide range of frequencies with similar energy (or amplitude), within a predictable and consistent cycle (Fig. 4.1d). Intermittent drilling noise was broadcasted 24 hours/day during two periods of 10 days each breeding season corresponding with the average duration of drilling operations for one well in this region (V. Dyck, *pers. comm.*). The start of the drilling playback periods were staggered by 3 days among the different replicates to allow us to distinguish effects of date and drilling noise, and all drilling playback were turned off approximately 15 days between the two 10 day broadcast period for a given site. Drilling rig noise is inconsistent, erratic, and changes throughout the recording and over the duration of the playback period (Fig. 4.1c). Drilling noises, such as loud clanking of pipes, powering of different generators, intercom systems and trucks, all have sudden onsets that are highly variable and unpredictable. Treatments included (1) intermittent drilling playbacks (*n* = 6 sites; 88 ± 4.0 dB(C)), (2) chronic generator pumpjack (*n* = 6; 73 ± 5.2 dB(C)) and (3) chronic power-grid pumpjack (*n* = 6; 62 ± 2.8 dB(C)) playbacks, (4) infrastructure-only playbacks that look identical to the other playbacks but emit no sound (*n* = 6), to control for effects driven by the presence of the playback units, and (5) controls (*n* = 17), with neither playback infrastructure nor real oil wells (Table 4.1). Noise playback and infrastructure-only treatments were rotated among sites randomly between 2014 and 2015 to ensure that differences among treatments were not caused by pre-existing differences among sites.

Table 4.1 Site and noise type, C-weighted time-averaged sound pressure level for broadband noise (LC_{eq}) 10 m from playback unit, and duration of playback periods per year for each treatment (± SD for both). Asterisks (*) indicates that LC_{eq} for infrastructure-only and control sites were estimated from background noise level measurements.

Site type	Noise type	LC_{eq}	Playback period (days) per year
Drilling activity	intermittent	88 ± 4.0	10 ± 0.6 x 2 periods
Generator pumpjack	chronic	73 ± 5.2	95 ± 11.0
Power-grid pumpjack	chronic	62 ± 2.8	87 ± 11.9
Infrastructure-only	natural ambient	$51 \pm 3.3^{*}$	N/A
Control	natural ambient	$51 \pm 3.3^{*}$	N/A

Field surveys

I conducted two rounds of avian abundance transect surveys at each study site radiating away from the playback structure or centre-point, in opposite directions (i.e., two 400 m x 200 m survey areas), between sunrise and 10:00, on days without rain or winds >20 km/h (Ralph et al. 1993) between mid-May to early July each year. Nests were found by flushing adults off nests by dragging a weighted 25-m rope, allowing for a systematic search (32 ha in 2013, 28 ha in 2014, 56 ha in 2015; Davis 2003, Winter et al. 2003). Nests were marked and monitored every 2–4 days (Winter et al. 2003) until broods fledged or were destroyed. The outcome of a nest was determined by observing the age and development of nestlings over a period of approximately 10 days after hatching (Ehrlich et al. 1988), and by recognizing disturbances indicative of predation (e.g., empty damaged nest at egg stage or young nestling stage). A nest was considered successful when a minimum of one juvenile fledged (Jones and Geupel 2007). To ensure that nesting success results were representative of effects of noise on nest predation, nests that were abandoned (*n* = 36) or that were unsuccessful due to unfavourable weather conditions (*n* = 9) were excluded from statistical analyses. Clutch size consisted of the final number of eggs laid by the female. If nests were found after hatching, I used number of nestlings as an estimate of clutch size.

I took morphometric measurements of Savannah Sparrow (*n* = 650 from 182 nests) and Chestnut-collared Longspur (*n* = 219 from 61 nests) nestlings at approximately day 5 (mean age = 5.04; SD ± 0.43) to minimise the risk of parents abandoning young nestlings or causing older nestlings to force fledge. Nestlings were weighed individually in holding bags using a Pesola micro-line spring scale (model #20030; 30 g capacity × 0.25 g resolution; ± 0.3% accuracy). I also measured the length of the left tarsometatarsal bone (i.e., tarsus length) from the notch of the intertarsal joint to the top of the bent foot using a SPI dial calliper (model #31-415-3; 0.1 mm graduation; ±0.0015 mm accuracy).

Each year, I also conducted 24 to 34 1-m^2 vegetation survey plots at each study site to account for potential confounding effects related to vegetation structure and composition (Fisher and Davis 2011; Appendix S4.2).

Statistical analyses

I compared the intermittent (acute) drilling rig treatment, chronic generator pumpjack, and chronic power-grid pumpjack treatments to both the control and infrastructure-only treatments. I used unadjusted counts of birds observed during abundance surveys as indices of relative abundance because previous studies in this region indicate that these focal species are highly perceptible (Leston et al. 2015) and song detection and distance estimates by human observers are not hindered by oil-well noise (Koper et al. 2016). I used generalised linear mixed models (PROC GLIMMIX; SAS 9.4; SAS Institute, Inc. 2012) to determine whether bird abundance, body condition (i.e., scaled mass index), and clutch size varied among treatments and with distance from the playback unit or centre-point at control sites. I used logistic-exposure models (PROC NLMIXED; SAS Institute, Inc. 2012) to assess relative effects of the treatments and distance to playbacks on nesting success (Shaffer 2004). Local-scale models for both relative abundance and nesting success included distance to playback unit or site center (for controls), and also an interaction term between treatment and distance (see Appendix S4.2 for additional methods).

RESULTS

Avian abundance

Both chronic and intermittent oil extraction noise negatively impacted relative abundance of some focal species. At the local scale, I detected fewer Chestnut-collared Longspurs at intermittent drilling and chronic power-grid pumpjack playback treatments, with a negative effect of proximity to noise, such that abundance was significantly reduced at 100 m from the playback unit compared to 400 m away (Fig. 4.3a; for details, see Table S4.2.8). However, these effects were not evident at the site scale ($P \geq 0.44$; for details, see Table S4.2.9). Although Chestnut-collared Longspurs avoided the drilling playback treatment, which was associated with the greatest surface area of acoustic disturbance, they also avoided the power-grid pumpjack treatment, which had the smallest surface area of impact (Fig. 4.2a; Table S4.1.1). At both the local and site scale, Savannah Sparrows avoided intermittent drilling noise (Fig. 4.3b).

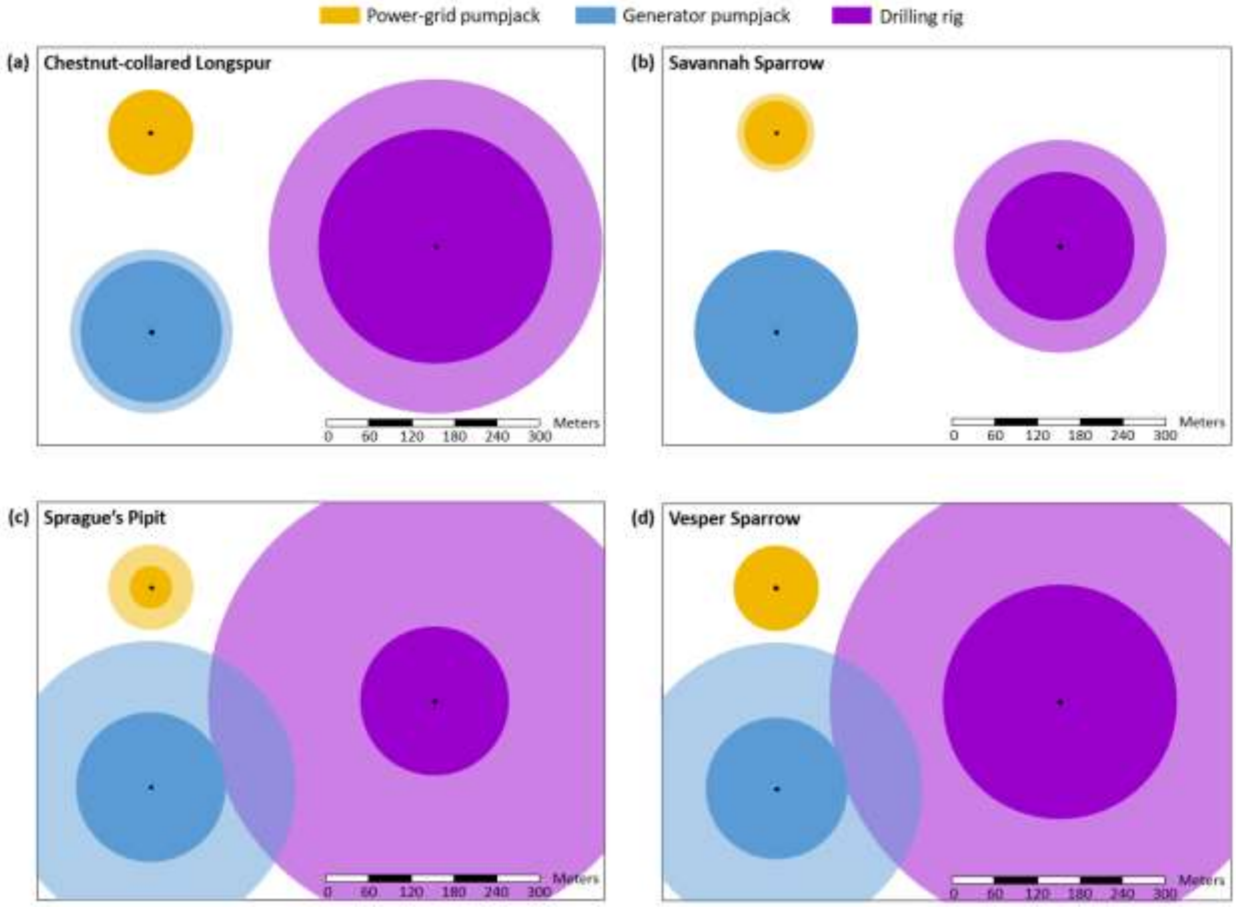


Figure 4.2 Acoustic footprint of intermittent (purple) and chronic (yellow and blue) oil development noise for (a) Chestnut-collared Longspur, (b) Savannah Sparrow, (c) Sprague's Pipit, and (d) Vesper Sparrow. Inner circles indicate surface area where noise can energetically mask signals (noise levels within peak frequency exceed ambient levels). Outer circles represent surface area where noise can interfere with signal transmission (noise levels within frequency range of vocalisation exceed ambient levels; see Appendix S4.1; Rosa and Koper 2018).

Two species' abundances were affected by the presence of the playback units, rather than the noise emitted from them. At the local scale, Sprague's Pipits were more abundant at controls compared to all treatments with structures present, except for generator pumpjack treatments (Fig. 4.3c; Table S2.4.8). Their abundance was independent of treatment at the site scale ($P \geq 0.36$; Table S4.2.9). Conversely, Vesper Sparrows were less abundant at controls compared to infrastructure-only and drilling playback sites at both the local ($P = 0.02$; Fig. 4.3d) and site scale ($P < 0.05$; Tables S4.2.8-9).

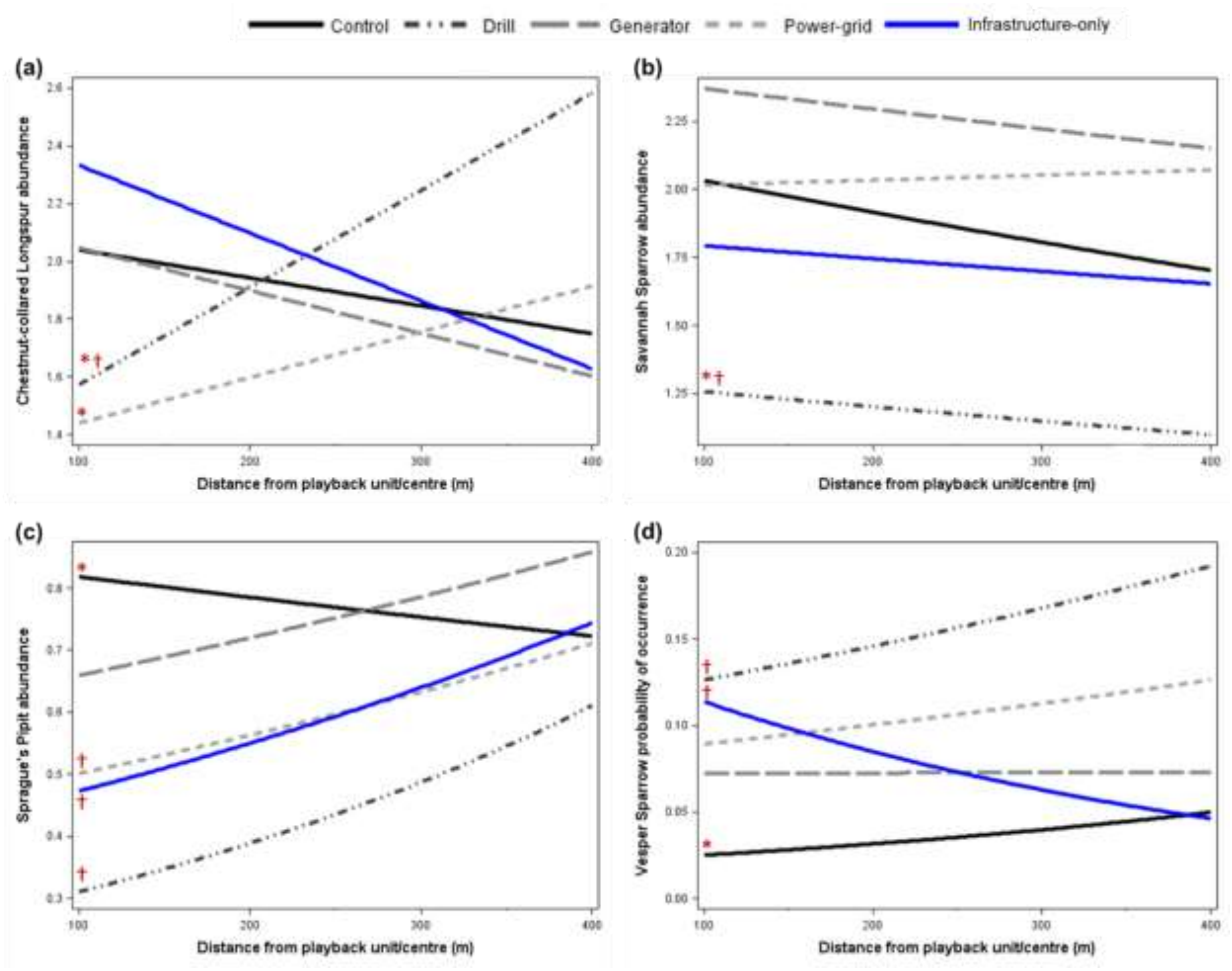


Figure 4.3 Effects of intermittent (drilling rig) and chronic (generator and power-grid pumpjack) playback noise and of presence of the playback unit at the local scale on abundance of four species of grassland songbirds for each experimental treatment, from 2013 to 2015, in Alberta, Canada. All treatments were compared to both infrastructure-only (blue line) and control treatments (solid black line). Significant differences ($P < 0.1$) compared to infrastructure-only are indicated by * and compared to control by †, for each species: (a) Chestnut-collared Longspur, (b) Savannah Sparrow, (c) Sprague's Pipit, and (d) Vesper Sparrow (probability of occurrence). To facilitate interpretation of graphs, 90% confidence intervals were omitted from this figure (for statistical results see Table S4.2.8; for confidence intervals see Fig. S4.2.2 in Appendix S4.2).

Nesting success

Intermittent drilling playback noise or the presence of the playback unit negatively affected nesting success of three of the four focal species at the site scale (Fig. 4.4; for details see Table S4.2.10). Savannah Sparrow and Sprague's Pipits experienced a lower probability of nest survival when exposed to drilling playback noise, which both species avoided. Sprague's Pipit also had greater nesting success at controls compared to chronic playback sites and the infrastructure-only treatment. Nesting success of Vesper Sparrow was greater at controls, which was the treatment at which they had the lowest abundances (Fig. 4.4). I found no significant effect of treatments on nesting success of Chestnut-collared Longspurs (Fig. 4.4).

I found no significant effects of distance to infrastructure or its interaction with treatment on nesting success of Chestnut-collared Longspur ($P \geq 0.12$) or Savannah Sparrow ($P \geq 0.24$). Local-scale models including distance to infrastructure did not converge for Sprague's Pipits or Vesper Sparrows, perhaps because of their smaller sample sizes, suggesting that the added distance variable overparameterized the models.

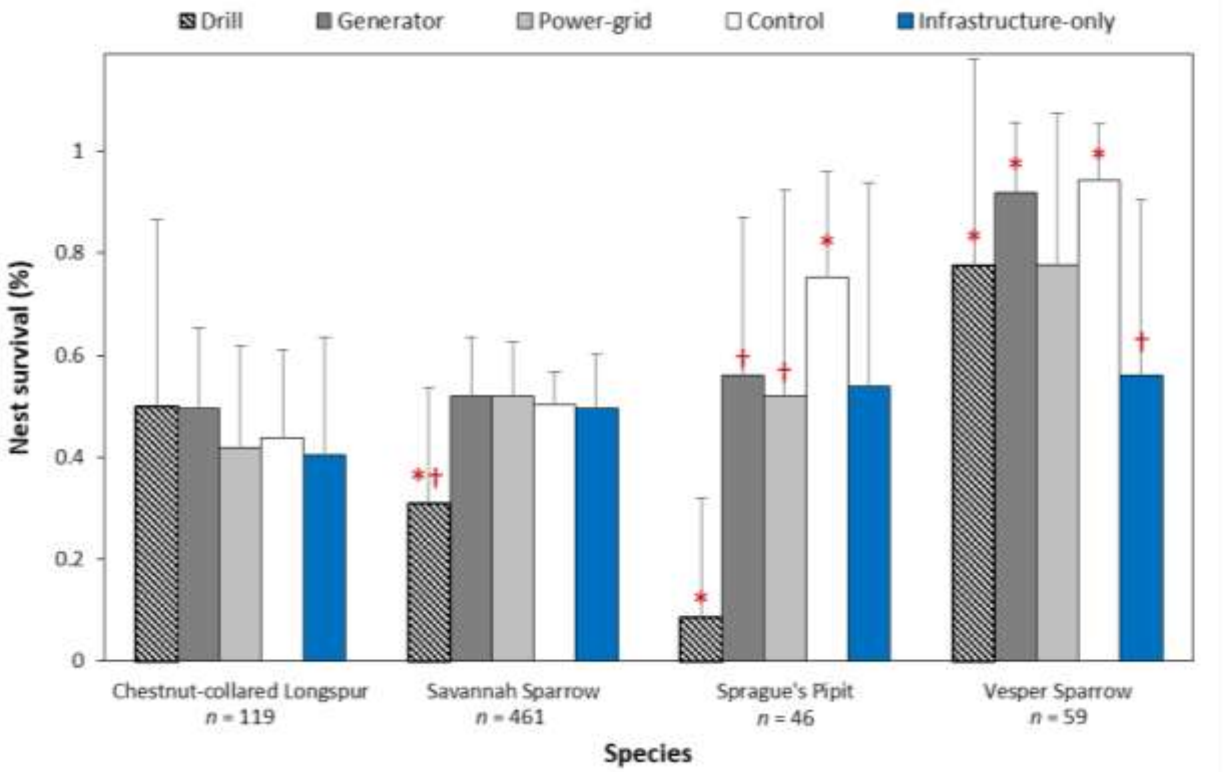


Figure 4.4 Effects of intermittent (drilling rig) and chronic (generator and power-grid pumpjack) playback noise and of presence of playback unit at the site scale on overall probability of nest survival (%) for four species of grassland songbirds at each experimental treatment, from 2013 to 2015, in Alberta, Canada. Noise-producing treatments were compared both to infrastructure-only (blue) and control (white) treatment. Significant differences ($P < 0.1$) compared to infrastructure-only are indicated by * and compared to control by †. Errors bars indicate 90% confidence intervals.

Nestling body condition and clutch size

Body condition of Savannah Sparrow nestlings was lower in the treatment they avoided (i.e., drilling playback), while body condition of Chestnut-collared Longspurs was higher in all noise-producing treatments and infrastructure sites including those they avoided (i.e., drilling and power-grid pumpjack playbacks) than in controls. There was no effect of noise or infrastructure on body condition of nestling Savannah Sparrows at the site scale ($P > 0.114$), but nestlings had lower body condition near intermittent drilling noise sources ($P = 0.098$), particularly closer to playback infrastructure (Fig. 4.5a). At the site scale, nestling Chestnut-collared Longspurs had significantly increased body condition at all noisy sites and the infrastructure-only treatment compared with controls ($\beta = 0.869$; $SE = 0.165$; $P = 0.008$), and this effect was independent of distance to infrastructure ($P > 0.940$).

Clutch sizes of Savannah Sparrow were independent of noise or infrastructure at the site scale ($P > 0.153$) and local scale ($P > 0.226$). At the site scale, Chestnut-collared Longspur produced larger clutches in intermittent drilling ($\beta = 4.269$; $SE = 1.838$; $P = 0.012$) and chronic power-grid ($\beta = 4.2268$; $SE = 1.884$; $P = 0.051$) playback treatments, when compared to both infrastructure-only ($\beta = 3.687$; $SE = 1.609$) and control ($\beta = 3.787$; $SE = 1.588$) treatments. At the local scale, I found larger Chestnut-collared Longspur clutch sizes at drilling playbacks ($P < 0.069$), particularly close to the playback unit ($P < 0.051$; Fig. 4.5b). Chestnut-collared Longspurs thus produced larger clutches in treatments with playback types they avoided.

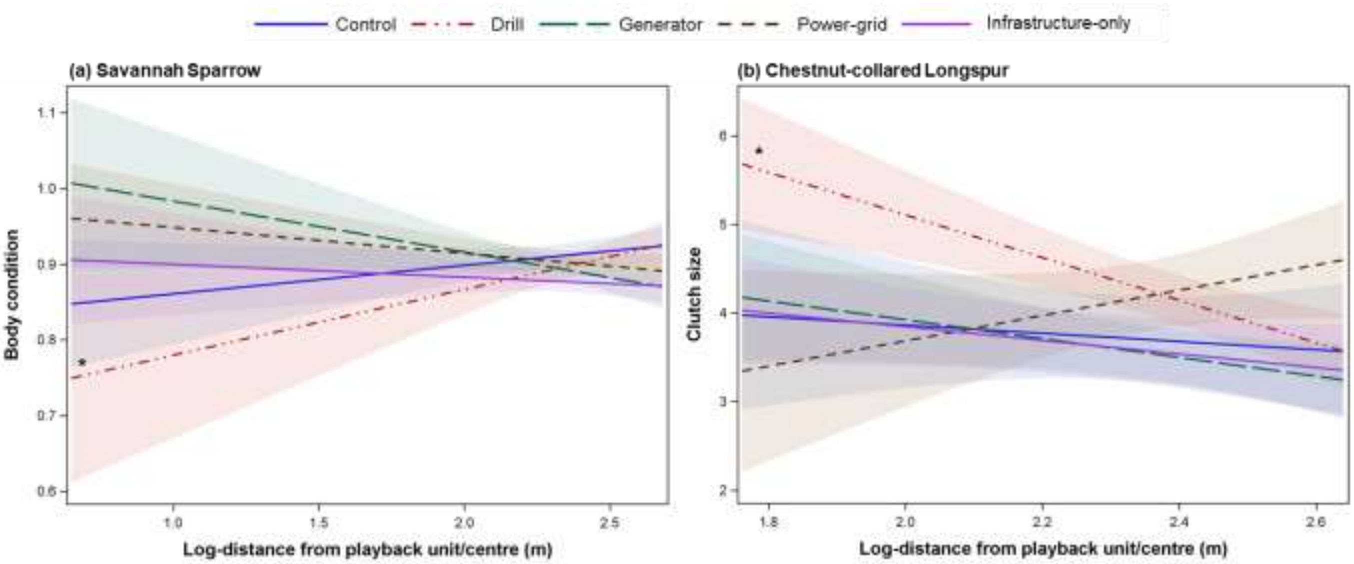


Figure 4.5 (a) Nestling body condition of Savannah Sparrow (*Passerculus sandwichensis*) and b) clutch size of Chestnut-collared Longspur (*Calcarius ornatus*) as a function of log-transformed distance from playback unit (or centre-point at control treatments). Significant site-scale effects (P < 0.1) are denoted by an asterisk (*).

DISCUSSION

Both noise and above-ground infrastructure can decouple apparent from realised habitat quality, as I observed for three out of the four focal species. Only Savannah Sparrows avoided treatments that resulted in poor nesting success and nestling quality; their ability to recognise sites with low reproductive potential may explain their ability to adapt relatively successfully to anthropogenically altered landscapes (e.g., Hamilton et al. 2011). Other species demonstrated maladaptive habitat selection in the presence of anthropogenic noise or infrastructure, including (1) avoidance of suitable sites (perceptual trap, Patten and Kelly 2010; Chestnut-collared Longspur and Vesper Sparrow), (2) selection of sites that had poor productivity (ecological trap, Schlaepfer et al. 2002; Chestnut-collared Longspur and Vesper Sparrow), and (3) lack of avoidance of some acoustically detrimental sites (Sprague’s Pipit).

Intermittent drilling noise had consistently greater ecological impacts than chronic oil-well noise. The sudden onset and frequent shifts in frequency and amplitude of drilling noise can be interpreted as alarming or threatening, and may be more distracting than cyclic oil well noise (e.g., Francis and Barber 2013). In contrast, chronic noise is conducive to acclimatisation (Wright et al. 2007), and its predictability may allow birds to adopt coping mechanisms that effectively mitigate its effects (Francis and Barber 2013). The size of the spatial footprint within which energetic masking may occur did not explain which treatments were most influential, or which species were most sensitive to noise (Fig. 4.2). Further, although generator-powered wells had a greater acoustic footprint than grid-powered wells, this did not result in greater ecological impacts. Both results suggest that effects of noise are more likely to be due to the acoustic structure of noise, which strongly impacts distraction and informational masking (Rosa and Koper 2018), rather than its power (see also Blickley et al. 2012a).

Both chronic and acute noises, however, resulted in ecological and perceptual traps for Chestnut-collared Longspurs. Noise may impact habitat selection differently from productivity for several reasons. Birds may select nest sites based on a variety of cues including apparent resource availability (Chalfoun and Martin 2007), conspecific attraction (Stamps 1988, Ahlering and Faaborg 2006), and cues that suggest protection from predators. Mechanisms that explain reproductive output may differ from these: for example, clutch size and nestling body condition are influenced by maternal condition and foraging opportunities and success (e.g. Remeš and Martin 2002), while nesting success of grassland songbirds is most heavily influenced by abundance and diversity of the local predator community (Vickery et al. 1992, Ludlow et al. 2014). Realized habitat quality may, therefore, differ from perceived habitat quality. Birds may not be able to detect altered predation risks if nest predators are susceptible to noise disturbances or rely on acoustic cues (Francis et al. 2009), which can result in lower avian abundance at suitable sites (i.e., perceptual traps) or higher avian abundance in sites with poor reproductive potential (i.e., ecological traps).A previous study investigating the predator community in our study area found grassland songbird nests were mostly depredated by predators with large home ranges (i.e., American Badgers [*Taxidea taxus*], domestic cattle [*Bos taurus*], and raptorssuch as Norther Harrier [Circus cyaneus] and Swainson's Hawk [*Buteo* swainsoni]) compared with predators with small home range (i.e., northern grasshopper mouse [*Onychomys leucogaster*], garter snake spp. [*Thamnophis spp.*]; Bernath-Plaisted 2015). Since songbirds generally respond to disturbance at smaller spatial scales than do nest predators (Chalfoun et al. 2002, Stephens et al. 2003), this may explain why effects of drilling noise on Savannah Sparrow abundance and nestling body condition were highest closer to wells, but its effects on nesting success occurred throughout the impacted sites.

Our results for both Sprague's Pipits and Vesper Sparrows also demonstrate that even diminutive above-ground infrastructure can affect habitat selection and quality. Playback infrastructure *per se* caused ecological traps for Vesper Sparrows. Infrastructure may be used as perch sites for territorial displays, or conversely, by nest predators; and infrastructure may mimic natural natural landscape features that affect habitat selection, such as shrubs (Rodgers and Koper 2017). This observation is critical to developing effective mitigation strategies, as minimizing infrastructure noise will not protect species whose habitat selection and reproductive output are affected by the infrastructure itself; conversely, minimizing industrial noise is necessary for protection of acoustically sensitive species, such as Chestnut-collared Longspur. It also highlights that noise playback experiments must be designed to allow researchers to disentangle effects of noise from effects of the presence of even small physical structures, particularly in open ecosystem types.

CONCLUSIONS

Both anthropogenic noise and above-ground infrastructure can decouple relative habitat use from habitat quality, depending on the species. Reducing noise amplitude at the source (e.g., mufflers, sound dampening walls) or shifting the timing of acute drilling activities away from the breeding period would reduce impacts of oil infrastructure on several grassland songbird species. Noise mitigation actions are more important when managing unpredictable noises, such as drilling noise, compared with noise from oil wells; most of the focal species seem able to adapt to chronic noise conditions, even at relatively loud amplitudes. Noise reduction technology is frequently employed in human-populated areas (Habib et al. 2007), demonstrating that effective mitigation strategies are immediately and commercially available. I also emphasize that reducing the presence of above-ground infrastructure is necessary to conserve some species. Instead of drilling multiple wells vertically throughout the landscape, horizontal drilling from centralized wells pads would facilitate this goal.

Although industry is constrained by setback buffers for drilling activities during peak breeding periods depending on the species (between May 1-15 and July 15-31), these buffer zones are only limited to 100 to 200 m for listed species (e.g., Chestnut-collared Longspur and Sprague's Pipit) and 5 to 50 m for unlisted migratory songbirds (Canadian Energy Pipeline Association 2013, Environment and Climate Change Canada 2017), which is insufficient to mitigate the effects observed. These results demonstrate that apparent habituation to noise or the presence of species in noisy areas do not imply a lack of fitness costs, in contrast with current industry policies (Canadian Energy Pipeline Association 2013). Since acute intermittent noise is not conducive to habituation (Francis and Barber 2013), both government and industry should revise their overarching regulations and policies regarding impacts of noise on wildlife populations to reflect the fact that best management practices are dependent on the type of noise to which wildlife are exposed.

LITERATURE CITED

Ahlering, M. A., and J. Faaborg. 2006. Avian habitat management meets conspecific attraction: If you build it, will they come? The Auk 123:301–312.

Antze, B., and Koper, N. 2018. Noisy anthropogenic infrastructure interferes with alarm responses in Savannah sparrows (*Passerculus sandwichensis*). Royal Society Open Science, 5:172168.

Arezki, M. R., Z. Jakab, M. D. Laxton, M. A. Matsumoto, A. Nurbekyan, H. Wang, H., and J. Yao. 2017. Oil prices and the global economy. IMF Working Paper. International Monetary Fund.

Barber, J. R., K. R. Crooks, and K. M. Fristrup. 2010. The costs of chronic noise exposure for terrestrial organisms. Trends in Ecology & Evolution 25:180–189.

Bayne, E. M., L. Habib, and S. Boutin. 2008. Impacts of chronic anthropogenic noise from energy-sector activity on abundance of songbirds in the boreal forest. Conservation Biology 22:1186–1193.

Bernath-Plaisted, J. 2015. The effects of oil and gas development on songbirds of the mixed-grass prairie: nesting success and identification of nest predators. Master's Thesis. University of Manitoba, Winnipeg. URI: http://hdl.handle.net/1993/31068

Blickley, J.L., D. Blackwood, and G. L. Patricelli. 2012a. Experimental evidence for the effects of chronic anthropogenic noise on abundance of Greater Sage-Grouse at leks. Conservation Biology 26:461–471.

Blickley, J. L., K. R Word, A. H. Krakauer, J. L. Phillips, S. N Sells, C. C. Taff, et al. 2012b. Experimental chronic noise is related to elevated fecal corticosteroid metabolites in lekking male greater sage-grouse (*Centrocercus urophasianus*). PLoS ONE 7:e50462.

Block, W. M., and L. A. Brennan. 1993. The habitat concept in ornithology. Pages 35–91 *in* D. M. Power, editor. Current Ornithology (Vol. 11). Plenum Press, New York.

Bock, C. E., and Z. F. Jones. 2004. Avian habitat evaluation: should counting birds count? Frontiers in Ecology and the Environment 2:403–410.

Canadian Energy Pipeline Association. 2013. Migratory Birds Convention Act: A best management practice for pipelines. Stantec Consulting Ltd., Calgary, Alberta, https://www.cepa.com/wp-content/uploads/2014/01/Migratory-Birds-Sept-26-2013-for-Publication.pdf.

Chalfoun, A. D., and T. E. Martin. 2007. Assessments of habitat preferences and quality depend on spatial scale and metrics of fitness. Journal of Applied Ecology 44:983–992.

Chalfoun, A. D., F. R. Thompson, and M. J. Ratnaswamy. 2002. Nest predators and fragmentation: a review and meta-analysis. Conservation Biology 16:306–318.

County of Newell. 2018. 2017 Annual Financial Report. Finance Department, County of Newell, Alberta, Canada. Published April 25, 2018. https://lfpublic.countyofnewell.ab.ca

Crino, O. L., B.K. Van Oorschot, E. E. Johnson, J. L. Malisch, and C. W. Breuner. 2011. Proximity to a high traffic road: glucocorticoid and life history consequences for nestling white-crowned sparrows. General and Comparative Endocrinology 173:323–332.

Curry, C. M., P. G. Des Brisay, P. Rosa, and N. Koper. 2018. Noise source and individual physiology mediate effectiveness of bird songs adjusted to anthropogenic noise. Scientific Reports 8:3942.

Davis, S. K. 2003. Nesting ecology of mixed-grass prairie songbirds in southern Saskatchewan. The Wilson Bulletin 115: 119–130.

Dooling, R. J., and A. N. Popper. 2007. The effects of highway noise on birds. The California Department of Transportation, Division of Environmental Analysis, Sacramento, California, USA.

Dyck, V. 2013, September. Personal communication with lead operator at Cenovus Energy.

Ehrlich, P. R., D. S. Dobkin, and D. Wheye. 1988. The birder’s handbook: A field guide to the natural history of North American birds. Simon and Schuster, New York, New York, USA.

Environment and Climate Change Canada. 2017. Avoiding harm to migratory birds: Technical information about the guidelines. Government of Canada, https://www.ec.gc.ca/paom-itmb/. Accessed September 21, 2017.

Fisher, R. J., and S. K Davis. 2011. Habitat use by Sprague's Pipits (*Anthus spragueii*) in native pastures and planted, non-native hay fields. The Auk 128:273–282.

Francis, C. D. 2015. Habitat loss and degradation. Pages 47–62 in M. L. Morrison, and H. A. Mathewson, editors. Wildlife Habitat Conservation, John Hopkins University Press, Baltimore.

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

Francis, C. D., C. P. Ortega, and A. Cruz. 2009. Noise pollution changes avian communities and species interactions. Current Biology 19:1415–1419.

Francis, C. D., J. Paritsis, C. P. Ortega, and A. Cruz. 2011. Landscape patterns of avian habitat use and nest success are affected by chronic gas well compressor noise. Landscape Ecology 26:1269–1280.

Frid, A., and L. Dill. 2002. Human-caused disturbance stimuli as a form of predation risk. Conservation Ecology 6:11.

Gillespie, M. K., and S. J. Dinsmore. 2014. Nest survival of Red-winged Blackbirds in agricultural areas developed for wind energy. Agriculture, Ecosystems & Environment 197:53–59.

Government of Alberta. 2014. Oil and gas. http://esrd.alberta.ca/lands-forests/land-industrial/education/industrial-land-use/oil-and-gas/default.aspx. Accessed May 5, 2018.

Government of Canada. 2018. Species at Risk Public Registry, https://www.sararegistry.gc.ca. Accessed May 5, 2018.

Habib, L., E. M. Bayne, and S. Boutin. 2007. Chronic industrial noise affects pairing success and age structure of ovenbirds *Seiurus aurocapilla*. Journal of Applied Ecology 44:176–184.

Halfwerk, W., L. J. Holleman, C. K. Lessells, and H. Slabbekoorn. 2011. Negative impact of traffic noise on avian reproductive success. Journal of Applied Ecology 48:210-219.

Hamilton, L., B. Dale, and C. Paszkowski. 2011. Effects of disturbance associated with natural gas extraction on the occurrence of three grassland songbirds. Avian Conservation and Ecology 6:7.

Huet des Aunay, G., M. Grenna, H. Slabbekoorn, P. Nicolas, L. Nagle, G. Leboucher, et al. 2017. Negative impact of urban noise on sexual receptivity and clutch size in female domestic canaries. Ethology 123:843–853.

Injaian, A. S., C. C. Taff, and G. L. Patricelli. 2018. Experimental anthropogenic noise impacts avian parental behaviour, nestling growth and nestling oxidative stress. Animal Behaviour 136:31–39.

International Energy Agency. 2018. Oil Market Report. https://www.iea.org/oilmarketreport/ Accessed May 16, 2018.

Jones, S. L., and G. R. Geupel. 2007. Beyond Mayfield: Measurements of nest-survival data. Studies in Avian Biology No. 34, Cooper Ornithological Society, Camarillo, CA.

Kleist, N. J., R. P. Guralnick, A. Cruz, and C. D. Francis. 2016. Anthropogenic noise weakens territorial response to intruder's songs. Ecosphere 7:e01259.

Kokko, H., and W. J. Sutherland. 2001. Ecological traps in changing environments: ecological and evolutionary consequences of a behaviourally mediated Allee effect. Evolutionary Ecology Research 3:603–610.

Koper, N., L. Leston, T. M. Baker, C. Curry, and P. Rosa. 2016. Effects of ambient noise on detectability and localization of avian songs and tones by observers in grasslands. Ecology and Evolution 6:245–255.

Leonard, M. L., and A. G. Horn. 2012. Ambient noise increases missed detections in nestling birds. Biology Letters 8:530–532.

Leston, L., N. Koper, and P. Rosa. 2015. Perceptibility of prairie songbirds using double-observer point counts. Great Plains Research 25:53–61.

Ludlow, S. M., R. M., Brigham, and S. K. Davis. 2014. Nesting ecology of grassland songbirds: effects of predation, parasitism, and weather. The Wilson Journal of Ornithology 126:686–699.

Martin, T. E. 1993. Nest predation and nest sites. BioScience 43:523.

Martin, T. E. 1995. Avian life history evolution in relation to nest sites, nest predation, and food. Ecological Monographs 65:101–127.

Mazerolle, D. F., and K. A. Hobson. 2002. Physiological ramifications of habitat selection in territorial male ovenbirds: consequences of landscape fragmentation. Oecologia 130:356–363.

McClure, C. J. W., H. E. Ware, J. Carlisle, G. Kaltenecker, and J. R. Barber. 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.

McClure, C. J. W., H. E. Ware, J. D. Carlisle, and J. R. Barber. 2017. Noise from a phantom road experiment alters the age structure of a community of migrating birds. Animal Conservation 20:164–172.

McIntyre, E., M. L. Leonard, and A. G. Horn. 2014. Ambient noise and parental communication of predation risk in tree swallows, Tachycineta bicolor. Animal Behaviour 87:85–89.

Mockford, E. J., and R. C. Marshall. 2009. Effects of urban noise on song and response behaviour in great tits. Proceedings of the Royal Society of London B: Biological Sciences 276:2979–2985.

Molles, L. E., and S. L. Vehrencamp. 2001. Neighbour recognition by resident males in the banded wren, *Thryothorus pleurostictus*, a tropical songbird with high song type sharing. Animal Behaviour 61:119–127.

Patten, M. A., and J. F. Kelly. 2010. Habitat selection and the perceptual trap. Ecological Applications 20:2148–2156.

Ralph, C. J., G. R. Geupel, P. Pyle, T. E. Martin, and D. F. DeSante. 1993. Handbook of field methods for monitoring landbirds. USDA Forest Service General Technical Report PSW-GTR-144, Pacific Southwest Research Station, Albany, California, USA.

Remeš, V., and T. E. Martin. 2002. Environmental influences on the evolution of growth and developmental rates in passerines. Evolution 56:2505–2518.

Robertson, B. A., and A. D. Chalfoun. 2016. Evolutionary traps as keys to understanding behavioral maladapation. Current Opinion in Behavioral Sciences 12:12–17.

Robertson, B. A., and R. L. Hutto. 2006. A framework for understanding ecological traps and an evaluation of existing evidence. Ecology 87:1075–1085.

Rodgers, J. A., and N. Koper. 2017. Shallow gas development and grassland songbirds: the importance of perches. The Journal of Wildlife Management 81:406–416.

Rosa, P., and N. Koper. 2018. Integrating multiple disciplines to understand effects of anthropogenic noise on animal communication. Ecosphere 9:e02127.

Rosa, P., C. R. Swider, L. Leston, and N. Koper. 2015. Disentangling effects of noise from presence of anthropogenic infrastructure: Design and testing of system for large-scale playback experiments. Wildlife Society Bulletin, 39:364–372.

SAS Institute, Inc. 2012. SAS Statistical Software. Version 9.4. SAS Institute, Cary, North Carolina, USA.

Sauer, J. R., D. K. Niven, J. E. Hines, D. J. Ziolkowski, Jr, K. L. Pardieck, J. E. Fallon, and W. A. Link. 2017. The North American Breeding Bird Survey, Results and Analysis 1966 - 2015. Version 2.07.2017 USGS Patuxent Wildlife Research Center, Laurel, MD, USA.

Schlaepfer, M. A., M. C. Runge, and P. W. Sherman. 2002. Ecological and evolutionary traps. Trends in Ecology & Evolution 17:474–480.

Shaffer, T. L. 2004. A unified approach to analyzing nest success. The Auk 121:526–540.

Shannon, G., M. F. McKenna, L. M. Angeloni, K. R. Crooks, K. M. Fristrup, E. Brown, et al. 2016. A synthesis of two decades of research documenting the effects of noise on wildlife. Biological Reviews 91:982–1005.

Shannon, G., K. R. Crooks, G. Wittemyer, K. M. Fristrup, and L. M. Angeloni. 2016b. Road noise causes earlier predator detection and flight response in a free-ranging mammal. Behavioral Ecology 27:1370–1375.

Shannon, G., M. F. McKenna, L. M. Angeloni, K. R. Crooks, K. M. Fristrup, E. Brown, et al. 2016a. A synthesis of two decades of research documenting the effects of noise on wildlife. Biological Reviews 91:982–1005.

Stamps, J. A. 1988. Conspecific attraction and aggregation in territorial species. The American Naturalist 131:329–347.

Stephens, S. E., D. N. Koons, J. J. Rotella, and D. W. Willey. 2003. Effects of habitat fragmentation on avian nesting success: a review of the evidence at multiple spatial scales. Biological Conservation 115:101–110.

Vickery, P. D., M. L. Hunter Jr., and J. V. Wells. 1992. Evidence of incidental nest predation and its effects on nests of threatened grassland birds. Oikos 63:281–288.

Ware, H. E., C. J. W McClure, J. D. Carlisle, and J. R. Barber. 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.

Warren, P. S., M. Katti, M. Ermann, and A. Brazel. 2006. Urban bioacoustics: it's not just noise. Animal Behaviour 71:491–502.

Winter, M., S. E. Hawks, J. A. Shaffer, and D. H. Johnson. 2003. Guidelines for finding nests of passerine birds in tallgrass prairie. Prairie Naturalist 35:197–211.

Wright, A. J., N. A. Aguilar, A. L. Baldwin, M. Bateson, C. M. Beale, C. Clark, et al. 2007. Anthropogenic noise as a stressor in animals: a multidisciplinary perspective. International Journal of Comparative Psychology 20:250–273.

Zwart, M. C., J. C. Dunn, P. J. McGowan, and M. J. Whittingham. 2015. Wind farm noise suppresses territorial defense behavior in a songbird. Behavioral Ecology 27:101–108.

CHAPTER 5. CONCLUSIONS AND MANAGEMENT IMPLICATIONS

CONCLUSIONS

The extent to which anthropogenic noise impacts wildlife is not well understood (Kight et al. 2012) because of the challenges associated with isolating effects of noise from potential confounding factors associated with the noise source (e.g., chemical pollution, visual stimuli, habitat alterations; Shannon et al. 2016). My experimental playback design proved to be a valuable method to understand behavioural and ecological impacts on birds exposed to oil development noise for several reasons. First, it was able to recreate the soundscape produced by real oil infrastructure very accurately, which I validated using appropriate acoustic metrics to characterise spectral composition and amplitude attenuation (Rosa et al. 2015; Chapter 2). Different noise treatments were replicated both spatially (i.e., minimum six of replicates per treatment) and temporally (i.e., three breeding seasons). I was able to distinguish between effects of noise from effects driven by the presence of above-ground structures by including infrastructure-only treatments that replicated the playback structure and control treatments. By integrating knowledge and findings from studies in the fields of psychoacoustics, psychophysics, and neurophysiology into applied ecology, I was able to develop a framework that would allow for a better assessment of noise impacts on wild populations (Rosa and Koper 2018; Chapter 3). Finally, measuring species' responses at two different spatial scales allowed for a more refined understanding of effects of noise on predator-prey interactions, habitat selection and quality, and reproductive output for multiple grassland songbird species (Chapter 4).

Findings from this research revealed that anthropogenic noise constrains animal communication across a much larger surface area when considering interferences with attentional processes in addition to energetic masking of signals (Rosa and Koper 2018; Chapter

3). Effects of oil infrastructure noise on communication were also species-specific, depending in part on each species vocalisation range. Further, I found that comparing the abundance of species among different noise treatments was not adequate to determine whether or not species had become habituated to the noise source (Chapter 4); noise influenced habitat selection and productivity differently. Chestnut-collared Longspur (*Calcarius ornatus*), Sprague’s Pipit (*Anthus spragueii*), and Vesper Sparrow (*Pooecetes gramineus*) showed a mismatch between relative habitat use (measured by species’ abundance) and habitat quality (estimated by productivity), while Savannah Sparrow (*Passerculus sandwichensis*) was the only species that avoided treatments where they experienced relatively poor nesting success and produce lower quality nestlings. Hence, for three of the four focal species, noise or infrastructure led to a decoupling of proximate factors used to select a habitat and ultimate factors (i.e., habitat quality; e.g., Block and Brennan 1993)

MANAGEMENT IMPLICATIONS

Current recommendations to minimise risks to migratory grassland songbirds (including avoiding disruption or damage to nests or eggs; Migratory Birds Convention Act 1994) or that can be easily circumvented by stipulating that birds present in areas exposed to oil development noise are likely habituated (Canadian Association of Petroleum Producers 2017) are too broad and ineffective to help mitigate further population declines. According to regulations, noise that is 10 dB above ambient levels or higher than 50 dB is considered to be a high-risk disturbance to migratory birds (Environment and Climate Change Canada 2017). However, noise produced by oil infrastructure is greater than the recommended threshold and these guidelines do no distinguish between chronic and acute noise sources. This study found that acute drilling noise was more detrimental than chronic oil well noise suggesting that the type of noise may be more important than amplitude in assessing potential negative noise impacts on migratory songbirds. Hence, my results demonstrate that migratory birds in affected areas are likely not habituated to these noise sources, which impact abundance, nesting success, and nestling quality.

Although measuring abundance of species present in these disturbed habitats is important, this metric is not indicative of the whole suite on costs incurred by exposed birds, particularly for threatened or specialist species whose ability to accurately assess habitat quality may have been altered in noise-disturbed environments. Since abundance can be a misleading indicator of habitat quality, I recommend that management practices based solely on this measure should proceed with caution, or opt to acquire additional data on other important measures (e.g., nesting success, body condition, clutch size) to better assess impacts of noise on avian populations.

Intermittent drilling noise is unlikely to result in species becoming habituated because it is inconsistent and unpredictable, and hence, potentially perceived as a threat (Francis and Barber 2013). Therefore, preventing drilling operations from taking place during the breeding season of migratory songbirds would be beneficial to most of the focal species studied here. Best management practices by the Alberta provincial government stipulate that a buffer of 100 m be maintained near active Chestnut-collared Longspur and Sprague's Pipit nests between April 15 and August 15 of each year (Government of Alberta 2017). However, noise from drilling operations is audible well beyond that buffer zone (e.g., up to 235 m for Chestnut-collared Longspur and 325 m for Sprague's Pipit; Table S4.1.1 in Appendix S4.1), resulting in additional habitat loss for species that perceive this noise as a threat to nestling or adult survival. When drilling operations occur in urban areas, temporary perimeter sound walls are regularly used to reduce noise levels by approximately 15 to 22 dB(A) (Environmental Noise Control 2018). Further, novel electric-hydraulic rotary drills with electric motors instead of the traditional diesel-hydraulic rotary drills are currently being used in Utah to create municipal water wells meeting 65 dB(A) zoning code requirements (Lamb 2017). Requiring that quieter drilling equipment or noise-mitigation measures be implemented in more rural areas where most of the sensitive species reside would be beneficial to nesting birds.

Since different oil well pumps produce different multimodal stimuli, managers could be more selective about the type of infrastructure employed to extract oil. For example, opting for screwpumps instead of pumpjacks may help decrease the effects of cross-modal distractions for nearby birds (Rosa and Koper 2018). Screwpumps have a lower vertical profile of approximately 2.7 m with little movement, while pumpjacks are approximately 4.5-m tall with multiple moving parts, such as a long walking beam that moves consistently in a vertical nodding motion. Savannah Sparrow males singing near noisy oil wells demonstrated higher adrenocortical responsiveness (i.e., a measure of stress levels) near pumpjacks than screwpumps, and this increased stress response resulted in more unnecessary aggressive behaviours in response to conspecific songs at pumpjacks sites (Curry et al. 2018). Although noise amplitude was higher at screwpumps, pumpjacks may be a more salient visual stimulus provoking greater stress responses and with greater potential to interfere with signals occurring in other modalities, such as acoustic signals in territorial males (Busch and Hayward 2009, Spence 2010, Curry et al. 2018). However, a previous study showed that nesting success of Savannah Sparrow and Vesper Sparrow was lower at sites with screwpumps compared to pumpjacks (Bernath-Plaisted and Koper 2016). Hence, there is a need to evaluate multiple co-occurring factors that could impact species exposed to anthropogenic disturbances, and investigating these effects on a species-specific basis may be necessary before developing management recommendations. Finally, enforcing the provincial regulation that non-operational oil wells be dismantled and sites be reclaimed within 12 months (Alberta Energy Regulator 2016) would benefit species sensitive to above-ground infrastructure (i.e., Chestnut-collared Longspur, Sprague’s Pipit, Vesper Sparrow).

Although effects of anthropogenic noise are complex and difficult to isolate from other habitat disturbances, the results of my research show that noise does present a threat to grassland songbirds, particularly if intermittent and unpredictable, and thus, noise itself is worth mitigating. Despite the availability of technology that reduces noise amplitude of oil extraction activities, few studies make concrete recommendations concerning how these noise-mitigation measures could benefit their study species (<10%; reviewed in Shannon et al. 2016). Future studies should propose applicable mitigation recommendations, but must also attempt to evaluate the effectiveness of these measures to determine if and how animals recuperate from exposure to noise (Shannon et al. 2016). Effective experimental studies are difficult to design and implement but are necessary to gain knowledge that can lead to useful management recommendations and practices to reduce impacts of anthropogenic noise on wildlife.

LITERATURE CITED

Alberta Energy Regulator. 2016. Directive 020: Well abandonment. Calgary, Alberta, Canada. March 15, 2016. https://www.aer.ca/documents/directives/Directive020.pdf

Bernath-Plaisted, J., and N. Koper. 2016. Physical footprint of oil and gas infrastructure, not anthropogenic noise, reduces nesting success of some grassland songbirds. Biological conservation 204:434–441.

Block, W. M., and L. A. Brennan. 1993. The habitat concept in ornithology. Pages 35–91 in D. M. Power, editor. Current Ornithology (Vol. 11). Plenum Press, New York.

Busch, D. S., and L. S. Hayward. 2009. Stress in a conservation context: a discussion of glucocorticoid actions and how levels change with conservation-relevant variables. Biological Conservation 142:2844–2853.

Canadian Association of Petroleum Producers. 2017. 2017 CAPP Crude oil forecast, markets & transportation. Canada's Oil & Natural Gas Producers, Calgary, Alberta, Canada. http://www.capp.ca/publications-and-statistics/publications/303440.

Curry, C. M., P. G. Des Brisay, P. Rosa, and N. Koper. 2018. Noise source and individual physiology mediate effectiveness of bird songs adjusted to anthropogenic noise. Scientific Reports 8:3942.

Environment and Climate Change Canada. 2017. Avoiding harm to migratory birds: Technical information about the guidelines. Government of Canada, https://www.ec.gc.ca/paom-itmb/. Accessed September 21, 2017.

Environmental Noise Control. 2018. Temporary Perimeter Sound Walls. Behrens and Associates. Accessed June 7, 2018. http://www.drillingnoisecontrol.com/tempwalls.html

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

Government of Alberta. 2017. Master schedule of standards and conditions. Version date July 28, 2017. Operations Division and Environment and Parks, Edmonton, Alberta, Canada. http://aep.alberta.ca/forms-maps-services/industry-online-services/public-lands-dispositions/step-one-pre-application/documents/MasterSchedStandardsConditions-Jun28-2017.pdf

Kight, C. R., M. S. Saha, and J. P. Swaddle. 2012. Anthropogenic noise is associated with reductions in the productivity of breeding Eastern Bluebirds (*Sialia sialis*). Ecological Applications 22:1989–1996.

Lamb, J. 2017. Drilling services achieves sound abatement with electric rotary rig. Published March 1, 2017. Accessed June 7, 2018. https://www.boartlongyear.com/insite/sound-abatement-electric-rotary-rig/

Migratory Birds Convention Act. (1994). (S.C. 1994, c.22). Minister of Justice, Government of Canada, current to August 27, 2017, http://laws-lois.justice.gc.ca/PDF/M-7.01.pdf.

Rosa, P., and N. Koper. 2018. Integrating multiple disciplines to understand effects of anthropogenic noise on animal communication. Ecosphere 9:e02127.

Rosa, P., C. R. Swider, L. Leston, and N. Koper. 2015. Disentangling effects of noise from presence of anthropogenic infrastructure: Design and testing of system for large-scale playback experiments. Wildlife Society Bulletin, 39:364–372.

Shannon, G., M. F. McKenna, L. M. Angeloni, K. R. Crooks, K. M. Fristrup, E. Brown, et al. 2016. A synthesis of two decades of research documenting the effects of noise on wildlife. Biological Reviews 91:982–1005.

Spence, C. 2010. Crossmodal spatial attention. Annals of the New York Academy of Sciences 1191:182–200.

APPENDIX S2.1 Supplemental technical details for the solar-powered broadcasting system design

The solar-powered broadcasting units each contained an array of 5 150-W (8.7-A, 12-V) solar panels (SunForce Products, Montreal, QC, Canada), for a potential 750-W (43.5-A) maximum power. I estimated the maximum power consumption of the system to be approximately 300 W by summing the expected power consumption of all the components (charge controller, inverter, speakers, and iPod; Morningstar 2009, LOUD 2011, Schumacher Electric 2012). I then designed the system so that the solar panels would generate a potential 750-W maximum power (350 W more than anticipated needing). Given the potential for cloudy days and the necessity to broadcast noise continuously throughout the night, this overcompensation ensured that the batteries could be recharged during a relatively short period of sunlight.

The panels were mounted on a frame constructed from 38-mm × 89-mm pressure-treated lumber. The dimensions of the frame were 3.8 m (l) × 1.1 m (h) × 1.5 m (w). This height and width combination held the solar panels at an angle of roughly 55° from vertical. This angle optimised solar irradiance on the panels, given the latitude of the study sites and the time of year the study was conducted (Boxwell 2013).

I wired the 12-V solar panels in parallel to maintain the voltage at 12 V throughout the system. Parallel wiring is also advantageous because if one of the panels fails, the rest of the array is still functional, whereas failure of a panel in a series circuit would result in failure of the entire system. I used weather-resistant, 6-AWG copper wire to accommodate the current and minimise voltage loss over the length of the wire in the system. Using wire that is too thin is inefficient because it results in voltage drops as wire length increases (Morningstar 2009). The stock wiring built into the solar panels was spliced onto the 6-AWG wire by crimping metal eyelets onto wire ends and connecting them with a nut and bolt. The exposed metal was then wrapped with electrical tape. This connection method was used to connect wires throughout the system.

The positive and negative leads from the solar panel array connected to the PV+ and PV− terminals in the charge controller. I interrupted the positive lead with an on/off kill switch that allowed to cut power from the solar panels to the rest of the system quickly and safely. I used a TriStar 45 charge controller (Morningstar Corporation, Newtown, PA) because its 45-A capacity exceeded the potential system maximum of 43.5 A. I grounded the system by wiring the charge controller to a grounding plate buried beneath the system. Copper grounding wire (6-AWG) was used for this connection.

The Battery+ and Battery− leads from the charge controller connected to the battery array. I used an array of four 6-V deep-cycle golf cart batteries (Exide, Milton, GA; Commercial Series, Product no. 10-2010-0). Deep cycle batteries provide constant current over long periods of time and can survive repeated discharge/recharge cycles. I wired them in a series-parallel arrangement to adapt the 6-V batteries into a 12-V configuration.

Current from the batteries was directed to a Schumacher 410-W power inverter, which converted direct current (DC) to alternating current (AC) and supplied the 8-GB iPod Nano and the 2 Mackie SRM350v2 loudspeakers (LOUD Technologies, Woodinville, WA) with AC power. I used this model of power inverter because the 410-W capacity exceeded the expected power consumption of the speakers and iPod. The iPod connected to the speakers with a 1/8” to dual ¼” audio cable. Powered speakers were used to eliminate the need for an amplifier. For a detailed rationale for speaker selection, see Discussion in Chapter 2.

The batteries, speakers, iPod, charge controller, and inverter were contained in a 1.2-m (l)

× 0.9-m (w) × 0.7-m (h) plywood box adjacent to the solar panel array, which protected the electronic components from the elements. The speakers projected sound through 36-cm (w) × 56-cm (h) screened holes in opposite sides of the boxes. Additional 75-cm (l) × 3-cm (h) screened slots located on the sides not containing speaker holes assisted in ventilation to prevent overheating. The boxes were painted white to reflect light and prevent heat absorption. The boxes were elevated approximately 0.2 m above the ground on cement cinder blocks, to prevent decay from moisture and to aid in sound projection. I installed a 1-m-high metal technical fence (Boomers Services, Brooks, AB, Canada) around each unit to prevent damage from cattle, for a fenced area of 7.3 m (l) × 4.9 m (w).

LITERATURE CITED

Boxwell, M. 2013. Solar angle calculator. *In* Solar electricity handbook. Greenstream, Warwickshire, England, United Kingdom. http://solarelectricityhandbook.com/solar-angle-calculator.html. Accessed 15 Jan 2014.

LOUD. 2011. SRM350v2 powered loudspeaker owner's manual. Loud Technologies, Woodinville, Washington, USA.

Morningstar. 2009. TriStar solar system controller: installation and operation manual. Morningstar, Washington Crossing, Pennsylvania, USA.

Schumacher Electric. 2012. Model PID-410 power inverter owner's manual. Schumacher Electric, Mount Prospect, Illinois, USA.

Supplemental material for: Rosa, P., C. R. Swider, L. Leston, and N. Koper. 2015. Disentangling effects of noise from presence of anthropogenic infrastructure: design and testing of system for large-scale playback experiments. Wildlife Society Bulletin 39:364–372.

APPENDIX S3.1 Literature review on effects of anthropogenic noise on animal communication from 2010 – 2017 (Fig. 3.1)

A recent review has found an increase in ecological assessment studies of anthropogenic noise impacts on wildlife with a particularly large increase in publications since 2010 (Shannon et al. 2016a). Hence, I assessed whether there was also an increase in the mention of energetic and informational masking, auditory scene analysis, multimodal communication, and cross-modal impacts from 2010 to 2017. I included publications (including research articles, reviews, perspectives) mentioning these mechanisms as potentially important in the assessment of anthropogenic noise effects on animal communication to evaluate awareness of these traditionally human-centric concepts in ecological literature. I conducted a literature search using Thompson Reuters' *ISI Web of Science* using the search terms outlined in Table S3.1.1a. I also cross-referenced recent literature reviews of effects of anthropogenic noise on wildlife (e.g. Halfwerk & Sabbekoorn 2015; Shannon et al. 2016a; Erbe et al. 2016). I examined each publication by searching specific terms (Table S3.1.1b), and the context in which they were mentioned. I excluded studies focused on human subjects, and publications focused exclusively on natural sources of ambient noise (e.g. morning chorus, wind, rain).

I used VIB-Ugent Center for Plant Systems Biology's Venn diagram webtool to calculate and draw Figure 3.1 (http://bioinformatics.psb.ugent.be/webtools/Venn/). This webtool also provided an input table (Table S3.1.2) with a summary of elements (i.e. publications) and an output table (Table S3.1.3) listing common elements of the sets (i.e. key concepts) represented by the overlapping area in Figure 3.1. To represent trends in awareness of these concepts across years from 2010 to 2017, I represented studies referencing 2 or more concepts as potential mechanisms affecting animal communication in noise for each years in Figure 3.1.

Table S3.1.1 Literature review search terms for each concept reviewed. *ISI Web of Science* search included search operators such as quotation marks to find exact phrases, asterisks following root words, and operators proposed in their guidelines (i.e. AND, OR, NEAR; a). Focused search of each publication was conducted in PDF XChange Viewer 2.5 (Tracker Software Products, 2012; b). Search terms related to scope (i.e. anthropogenic noise, animal communication) were employed for each search concerning focal mechanisms.

Scope topics	**(a) *ISI Search***	**(b) Focused search**
Anthropogenic noise	(noise* NEAR/3 pollution*) OR (noise* NEAR/3 anthropogenic*) OR (noise* NEAR/3 disturbance*)	noise anthropo* distrurb*
Animal communication	[wildlife OR animal OR mammal OR reptile OR amphibian OR bird OR fish OR invertebrate] AND [communicat* OR calling* OR "alarm" OR "call*" OR "song" OR "cue" OR "display" OR (signal* NEAR/3 acoustic*)]	communicat* signal
Focal mechanisms	**(a) *ISI Search***	**(b) Focused search**
Energetic masking	"energetic mask*" OR (frequency* NEAR/3 mask*) OR "acoustic mask*" OR "co-modulat*" OR "comodulat*" OR "spatial release" OR (mask* NEAR/3 noise*) OR (mask* NEAR/3 signal*)	energetic mask* mask*
Informational masking	"informational mask*" OR distract* OR (distraction AND attention*)	informational mask* distract* attention*
Auditory scene analysis	"auditory scene analysis" OR "scene analysis" OR "source segregat*" OR "stream segregat*" OR "auditory object"	scene segregat*
Multimodal signals	"multimodal" OR "multi-modal"	modal multimodal OR multi-modal
Cross-modal interference	"crossmodal" OR "cross-modal" OR "across modalities" OR "across sensory modalities"	modal crossmodal OR cross-modal across modal* across sensory modal*

Table S3.1.2 Summary of publications considered for each concept and number of overall unique publications inputted into Venn diagram webtool for comparison.

Concepts	Number of publications
Energetic masking	174
Informational masking	57
Auditory scene analysis	41
Multimodal signals	39
Cross-modal impacts	33
Overall number of unique elements	241

Table S3.1.3 Summary of publications referencing two or more of the concepts reviewed (a) i.e. energetic (A) and informational masking (B), auditory scene analysis (C), multimodal signals (D), and cross-modal impacts (E) in relation to effects on animal communication in anthropogenic noise, and publications referencing only one of these concepts (b).

(a)

Concepts	Total	Citations
A B C D E	2	Bee & Miller 2016; Miller & Bee 2012
A B C D	1	Farris & Taylor 2016
A B D E	2	Swaddle et al. 2015; Francis 2015
A C D E	1	van der Sluijs et al. 2011
A B C	5	Popper & Hawkins 2016; Bee 2015; Branstetter et al. 2016; Dooling & Blumenrath 2013; Bee & Christensen-Dalsgaard 2016
A B D	1	Potvin 2017
A B E	9	Meillere et al. 2015; Halfwerk et al. 2016; Shannon et al. 2016b; Shannon et al. 2016a; Purser & Radford 2011; Francis & Barber 2013; Shannon et al. 2014; Ware et al. 2015; McGregor et al. 2013
A C D	2	Velez et al. 2013; Wiley 2015
A D E	3	Romer 2013; Gordon & Uetz 2012; Brumm 2013
A B	16	Schmidt et al. 2014; Naguib 2013; Kleist et al. 2016; Wiley 2013; Brown et al. 2012; Pohl et al. 2015; Kern & Radford 2016; Sabet et al. 2016a; Naguib et al. 2013; Radford et al. 2014; Leonard & Horn 2012; Owens et al. 2012; Shier et al. 2012; Grade & Sieving 2016; Senzaki et al. 2016; McClure et al. 2013
A C	9	Klump 2016; Casper et al. 2013; Gutscher et al. 2011; Branstetter et al. 2013b; Schmidt & Roemer 2011; Dooling & Popper 2016; Hatch et al. 2012; Branstetter et al. 2013a; Finneran & Branstetter 2013
A D	5	Brumm & Zollinger 2013; Hage et al. 2013; Schwartz & Bee 2013; Rios-Chelen et al. 2015; Preininger et al. 2013
A E	2	McNett et al. 2010; Goodwin & Podos 2013
B E	6	Chan et al. 2010a; Kunc et al. 2016; Chan et al. 2010b; Morris-Drake et al. 2016; Chan & Blumstein 2011; Blumstein 2014
C D	2	Taylor & Ryan 2013; Holt et al. 2010
D E	3	Munoz & Blumstein 2012; Halfwerk & Slabbekoorn 2015; Page & Jones 2016

(b)

Concepts	Total	Citations
A	116	Bermúdez-Cuamatzin et al. 2011; Halfwerk et al. 2011b; Halfwerk & Slabbekoorn 2013; Melcon et al. 2012; Ladick & Schulz-Mirbach 2013; Gross et al. 2010; Cardoso 2014; Dominoni et al. 2016; Nieukirk et al. 2012; Francis et al. 2011c; Nemeth & Brumm 2010; Potvin & Mulder 2013; Mockford et al. 2011; Mendes et al. 2011a; Redondo et al. 2013; Lackey et al. 2011; Grace & Anderson 2015; Shieh et al. 2016; Balakrishnan 2016; Guo et al. 2016; Luther & Gentry 2013; Pieretti & Farina 2013; Rice et al. 2014; Gough et al. 2014; Swaddle et al. 2012; Kight et al. 2012; Nowacek et al. 2015; Terhune & Bosker 2016; Job et al. 2016; Mendes et al. 2011b; Schroeder et al. 2012; Blickley & Patricelli 2012; Diaz et al. 2011; Tennessen et al. 2016; Moiron et al. 2015; Roca et al. 2016; Swaddle et al. 2016; Henry et al. 2016; Templeton et al. 2016; Lackey et al. 2012; Byrnes et al. 2012; Nemeth et al. 2013; Cartwright et al. 2014; Lammers et al. 2012; Pine et al. 2012; Oden et al. 2015; Lucass et al. 2016; Holt et al. 2015; Schmidt & Balakrishnan 2015; Costello & Symes 2014; Tyack & Janik 2013; Cardoso & Atwell 2011; Luther & Magnotti 2014; Seger-Fullman et al. 2012; Slabbekoorn 2013; Luther et al. 2015; Arroyo-Solis et al. 2013; Colino-Rabanal et al. 2016; Ellison et al. 2012; Potvin & MacDougall-Shackleton 2015; Simard et al. 2011; Miksis-Olds & Wagner 2011; Potvin et al. 2014; Lowry et al. 2012; Arevalo & Newhard 2011; Francis et al. 2011d; Hobel 2014; Orci et al. 2016; Vargas-Salinas et al. 2014; Holt et al. 2011; La Manna et al. 2013; Gill et al. 2014; Cunnington & Fahrig 2010; Goodwin & Shriver 2010; Bunkley et al. 2015 Francis et al. 2011b; Parris & McCarthy 2013; Blackwell et al. 2013; Rios-Chelen et al. 2017; McCarthy et al. 2011; Huet des Aunay et al. 2014; Castellote et al. 2012; Blickley et al. 2012a; Francis et al. 2012; Luther & Derryberry 2012; Rios-Chelen et al. 2012; Francis et al. 2011a; Ortega 2012; Laiolo 2011; Halfwerk et al. 2011a; Neenan et al. 2016; Herrera-Montes & Aide 2011; Kruger & Du Preez 2016; Lowry et al. 2013; Vargas-Salinas & Amezquita 2013; Erbe et al. 2016; Moore et al. 2012; Proppe et al. 2013; Ladich 2013; McMullen et al. 2014; Iglesias-Merchan et al. 2016; Huffeldt & Dabelsteen 2013; Lampe et al. 2014; Lampe et al. 2013; McIntyre et al. 2014; Fay 2011; Dowling et al. 2012; Sabet et al. 2016b; Kostarakos & Romer 2015; Blickley et al. 2012b; Verzijden et al. 2010; Dorado-Correa et al. 2016; Cunningham & Mountain 2014; Pohl et al. 2012; Hanna et al. 2011; Hu & Cardoso 2010
B	15	Read et al. 2014; Klett-Mingo et al. 2016; Simpson et al. 2015; Akre & Johnsen 2016; Owen et al. 2014; Simpson et al. 2016; Hubbard et al. 2015; Siemers & Schaub 2011; Vélez et al. 2013; Grubb et al. 2013; Römer 2013; Luo et al. 2015; Sabet et al. 2015; Wale et al. 2013; Everley et al. 2016
C	19	Klink et al. 2010; Blesdoe & Blumstein 2014; Bee 2012; Farris & Ryan 2011; Ponnath & Farris 2014; Mouterde et al. 2014; Willis 2016;

		Larsson 2012; Itatani & Klum 2017; Neilans & Dent 2015a; Tarano 2015; Jarvis et al. 2013; Mooney et al. 2016; Slabbekoorn et al. 2012; Dent et al. 2016; Lewicki et al. 2014; Neilans & Dent 2015b; Seeba et al. 2010; Velez & Bee 2011
D	17	Gomez et al. 2011; Highman & Hebets 2013; Reichert et al. 2016; Troianowski et al. 2014; Troianowski et al. 2015; Taylor et al. 2011; Lecker et al. 2015; Uetz et al. 2013; Wilson et al. 2013; Rhebergen et al. 2015; Partan 2013; Rubi & Stephens 2016; Maruska et al. 2012; Halfwerk et al. 2014; Arch et al. 2011; Weissburg et al. 2014; Grafe et al. 2012
E	5	Estramil et al. 2014; Higham & Hebets 2013; Kunc et al. 2014; McLaughlin & Kunc 2015; Reichert & Hobel 2015

LITERATURE CITED

Energetic masking

Arévalo, J. E., & Newhard, K. (2011). Traffic noise affects forest bird species in a protected tropical forest. Revista de Biologia Tropical, 59, 969-980.

Arroyo-Solís, A., Castillo, J. M., Figueroa, E., López-Sánchez, J. L., & Slabbekoorn, H. (2013). Experimental evidence for an impact of anthropogenic noise on dawn chorus timing in urban birds. Journal of Avian Biology, 44, 288-296.

Balakrishnan, R. (2016). Behavioral Ecology of Insect Acoustic Communication. In Insect Hearing (pp. 49-80). Springer International Publishing.

Bee, M. A. (2015). Treefrogs as animal models for research on auditory scene analysis and the cocktail party problem. International Journal of Psychophysiology, 95, 216-237.

Bee, M. A., & Christensen-Dalsgaard, J. (2016). Sound source localization and segregation with internally coupled ears: the treefrog model. Biological Cybernetics, 110, 271-290.

Bee, M. A., & Miller, C. T. (2016). Signaler and receiver psychology. In Psychological mechanisms in animal communication (pp. 1-16). Springer International Publishing.

Bermúdez-Cuamatzin, E., Ríos-Chelén, A. A., Gil, D., & Garcia, C. M. (2011). Experimental evidence for real-time song frequency shift in response to urban noise in a passerine bird. Biology Letters, 8, 36-38.

Blackwell, S. B., Nations, C. S., McDonald, T. L., Greene, C. R., Thode, A. M., Guerra, M., & Michael Macrander, A. (2013). Effects of airgun sounds on bowhead whale calling rates in the Alaskan Beaufort Sea. Marine Mammal Science, 29, E342-E365.

Blickley, J. L., & Patricelli, G. L. (2012). Potential acoustic masking of greater sage-grouse (*Centrocercus urophasianus*) display components by chronic industrial noise. Ornithological Monographs, 74, 23-35.

Blickley, J. L., Blackwood, D., & Patricelli, G. L. (2012a). Experimental evidence for the effects of chronic anthropogenic noise on abundance of greater sage-grouse at leks. Conservation Biology, 26, 461-471.

Blickley, J. L., Word, K. R., Krakauer, A. H., Phillips, J. L., Sells, S. N., Taff, C. C., *et al.* (2012b). Experimental chronic noise is related to elevated fecal corticosteroid metabolites in lekking male greater sage-grouse (*Centrocercus urophasianus*). PLoS One, 7, e50462.

Branstetter, B. K., Trickey, J. S., Aihara, H., Finneran, J. J., & Liberman, T. R. (2013a). Time and frequency metrics related to auditory masking of a 10 kHz tone in bottlenose dolphins (*Tursiops truncatus*). The Journal of the Acoustical Society of America, 134, 4556-4565.

Branstetter, B. K., Trickey, J. S., Bakhtiari, K., Black, A., Aihara, H., & Finneran, J. J. (2013b). Auditory masking patterns in bottlenose dolphins (*Tursiops truncatus*) with natural, anthropogenic, and synthesized noise. The Journal of the Acoustical Society of America, 133, 1811-1818.

Branstetter, B. K., Bakhtiari, K., Black, A., Trickey, J. S., Finneran, J. J., & Aihara, H. (2016). Energetic and informational masking of complex sounds by a bottlenose dolphin (*Tursiops truncatus*). The Journal of the Acoustical Society of America, 140, 1904-1917.

Brown, C. L., Hardy, A. R., Barber, J. R., Fristrup, K. M., Crooks, K. R., & Angeloni, L. M. (2012). The effect of human activities and their associated noise on ungulate behavior. PloS One, 7, e40505.

Brumm, H. (2013). Introduction. In Animal Communication and Noise (pp. 187-227). Springer Berlin Heidelberg.

Brumm, H., & Zollinger, S. A. (2013). Avian vocal production in noise. In Animal Communication and Noise (pp. 187-227). Springer Berlin Heidelberg.

Bunkley, J. P., McClure, C. J., Kleist, N. J., Francis, C. D., & Barber, J. R. (2015). Anthropogenic noise alters bat activity levels and echolocation calls. Global Ecology and Conservation, 3, 62-71.

Byrnes, P., Goosem, M., & Turton, S. M. (2012). Are less vocal rainforest mammals susceptible to impacts from traffic noise? Wildlife Research, 39, 355-365.

Cardoso, G. C. (2014). Nesting and acoustic ecology, but not phylogeny, influence passerine urban tolerance. Global Change Biology, 20, 803-810.

Cardoso, G. C., & Atwell, J. W. (2011). On the relation between loudness and the increased song frequency of urban birds. Animal Behaviour, 82, 831-836.

Cartwright, L. A., Taylor, D. R., Wilson, D. R., & Chow-Fraser, P. (2014). Urban noise affects song structure and daily patterns of song production in Red-winged Blackbirds (*Agelaius phoeniceus*). Urban Ecosystems, 17, 561-572.

Casper, B. M., Smith, M. E., Halvorsen, M. B., Sun, H., Carlson, T. J., & Popper, A. N. (2013). Effects of exposure to pile driving sounds on fish inner ear tissues. Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology, 166, 352-360.

Castellote, M., Clark, C. W. & Lammers, M. O. (2012). Acoustic and behavioural changes by fin whales (*Balaenoptera physalus*) in response to shipping and airgun noise. Biological Conservation, 147, 115–122.

Colino-Rabanal, V. J., Mendes, S., Peris, S. J., & Pescador, M. (2016). Does the song of the Wren Troglodytes troglodytes change with different environmental sounds? Acta Ornithologica, 51, 13-22.

Costello, R. A., & Symes, L. B. (2014). Effects of anthropogenic noise on male signalling behaviour and female phonotaxis in Oecanthus tree crickets. Animal Behaviour, 95, 15-22.

Cunnington, G. M., & Fahrig, L. (2010). Plasticity in the vocalizations of anurans in response to traffic noise. Acta Oecologica, 36, 463-470.

Cunningham, K. A., & Mountain, D. C. (2014). Simulated masking of right whale sounds by shipping noise: Incorporating a model of the auditory periphery. The Journal of the Acoustical Society of America, 135, 1632-1640.

Huet des Aunay, G. H., Slabbekoorn, H., Nagle, L., Passas, F., Nicolas, P., & Draganoiu, T. I. (2014). Urban noise undermines female sexual preferences for low-frequency songs in domestic canaries. Animal Behaviour, 87, 67-75.

Díaz, M., Parra, A., & Gallardo, C. (2011). Serins respond to anthropogenic noise by increasing vocal activity. Behavioral Ecology, 22, 332-336.

Dominoni, D. M., Greif, S., Nemeth, E., & Brumm, H. (2016). Airport noise predicts song timing of European birds. Ecology and Evolution, 6, 6151-6159.

Dooling, R. J., & Blumenrath, S. H. (2013). Avian sound perception in noise. In Animal communication and noise (pp. 229-250). Springer Berlin Heidelberg.

Dooling, R. J., & Popper, A. N. (2016). Technical guidance for assessment and mitigation of the effects of highway and road construction noise on birds. The California Department of Transportation, Division of Environmental Analysis, Sacramento, California, USA.

Dorado-Correa, A. M., Rodríguez-Rocha, M., & Brumm, H. (2016). Anthropogenic noise, but not artificial light levels predicts song behaviour in an equatorial bird. Royal Society Open Science, 3, 160231.

Dowling, J. L., Luther, D. A., & Marra, P. P. (2012). Comparative effects of urban development and anthropogenic noise on bird songs. Behavioral Ecology, 23, 201-209.

Ellison, W. T., Southall, B. L., Clark, C. W., & Frankel, A. S. (2012). A new context-based approach to assess marine mammal behavioral responses to anthropogenic sounds. Conservation Biology, 26, 21-28.

Erbe, C., Reichmuth, C., Cunningham, K., Lucke, K., & Dooling, R. (2016). Communication masking in marine mammals: A review and research strategy. Marine Pollution Bulletin, 103, 15-38.

Farris, H. E., & Taylor, R. C. (2016). Mate searching animals as model systems for understanding perceptual grouping. In Psychological Mechanisms in Animal Communication (pp. 89-118). Springer International Publishing.

Fay, R. R. (2011). Signal-to-noise ratio for source determination and for a comodulated masker in goldfish, *Carassius auratus*. The Journal of the Acoustical Society of America, 129, 3367-3372.

Finneran, J. J., & Branstetter, B. K. (2013). Effects of noise on sound perception in marine mammals. In Animal Communication and Noise (pp. 273-308). Springer Berlin Heidelberg.

Francis, C. D. (2015). Vocal traits and diet explain avian sensitivities to anthropogenic noise. Global Change Biology, 21, 1809-1820.

Francis, C. D., & Barber, J. R. (2013). A framework for understanding noise impacts on wildlife: an urgent conservation priority. Frontiers in Ecology and the Environment, 11, 305-313.

Francis, C. D., Ortega, C. P., & Cruz, A. (2011a). Noise pollution filters bird communities based on vocal frequency. PLoS One, 6, e27052.

Francis, C. D., Ortega, C. P., & Cruz, A. (2011b). Different behavioural responses to anthropogenic noise by two closely related passerine birds. Biology Letters, rsbl20110359.

Francis, C. D., Ortega, C. P., & Cruz, A. (2010c). Vocal frequency change reflects different responses to anthropogenic noise in two suboscine tyrant flycatchers. Proceedings of the Royal Society of London B: Biological Sciences, rspb20101847.

Francis, C. D., Paritsis, J., Ortega, C. P., & Cruz, A. (2011d). Landscape patterns of avian habitat use and nest success are affected by chronic gas well compressor noise. Landscape Ecology, 26(9), 1269-1280.

Francis, C. D., Kleist, N. J., Davidson, B. J., Ortega, C. P., & Cruz, A. (2012). Behavioral responses by two songbirds to natural-gas-well compressor noise. Ornithological Monographs, 74, 36-46.

Gill, S. A., Job, J. R., Myers, K., Naghshineh, K., & Vonhof, M. J. (2015). Toward a broader characterization of anthropogenic noise and its effects on wildlife. Behavioral Ecology, 26, 328-333.

Goodwin, S. E., & Podos, J. (2013). Shift of song frequencies in response to masking tones. Animal Behaviour, 85, 435-440.

Goodwin, S. E., & Shriver, W. G. (2011). Effects of traffic noise on occupancy patterns of forest birds. Conservation Biology, 25, 406-411.

Gordon, S. D., & Uetz, G. W. (2012). Environmental interference: impact of acoustic noise on seismic communication and mating success. Behavioral Ecology, 23, 707-714.

Gough, D. C., Mennill, D. J., & Nol, E. (2014). Singing seaside: Pacific Wrens (*Troglodytes pacificus*) change their songs in the presence of natural and anthropogenic noise. Wilson Journal of Ornithology, 126, 269-278.

Grace, M. K., & Anderson, R. C. (2015). No frequency shift in the "D" notes of Carolina chickadee calls in response to traffic noise. Behavioral ecology and sociobiology, 69, 253-263.

Grade, A. M., & Sieving, K. E. (2016). When the birds go unheard: highway noise disrupts information transfer between bird species. Biology Letters, 12, 20160113.

Gross, K., Pasinelli, G., & Kunc, H. P. (2010). Behavioral plasticity allows short-term adjustment to a novel environment. The American Naturalist, 176, 456-464.

Guo, F., Bonebrake, T. C., & Dingle, C. (2016). Low frequency dove coos vary across noise gradients in an urbanized environment. Behavioural Processes, 129, 86-93.

Gutscher, M., Wysocki, L. E., & Ladich, F. (2011). Effects of aquarium and pond noise on hearing sensitivity in an otophysine fish. Bioacoustics, 20, 117-136.

Hage, S. R., Jiang, T., Berquist, S. W., 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.

Halfwerk, W., & Slabbekoorn, H. (2013). The impact of anthropogenic noise on avian communication and fitness. Avian Urban Ecology, 84-97.

Halfwerk, W., Both, C., & Slabbekoorn, H. (2016). Noise affects nest-box choice of 2 competing songbird species, but not their reproduction. Behavioral Ecology, 27, 1592-1600.

Halfwerk, W., Bot, S., Buikx, J., van der Velde, M., Komdeur, J., ten Cate, C., & Slabbekoorn, H. (2011a). Low-frequency songs lose their potency in noisy urban conditions. Proceedings of the National Academy of Sciences, 108, 14549-14554.

Halfwerk, W., Holleman, L. J., Lessells, C. K., & Slabbekoorn, H. (2011b). Negative impact of traffic noise on avian reproductive success. Journal of applied Ecology, 48, 210-219.

Hanna, D., Blouin-Demers, G., Wilson, D. R., & Mennill, D. J. (2011). Anthropogenic noise affects song structure in red-winged blackbirds (*Agelaius phoeniceus*). Journal of experimental Biology, 214, 3549-3556.

Hatch, L. T., Clark, C. W., Van Parijs, S. M., Frankel, A. S., & Ponirakis, D. W. (2012). Quantifying loss of acoustic communication space for right whales in and around a US National Marine Sanctuary. Conservation Biology, 26, 983-994.

Henry, K. S., Gall, M. D., Vélez, A., & Lucas, J. R. (2016). Avian auditory processing at four different scales: variation among species, seasons, sexes, and individuals. In Psychological Mechanisms in Animal Communication (pp. 17-55). Springer International Publishing.

Herrera-Montes, M. I., & Aide, T. M. (2011). Impacts of traffic noise on anuran and bird communities. Urban Ecosystems, 14, 415-427.

Höbel, G. (2014). Effect of temporal and spectral noise features on gap detection behavior by calling green treefrogs. Behavioural Processes, 108, 43-49.

Holt, M. M., Noren, D. P., & Emmons, C. K. (2011). Effects of noise levels and call types on the source levels of killer whale calls. The Journal of the Acoustical Society of America, 130, 3100-3106.

Holt, M. M., Noren, D. P., Dunkin, R. C., & Williams, T. M. (2015). Vocal performance affects metabolic rate in dolphins: implications for animals communicating in noisy environments. Journal of Experimental Biology, 218, 1647-1654.

Hu, Y., & Cardoso, G. C. (2010). Which birds adjust the frequency of vocalizations in urban noise? Animal Behaviour, 79, 863-867.

Huffeldt, N. P., & Dabelsteen, T. (2013). Impact of a noise-polluted urban environment on the song frequencies of a cosmopolitan songbird, the Great Tit (*Parus major*), in Denmark. Ornis Fennica, 90, 94-102.

Iglesias-Merchán, C., Diaz-Balteiro, L., & de la Puente, J. (2016). Road traffic noise impact assessment in a breeding colony of cinereous vultures (Aegypius monachus) in Spain. The Journal of the Acoustical Society of America, 139, 1124-1131.

Job, J. R., Kohler, S. L., & Gill, S. A. (2016). Song adjustments by an open habitat bird to anthropogenic noise, urban structure, and vegetation. Behavioral Ecology, 27, 1734-1744.

Kern, J. M., & Radford, A. N. (2016). Anthropogenic noise disrupts use of vocal information about predation risk. Environmental Pollution, 218, 988-995.

Kight, C. R., Saha, M. S., & Swaddle, J. P. (2012). Anthropogenic noise is associated with reductions in the productivity of breeding Eastern Bluebirds (*Sialia sialis*). Ecological Applications, 22, 1989-1996.

Kleist, N. J., Guralnick, R. P., Cruz, A., & Francis, C. D. (2016). Anthropogenic noise weakens territorial response to intruder's songs. Ecosphere, 7, e01259.

Klump, G. M. (2016). Perceptual and neural mechanisms of auditory scene analysis in the European starling. In Psychological Mechanisms in Animal Communication (pp. 57-88). Springer International Publishing.

Kostarakos, K., & Römer, H. (2015). Neural mechanisms for acoustic signal detection under strong masking in an insect. Journal of Neuroscience, 35, 10562-10571.

Kruger, D. J., & Du Preez, L. H. (2016). The effect of airplane noise on frogs: a case study on the Critically Endangered Pickersgill's reed frog (*Hyperolius pickersgilli*). Ecological Research, 31, 393-405.

La Manna, G., Manghi, M., Pavan, G., Lo Mascolo, F., & Sarà, G. (2013). Behavioural strategy of common bottlenose dolphins (Tursiops truncatus) in response to different kinds of boats in the waters of Lampedusa Island (Italy). Aquatic Conservation: Marine and Freshwater Ecosystems, 23, 745-757.

Lackey, M. A., Morrison, M. L., Loman, Z. G., Fisher, N., Farrell, S. L., Collier, B. A., & Wilkins, R. N. (2011). Effects of road construction noise on the endangered golden-cheeked warbler. Wildlife Society Bulletin, 35, 15-19.

Lackey, M. A., Morrison, M. L., Loman, Z. G., Collier, B. A., & Wilkins, R. N. (2012). Experimental determination of the response of Golden-cheeked Warblers (*Setophaga chrysoparia*) to road construction noise. Ornithological Monographs, 74, 91-100.

Ladich, F. (2013). Effects of noise on sound detection and acoustic communication in fishes. In Animal communication and noise (pp. 65-90). Springer Berlin Heidelberg.

Ladich, F., & Schulz-Mirbach, T. (2013). Hearing in cichlid fishes under noise conditions. PLoS One, 8, e57588.

Laiolo, P. (2011). Homogenisation of birdsong along a natural–urban gradient in Argentina. Ethology Ecology & Evolution, 23, 274-287.

Lammers, M. O., Castellote, M., Small, R. J., Atkinson, S., Jenniges, J., Rosinski, A., *et al.* (2013). Passive acoustic monitoring of Cook Inlet beluga whales (Delphinapterus leucas). The Journal of the Acoustical Society of America, 134, 2497-2504.

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.

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.

Leonard, M. L., & Horn, A. G. (2012). Ambient noise increases missed detections in nestling birds. Biology Letters, 8, 530-532.

Lowry, H., Lill, A., & Wong, B. B. (2012). How noisy does a noisy miner have to be? Amplitude adjustments of alarm calls in an avian urban ‘adapter’. PLoS One, 7, e29960.

Lowry, H., Lill, A., & Wong, B. (2013). Behavioural responses of wildlife to urban environments. Biological Reviews, 88, 537-549.

Lucass, C., Eens, M., & Müller, W. (2016). When ambient noise impairs parent-offspring communication. Environmental Pollution, 212, 592-597.

Luther, D. A., & Derryberry, E. P. (2012). Birdsongs keep pace with city life: changes in song over time in an urban songbird affects communication. Animal Behaviour, 83, 1059-1066.

Luther, D., & Gentry, K. (2013). Sources of background noise and their influence on vertebrate acoustic communication. Behaviour, 150, 1045-1068.

Luther, D., & Magnotti, J. (2014). Can animals detect differences in vocalizations adjusted for anthropogenic noise? Animal Behaviour, 92, 111-116.

Luther, D. A., Phillips, J., & Derryberry, E. P. (2015). Not so sexy in the city: urban birds adjust songs to noise but compromise vocal performance. Behavioral Ecology, 27, 332-340.

McCarthy, E., Moretti, D., Thomas, L., DiMarzio, N., Morrissey, R., Jarvis, S., *et al.* (2011). Changes in spatial and temporal distribution and vocal behavior of Blainville's beaked whales (*Mesoplodon densirostris*) during multiship exercises with mid-frequency sonar. Marine Mammal Science, 27, E206-E226.

McClure, C. J., Ware, H. E., Carlisle, J., Kaltenecker, G., & Barber, J. R. (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.

McGregor, P. K., Horn, A. G., Leonard, M. L., & Thomsen, F. (2013). Anthropogenic noise and conservation. In Animal communication and noise (pp. 409-444). Springer Berlin Heidelberg.

McIntyre, E., Horn, A. G., & Leonard, M. L. (2014). Do nestling Tree Swallows (*Tachycineta bicolor*) respond to parental alarm calls? The Auk, 13, 314-320.

McMullen, H., Schmidt, R., & Kunc, H. P. (2014). Anthropogenic noise affects vocal interactions. Behavioural Processes, 103, 125-128.

McNett, G. D., Luan, L. H., & Cocroft, R. B. (2010). Wind-induced noise alters signaler and receiver behavior in vibrational communication. Behavioral Ecology and Sociobiology, 64, 2043-2051.

Meillère, A., Brischoux, F., & Angelier, F. (2015). Impact of chronic noise exposure on antipredator behavior: an experiment in breeding house sparrows. Behavioral Ecology, 26, 569-577.

Melcon, M. L., Cummins, A. J., Kerosky, S. M., Roche, L. K., Wiggins, S. M., & Hildebrand, J. A. (2012). Blue whales respond to anthropogenic noise. PLoS One, 7, e32681.

Mendes, S., Colino-Rabanal, V. J., & Peris, S. J. (2011a). Bird song variations along an urban gradient: The case of the European blackbird (*Turdus merula*). Landscape and Urban Planning, 99, 51-57.

Mendes, S., Colino-Rabanal, V. J., & Peris, S. J. (2011b). Changes in the vocalization of the Southern House Wren (*Troglodytes musculus*) in environments with different levels of human disturbance. Hornero, 26, 85-93.

Miksis-Olds, J. L., & Wagner, T. (2011). Behavioral response of manatees to variations in environmental sound levels. Marine Mammal Science, 27, 130-148.

Miller, C. T., & Bee, M. A. (2012). Receiver psychology turns 20: is it time for a broader approach? Animal Behaviour, 83, 331-343.

Mockford, E. J., Marshall, R. C., & Dabelsteen, T. (2011). Degradation of rural and urban great tit song: testing transmission efficiency. PLoS One, 6, e28242.

Moiron, M., González-Lagos, C., Slabbekoorn, H., & Sol, D. (2015). Singing in the city: high song frequencies are no guarantee for urban success in birds. Behavioral Ecology, 26, 843-850.

Moore, S. E., Reeves, R. R., Southall, B. L., Ragen, T. J., Suydam, R. S., & Clark, C. W. (2012). A new framework for assessing the effects of anthropogenic sound on marine mammals in a rapidly changing Arctic. BioScience, 62, 289-295.

Naguib, M. (2013). Living in a noisy world: indirect effects of noise on animal communication. Behaviour, 150, 1069-1084.

Naguib, M., van Oers, K., Braakhuis, A., Griffioen, M., de Goede, P., & Waas, J. R. (2013). Noise annoys: effects of noise on breeding great tits depend on personality but not on noise characteristics. Animal Behaviour, 85, 949-956.

Neenan, S. T., Piper, R., White, P. R., Kemp, P., Leighton, T. G., & Shaw, P. J. (2016). Does Masking Matter? Shipping Noise and Fish Vocalizations. In The Effects of Noise on Aquatic Life II (pp. 747-753). Springer New York.

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

Nemeth, E., Pieretti, N., Zollinger, S. A., Geberzahn, N., Partecke, J., Miranda, A. C., & 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, 280, 20122798.

Nieukirk, S. L., Mellinger, D. K., Moore, S. E., Klinck, K., Dziak, R. P., & Goslin, J. (2012). Sounds from airguns and fin whales recorded in the mid-Atlantic Ocean, 1999–2009. The Journal of the Acoustical Society of America, 131, 1102-1112.

Nowacek, D. P., Clark, C. W., Mann, D., Miller, P. J., Rosenbaum, H. C., Golden, J. S., ... & Southall, B. L. (2015). Marine seismic surveys and ocean noise: time for coordinated and prudent planning. Frontiers in Ecology and the Environment, 13, 378-386.

Oden, A. I., Bomberger Brown, M., Burbach, M. E., Brandle, J. R., & Quinn, J. E. (2015). Variation in avian vocalizations during the non-breeding season in response to traffic noise. Ethology, 121, 472-479.

Orci, K. M., 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, C. P. (2012). Effects of noise pollution on birds: a brief review of our knowledge. Ornithological Monographs, 74, 6-22.

Owens, J. L., Stec, C. L., & O'Hatnick, A. (2012). The effects of extended exposure to traffic noise on parid social and risk-taking behavior. Behavioural Processes, 91, 61-69.

Parris, K. M., & McCarthy, M. A. (2013). Predicting the effect of urban noise on the active space of avian vocal signals. The American Naturalist, 182, 452-464.

Pieretti, N., & Farina, A. (2013). Application of a recently introduced index for acoustic complexity to an avian soundscape with traffic noise. The Journal of the Acoustical Society of America, 134, 891-900.

Pine, M. K., Jeffs, A. G., & Radford, C. A. (2012). Turbine sound may influence the metamorphosis behaviour of estuarine crab megalopae. PLoS One, 7, e51790.

Pohl, N. U., Klump, G. M., & Langemann, U. (2015). Effects of signal features and background noise on distance cue discrimination by a songbird. Journal of Experimental Biology, 218, 1006-1015.

Pohl, N. U., Leadbeater, E., Slabbekoorn, H., Klump, G. M., & Langemann, U. (2012). Great tits in urban noise benefit from high frequencies in song detection and discrimination. Animal Behaviour, 83, 711-721.

Popper, A. N., & Hawkins, A. (Eds.). (2016). The effects of noise on aquatic life II (Vol. 875). Springer.

Potvin, D. A. (2017). Coping with a changing soundscape: avoidance, adjustments and adaptations. Animal Cognition, 20, 9-18.

Potvin, D. A., & MacDougall-Shackleton, S. A. (2015). Experimental chronic noise exposure affects adult song in zebra finches. Animal Behaviour, 107, 201-207.

Potvin, D. A., & Mulder, R. A. (2013). Immediate, independent adjustment of call pitch and amplitude in response to varying background noise by silvereyes (*Zosterops lateralis*). Behavioral Ecology, 24, 1363-1368.

Potvin, D. A., Mulder, R. A., & Parris, K. M. (2014). Silvereyes decrease acoustic frequency but increase efficacy of alarm calls in urban noise. Animal Behaviour, 98, 27-33.

Preininger, D., Boeckle, M., Freudmann, A., Starnberger, I., Sztatecsny, M., & Hödl, W. (2013). Multimodal signaling in the small torrent frog (*Micrixalus saxicola*) in a complex acoustic environment. Behavioral Ecology and Sociobiology, 67, 1449-1456.

Proppe, D. S., Sturdy, C. B., & St Clair, C. C. (2013). Anthropogenic noise decreases urban songbird diversity and may contribute to homogenization. Global Change Biology, 19, 1075-1084.

Purser, J., & Radford, A. N. (2011). Acoustic noise induces attention shifts and reduces foraging performance in three-spined sticklebacks (*Gasterosteus aculeatus*). PLoS One, 6, e17478.

Radford, A. N., Kerridge, E., & Simpson, S. D. (2014). Acoustic communication in a noisy world: can fish compete with anthropogenic noise? Behavioral Ecology, 25, 1022-1030.

Redondo, P., Barrantes, G., & Sandoval, L. (2013). Urban noise influences vocalization structure in the House Wren *Troglodytes aedon*. Ibis, 155, 621-625.

Rice, A. N., Tielens, J. T., Estabrook, B. J., Muirhead, C. A., Rahaman, A., Guerra, M., & Clark, C. W. (2014). Variation of ocean acoustic environments along the western north Atlantic coast: a case study in context of the right whale migration route. Ecological Informatics, 21, 89-99.

Ríos-Chelén, A. A., Lee, G. C., & Patricelli, G. L. (2015). Anthropogenic noise is associated with changes in acoustic but not visual signals in red-winged blackbirds. Behavioral Ecology and Sociobiology, 69, 1139-1151.

Ríos-Chelén, A. A., McDonald, A. N., Berger, A., Perry, A. C., Krakauer, A. H., & Patricelli, G. L. (2017). Do birds vocalize at higher pitch in noise, or is it a matter of measurement? Behavioral Ecology and Sociobiology, 71, 29.

Ríos-Chelén, A. A., Salaberria, C., Barbosa, I., Macías Garcia, C., & Gil, D. (2012). The learning advantage: Bird species that learn their song show a tighter adjustment of song to noisy environments than those that do not learn. Journal of Evolutionary Biology, 25, 2171-2180.

Roca, I. T., Desrochers, L., Giacomazzo, M., Bertolo, A., Bolduc, P., Deschesnes, R., *et al.* (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 (pp. 33-63). Springer Berlin Heidelberg.

Sabet, S. S., Neo, Y. Y., & Slabbekoorn, H. (2016a). Impact of anthropogenic noise on aquatic animals: From single species to community-level effects. In The Effects of Noise on Aquatic Life II (pp. 957-961). Springer New York.

Sabet, S. S., Wesdorp, K., Campbell, J., Snelderwaard, P., & Slabbekoorn, H. (2016b). Behavioural responses to sound exposure in captivity by two fish species with different hearing ability. Animal Behaviour, 116, 1-11.

Schmidt, A. K., & Balakrishnan, R. (2015). Ecology of acoustic signalling and the problem of masking interference in insects. Journal of Comparative Physiology A, 201, 133-142.

Schmidt, A. K., & 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.

Schmidt, R., Morrison, A., & Kunc, H. P. (2014). Sexy voices–no choices: male song in noise fails to attract females. Animal Behaviour, 94, 55-59.

Schroeder, J., Nakagawa, S., Cleasby, I. R., & Burke, T. (2012). Passerine birds breeding under chronic noise experience reduced fitness. PLoS One, 7, e39200.

Schwartz, J. J., & Bee, M. A. (2013). Anuran acoustic signal production in noisy environments. In Animal communication and noise (pp. 91-132). Springer Berlin Heidelberg.

Seger-Fullam, K. D., Rodewald, A. D., & Soha, J. A. (2012). Urban noise predicts song frequency in northern cardinals and American robins. Bioacoustics, 20, 267-276.

Senzaki, M., Yamaura, Y., Francis, C. D., & Nakamura, F. (2016). Traffic noise reduces foraging efficiency in wild owls. Scientific Reports, 6, 30602.

Shannon, G., Angeloni, L. M., Wittemyer, G., Fristrup, K. M., & Crooks, K. R. (2014). Road traffic noise modifies behaviour of a keystone species. Animal Behaviour, 94, 135-141.

Shannon, G., Crooks, K. R., Wittemyer, G., Fristrup, K. M., & Angeloni, L. M. (2016b). Road noise causes earlier predator detection and flight response in a free-ranging mammal. Behavioral Ecology, 27, 1370-1375.

Shannon, G., McKenna, M. F., Angeloni, L. M., Crooks, K. R., Fristrup, K. M., Brown, E., *et al.* (2016a). A synthesis of two decades of research documenting the effects of noise on wildlife. Biological Reviews, 91, 982-1005.

Shieh, B. S., Liang, S. H., Chiu, Y. W., & Lin, S. Y. (2016). Interspecific comparison of traffic noise effects on dove coo transmission in urban environments. Scientific Reports, 6, 32519.

Shier, D. M., Lea, A. J., & Owen, M. A. (2012). Beyond masking: Endangered Stephen's kangaroo rats respond to traffic noise with footdrumming. Biological Conservation, 150, 53-58.

Simard, P., Lace, N., Gowans, S., Quintana-Rizzo, E., Kuczaj, S. A., Wells, R. S., & Mann, D. A. (2011). Low frequency narrow-band calls in bottlenose dolphins (Tursiops truncatus): signal properties, function, and conservation implications. The Journal of the Acoustical Society of America, 130, 3068-3076.

Slabbekoorn, H. (2013). Songs of the city: noise-dependent spectral plasticity in the acoustic phenotype of urban birds. Animal Behaviour, 85, 1089-1099.

Swaddle, J. P., Francis, C. D., Barber, J. R., Cooper, C. B., Kyba, C. C., Dominoni, D. M., ... & Luther, D. (2015). A framework to assess evolutionary responses to anthropogenic light and sound. Trends in Ecology & Evolution, 30, 550-560.

Swaddle, J. P., Kight, C. R., Perera, S., Davila-Reyes, E., & Sikora, S. (2012). Constraints on acoustic signaling among birds breeding in secondary cavities: The effects of weather, cavity material, and noise on sound propagation. Ornithological Monographs, 74, 63-77.

Swaddle, J. P., Moseley, D. L., Hinders, M. K., & P Smith, E. (2016). A sonic net excludes birds from an airfield: implications for reducing bird strike and crop losses. Ecological Applications, 26, 339-345.

Templeton, C. N., Zollinger, S. A., & Brumm, H. (2016). Traffic noise drowns out great tit alarm calls. Current Biology, 26, R1173-R1174.

Tennessen, J. B., Parks, S. E., & Langkilde, T. L. (2016). Anthropogenic noise and physiological stress in wildlife. In The Effects of Noise on Aquatic Life II (pp. 1145-1148). Springer New York.

Terhune, J. M., & Bosker, T. (2016). Harp Seals Do Not Increase Their Call Frequencies When It Gets Noisier. In The Effects of Noise on Aquatic Life II (pp. 1149-1153). Springer New York.

Tyack, P. L., & Janik, V. M. (2013). Effects of noise on acoustic signal production in marine mammals. In Animal communication and noise (pp. 251-271). Springer Berlin Heidelberg.

van der Sluijs, I., Gray, S. M., Amorim, M. C. P., Barber, I., Candolin, U., Hendry, A. P., *et al.* (2011). Communication in troubled waters: responses of fish communication systems to changing environments. Evolutionary Ecology, 25, 623-640.

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., Cunnington, G. M., Amézquita, A., & Fahrig, L. (2014). Does traffic noise alter calling time in frogs and toads? A case study of anurans in Eastern Ontario, Canada. Urban ecosystems, 17, 945-953.

Vélez, A., Schwartz, J. J., & Bee, M. A. (2013). Anuran acoustic signal perception in noisy environments. In Animal communication and noise (pp. 133-185). Springer Berlin Heidelberg.

Verzijden, M. N., Ripmeester, E. A. P., Ohms, V. R., Snelderwaard, P., & Slabbekoorn, H. (2010). Immediate spectral flexibility in singing chiffchaffs during experimental exposure to highway noise. Journal of Experimental Biology, 213, 2575-2581.

Ware, H. E., McClure, C. J., Carlisle, J. D., & Barber, J. R. (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.

Wiley, R.H. (2013). Signal detection, noise, and the evolution of communication. In Animal communication and noise (pp. 7–30). Springer Berlin Heidelberg.

Wiley, R. H. (2015). Noise matters: The evolution of communication. Harvard University Press. Cambridge, Massachusetts.

Informational masking

Akre, K. L., & Johnsen, S. (2016). Communication through a window of error: Proportional processing and signal categorization. In Psychological Mechanisms in Animal Communication (pp. 137-167). Springer International Publishing.

Bee, M. A. (2015). Treefrogs as animal models for research on auditory scene analysis and the cocktail party problem. International Journal of Psychophysiology, 95, 216-237.

Bee, M. A., & Christensen-Dalsgaard, J. (2016). Sound source localization and segregation with internally coupled ears: the treefrog model. Biological Cybernetics, 110, 271-290.

Bee, M. A., & Miller, C. T. (2016). Signaler and receiver psychology. In Psychological mechanisms in animal communication (pp. 1-16). Springer International Publishing.

Blumstein, D. T. (2014). Attention, habituation, and antipredator behaviour: implications for urban birds. Avian urban ecology: Behavioural and physiological adaptations, 41e53.

Branstetter, B. K., Bakhtiari, K., Black, A., Trickey, J. S., Finneran, J. J., & Aihara, H. (2016). Energetic and informational masking of complex sounds by a bottlenose dolphin (*Tursiops truncatus*). The Journal of the Acoustical Society of America, 140, 1904-1917.

Brown, C. L., Hardy, A. R., Barber, J. R., Fristrup, K. M., Crooks, K. R., & Angeloni, L. M. (2012). The effect of human activities and their associated noise on ungulate behavior. PloS One, 7, e40505.

Chan, A. A. Y. H., & Blumstein, D. T. (2011). Attention, noise, and implications for wildlife conservation and management. Applied Animal Behaviour Science, 131, 1-7.

Chan, A. A. Y. H., Giraldo-Perez, P., Smith, S., & Blumstein, D. T. (2010a). Anthropogenic noise affects risk assessment and attention: the distracted prey hypothesis. Biology Letters, 6, 458-461.

Chan, A. A. Y. H., Stahlman, W. D., Garlick, D., Fast, C. D., Blumstein, D. T., & Blaisdell, A. P. (2010b). Increased amplitude and duration of acoustic stimuli enhance distraction. Animal Behaviour, 80, 1075-1079.

Dooling, R. J., & Blumenrath, S. H. (2013). Avian sound perception in noise. In Animal communication and noise (pp. 229-250). Springer Berlin Heidelberg.

Everley, K. A., Radford, A. N., & Simpson, S. D. (2016). Pile-driving noise impairs antipredator behavior of the European sea bass *Dicentrarchus labrax.* In The Effects of Noise on Aquatic Life II (pp. 273-279). Springer New York.

Farris, H. E., & Taylor, R. C. (2016). Mate searching animals as model systems for understanding perceptual grouping. In Psychological Mechanisms in Animal Communication (pp. 89-118). Springer International Publishing.

Francis, C. D. (2015). Vocal traits and diet explain avian sensitivities to anthropogenic noise. Global Change Biology, 21, 1809-1820.

Francis, C. D., & Barber, J. R. (2013). A framework for understanding noise impacts on wildlife: an urgent conservation priority. Frontiers in Ecology and the Environment, 11, 305-313.

Grade, A. M., & Sieving, K. E. (2016). When the birds go unheard: highway noise disrupts information transfer between bird species. Biology Letters, 12, 20160113.

Grubb, T. G., Pater, L. L., Gatto, A. E., & Delaney, D. K. (2013). Response of nesting northern goshawks to logging truck noise in northern Arizona. The Journal of Wildlife Management, 77, 1618-1625.

Halfwerk, W., Both, C., & Slabbekoorn, H. (2016). Noise affects nest-box choice of 2 competing songbird species, but not their reproduction. Behavioral Ecology, 27, 1592-1600.

Hubbard, L., King, W., Vu, A., & Blumstein, D. T. (2015). Heterospecific nonalarm vocalizations enhance risk assessment in common mynas. Behavioral Ecology, 26, 632-638.

Kern, J. M., & Radford, A. N. (2016). Anthropogenic noise disrupts use of vocal information about predation risk. Environmental Pollution, 218, 988-995.

Kleist, N. J., Guralnick, R. P., Cruz, A., & Francis, C. D. (2016). Anthropogenic noise weakens territorial response to intruder's songs. Ecosphere, 7, e01259.

Klett-Mingo, J. I., Pavón, I., & Gil, D. (2016). Great tits, *Parus major*, increase vigilance time and reduce feeding effort during peaks of aircraft noise. Animal Behaviour, 115, 29-34.

Kunc, H. P., McLaughlin, K. E., & Schmidt, R. (2016). Aquatic noise pollution: implications for individuals, populations, and ecosystems. Proceedings of the Royal Society of London B: Biological Sciences, 283, 20160839.

Leonard, M. L., & Horn, A. G. (2012). Ambient noise increases missed detections in nestling birds. Biology Letters, 8, 530-532.

Luo, J., Siemers, B. M., & Koselj, K. (2015). How anthropogenic noise affects foraging. Global Change Biology, 21, 3278-3289.

McClure, C. J., Ware, H. E., Carlisle, J., Kaltenecker, G., & Barber, J. R. (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.

McGregor, P. K., Horn, A. G., Leonard, M. L., & Thomsen, F. (2013). Anthropogenic noise and conservation. In Animal communication and noise (pp. 409-444). Springer Berlin Heidelberg.

Meillère, A., Brischoux, F., & Angelier, F. (2015). Impact of chronic noise exposure on antipredator behavior: an experiment in breeding house sparrows. Behavioral Ecology, 26, 569-577.

Miller, C. T., & Bee, M. A. (2012). Receiver psychology turns 20: is it time for a broader approach? Animal Behaviour, 83, 331-343.

Morris-Drake, A., Kern, J. M., & Radford, A. N. (2016). Cross-modal impacts of anthropogenic noise on information use. Current Biology, 26, R911-R912.

Naguib, M. (2013). Living in a noisy world: indirect effects of noise on animal communication. Behaviour, 150, 1069-1084.

Naguib, M., van Oers, K., Braakhuis, A., Griffioen, M., de Goede, P., & Waas, J. R. (2013). Noise annoys: effects of noise on breeding great tits depend on personality but not on noise characteristics. Animal Behaviour, 85, 949-956.

Owen, M. A., Hall, S., Bryant, L., & Swaisgood, R. R. (2014). The influence of ambient noise on maternal behavior in a Bornean sun bear (*Helarctos malayanus euryspilus*). Zoo biology, 33, 49-53.

Owens, J. L., Stec, C. L., & O’Hatnick, A. (2012). The effects of extended exposure to traffic noise on parid social and risk-taking behavior. Behavioural Processes, 91, 61-69.

Pohl, N. U., Klump, G. M., & Langemann, U. (2015). Effects of signal features and background noise on distance cue discrimination by a songbird. Journal of Experimental Biology, 218, 1006-1015.

Popper, A. N., & Hawkins, A. (Eds.). (2016). The effects of noise on aquatic life II (Vol. 875). Springer.

Potvin, D. A. (2017). Coping with a changing soundscape: avoidance, adjustments and adaptations. Animal Cognition, 20, 9-18.

Purser, J., & Radford, A. N. (2011). Acoustic noise induces attention shifts and reduces foraging performance in three-spined sticklebacks (*Gasterosteus aculeatus*). PLoS One, 6, e17478.

Radford, A. N., Kerridge, E., & Simpson, S. D. (2014). Acoustic communication in a noisy world: can fish compete with anthropogenic noise? Behavioral Ecology, 25, 1022-1030.

Read, J., Jones, G., & Radford, A. N. (2014). Fitness costs as well as benefits are important when considering responses to anthropogenic noise. Behavioral Ecology, 25, 4-7.

Römer, H. (2013). Masking by noise in acoustic insects: problems and solutions. In Animal communication and noise (pp. 33-63). Springer Berlin Heidelberg.

Sabet, S. S., Neo, Y. Y., & Slabbekoorn, H. (2015). The effect of temporal variation in sound exposure on swimming and foraging behaviour of captive zebrafish. Animal Behaviour, 107, 49-60.

Sabet, S. S., Neo, Y. Y., & Slabbekoorn, H. (2016a). Impact of anthropogenic noise on aquatic animals: From single species to community-level effects. In The Effects of Noise on Aquatic Life II (pp. 957-961). Springer New York.

Schmidt, R., Morrison, A., & Kunc, H. P. (2014). Sexy voices–no choices: male song in noise fails to attract females. Animal Behaviour, 94, 55-59.

Senzaki, M., Yamaura, Y., Francis, C. D., & Nakamura, F. (2016). Traffic noise reduces foraging efficiency in wild owls. Scientific reports, 6, 30602.

Shannon, G., Angeloni, L. M., Wittemyer, G., Fristrup, K. M., & Crooks, K. R. (2014). Road traffic noise modifies behaviour of a keystone species. Animal Behaviour, 94, 135-141.

Shannon, G., Crooks, K. R., Wittemyer, G., Fristrup, K. M., & Angeloni, L. M. (2016b). Road noise causes earlier predator detection and flight response in a free-ranging mammal. Behavioral Ecology, 27, 1370-1375.

Shannon, G., McKenna, M. F., Angeloni, L. M., Crooks, K. R., Fristrup, K. M., Brown, E., *et al.* (2016a). A synthesis of two decades of research documenting the effects of noise on wildlife. Biological Reviews, 91, 982-1005.

Shier, D. M., Lea, A. J., & Owen, M. A. (2012). Beyond masking: Endangered Stephen's kangaroo rats respond to traffic noise with footdrumming. Biological Conservation, 150, 53-58.

Siemers, B. M., & 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.

Simpson, S. D., Purser, J., & Radford, A. N. (2015). Anthropogenic noise compromises antipredator behaviour in European eels. Global Change Biology, 21, 586-593.

Simpson, S. D., Radford, A. N., Nedelec, S. L., Ferrari, M. C., Chivers, D. P., McCormick, M. I., & Meekan, M. G. (2016). Anthropogenic noise increases fish mortality by predation. Nature Communications, 7, 10544.

Swaddle, J. P., Francis, C. D., Barber, J. R., Cooper, C. B., Kyba, C. C., Dominoni, D. M., ... & Luther, D. (2015). A framework to assess evolutionary responses to anthropogenic light and sound. Trends in Ecology & Evolution, 30, 550-560.

Vélez, A., Schwartz, J. J., & Bee, M. A. (2013). Anuran acoustic signal perception in noisy environments. In Animal communication and noise (pp. 133-185). Springer Berlin Heidelberg.

Wale, M. A., Simpson, S. D., & Radford, A. N. (2013). Noise negatively affects foraging and antipredator behaviour in shore crabs. Animal Behaviour, 86, 111-118.

Ware, H. E., McClure, C. J., Carlisle, J. D., & Barber, J. R. (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.

Wiley, R.H. (2013). Signal detection, noise, and the evolution of communication. In Animal communication and noise (pp. 7–30). Springer Berlin Heidelberg.

Auditory scene analysis

Bee, M. A. (2012). Sound source perception in anuran amphibians. Current opinion in neurobiology, 22, 301-310.

Bee, M. A. (2015). Treefrogs as animal models for research on auditory scene analysis and the cocktail party problem. International Journal of Psychophysiology, 95, 216-237.

Bee, M. A., & Christensen-Dalsgaard, J. (2016). Sound source localization and segregation with internally coupled ears: the treefrog model. Biological Cybernetics, 110, 271-290.

Bee, M. A., & Miller, C. T. (2016). Signaler and receiver psychology. In Psychological mechanisms in animal communication (pp. 1-16). Springer International Publishing.

Blesdoe, E. K., & Blumstein, D. T. (2014). What is the sound of fear? Behavioral responses of white-crowned sparrows Zonotrichia leucophrys to synthesized nonlinear acoustic phenomena. Current Zoology, 60, 534-541.

Branstetter, B. K., Trickey, J. S., Aihara, H., Finneran, J. J., & Liberman, T. R. (2013a). Time and frequency metrics related to auditory masking of a 10 kHz tone in bottlenose dolphins (*Tursiops truncatus*). The Journal of the Acoustical Society of America, 134, 4556-4565.

Branstetter, B. K., Trickey, J. S., Bakhtiari, K., Black, A., Aihara, H., & Finneran, J. J. (2013b). Auditory masking patterns in bottlenose dolphins (*Tursiops truncatus*) with natural, anthropogenic, and synthesized noise. The Journal of the Acoustical Society of America, 133, 1811-1818.

Branstetter, B. K., Bakhtiari, K., Black, A., Trickey, J. S., Finneran, J. J., & Aihara, H. (2016). Energetic and informational masking of complex sounds by a bottlenose dolphin (*Tursiops truncatus*). The Journal of the Acoustical Society of America, 140, 1904-1917.

Casper, B. M., Smith, M. E., Halvorsen, M. B., Sun, H., Carlson, T. J., & Popper, A. N. (2013). Effects of exposure to pile driving sounds on fish inner ear tissues. Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology, 166, 352-360.

Dent, M. L., Martin, A. K., Flaherty, M. M., & Neilans, E. G. (2016). Cues for auditory stream segregation of birdsong in budgerigars and zebra finches: effects of location, timing, amplitude, and frequency. The Journal of the Acoustical Society of America, 139, 674-683.

Dooling, R. J., & Blumenrath, S. H. (2013). Avian sound perception in noise. In Animal communication and noise (pp. 229-250). Springer Berlin Heidelberg.

Dooling, R. J., & Popper, A. N. (2016). Technical guidance for assessment and mitigation of the effects of highway and road construction noise on birds. The California Department of Transportation, Division of Environmental Analysis, Sacramento, California, USA.

Farris, H. E., & Ryan, M. J. (2011). Relative comparisons of call parameters enable auditory grouping in frogs. Nature Communications, 2, 410.

Farris, H. E., & Taylor, R. C. (2016). Mate searching animals as model systems for understanding perceptual grouping. In Psychological Mechanisms in Animal Communication (pp. 89-118). Springer International Publishing.

Finneran, J. J., & Branstetter, B. K. (2013). Effects of noise on sound perception in marine mammals. In Animal Communication and Noise (pp. 273-308). Springer Berlin Heidelberg.

Gutscher, M., Wysocki, L. E., & Ladich, F. (2011). Effects of aquarium and pond noise on hearing sensitivity in an otophysine fish. Bioacoustics, 20, 117-136.

Hatch, L. T., Clark, C. W., Van Parijs, S. M., Frankel, A. S., & Ponirakis, D. W. (2012). Quantifying loss of acoustic communication space for right whales in and around a US National Marine Sanctuary. Conservation Biology, 26, 983-994.

Holt, M. M., Southall, B. L., Insley, S. J., & Schusterman, R. J. (2010). Call directionality and its behavioural significance in male northern elephant seals, *Mirounga angustirostris.* Animal Behaviour, 80, 351-361.

Itatani, N., & Klump, G. M. (2017). Animal models for auditory streaming. Philosophical Transactions of the Royal Society B, 372, 20160112.

Jarvis, J., Jackson, W., & Smotherman, M. (2013). Groups of bats improve sonar efficiency through mutual suppression of pulse emissions. Frontiers in Physiology, 4, 140.

Klink, K. B., Dierker, H., Beutelmann, R., & Klump, G. M. (2010). Comodulation masking release determined in the mouse (*Mus musculus*) using a flanking-band paradigm. Journal of the Association for Research in Otolaryngology, 11, 79-88.

Klump, G. M. (2016). Perceptual and neural mechanisms of auditory scene analysis in the European starling. In Psychological Mechanisms in Animal Communication (pp. 57-88). Springer International Publishing.

Larsson, M. (2012). Incidental sounds of locomotion in animal cognition. Animal Cognition, 15, 1-13.

Lewicki, M. S., Olshausen, B. A., Surlykke, A., & Moss, C. F. (2014). Scene analysis in the natural environment. Frontiers in Psychology, 5, 199.

Miller, C. T., & Bee, M. A. (2012). Receiver psychology turns 20: is it time for a broader approach? Animal Behaviour, 83, 331-343.

Mooney, T. A., Samson, J. E., Schlunk, A. D., & 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.

Mouterde, S. C., Elie, J. E., Theunissen, F. E., & Mathevon, N. (2014). Learning to cope with degraded sounds: female zebra finches can improve their expertise in discriminating between male voices at long distances. Journal of Experimental Biology, 217, 3169-3177.

Neilans, E. G., & Dent, M. L. (2015q). Temporal coherence for complex signals in budgerigars (*Melopsittacus undulatus*) and humans (*Homo sapiens*). Journal of Comparative Psychology, 129, 174-180.

Neilans, E. G., & Dent, M. L. (2015b). Temporal coherence for pure tones in budgerigars (*Melopsittacus undulatus*) and humans (*Homo sapiens*). Journal of Comparative Psychology, 129, 52-61.

Ponnath, A., & Farris, H. E. (2014). Sound-by-sound thalamic stimulation modulates midbrain auditory excitability and relative binaural sensitivity in frogs. Frontiers in Neural Circuits, 8, 85.

Popper, A. N., & Hawkins, A. (Eds.). (2016). The effects of noise on aquatic life II (Vol. 875). Springer.

Schmidt, A. K., & 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.

Seeba, F., Schwartz, J. J., & Bee, M. A. (2010). Testing an auditory illusion in frogs: Perceptual restoration or sensory bias? Animal Behaviour, 79, 1317-1328.

Slabbekoorn, H., Verzijden, M., & May, C. (2012). Cichlid courtship acoustics: signals and noise influence reproductive behavior. In The Effects of Noise on Aquatic Life (pp. 407-409). Springer New York.

Tárano, Z. (2015). Choosing a Mate in a Cocktail Party-Like Situation: The Effect of Call Complexity and Call Timing between Two Rival Males on Female Mating Preferences in the Túngara Frog *Physalaemus pustulosus*. Ethology, 121, 749-759.

Taylor, R. C., & Ryan, M. J. (2013). Interactions of multisensory components perceptually rescue túngara frog mating signals. Science, 341, 273-274.

van der Sluijs, I., Gray, S. M., Amorim, M. C. P., Barber, I., Candolin, U., Hendry, A. P., et al. (2011). Communication in troubled waters: responses of fish communication systems to changing environments. Evolutionary Ecology, 25, 623-640.

Vélez, A., & Bee, M. A. (2011). Dip listening and the cocktail party problem in grey treefrogs: signal recognition in temporally fluctuating noise. Animal Behaviour, 82, 1319-1327.

Vélez, A., Schwartz, J. J., & Bee, M. A. (2013). Anuran acoustic signal perception in noisy environments. In Animal communication and noise (pp. 133-185). Springer Berlin Heidelberg.

Wiley, R. H. (2015). Noise matters: The evolution of communication. Harvard University Press. Cambridge, Massachusetts.

Willis, K. L. (2016). Underwater hearing in turtles. In The Effects of Noise on Aquatic Life II (pp. 1229-1235). Springer New York.

Multimodal signals

Arch, V. S., Richards-Zawaki, C. L., & Feng, A. S. (2011). Acoustic communication in the Kihansi spray toad (*Nectophrynoides asperginis*): insights from a captive population. Journal of Herpetology, 45, 45-49.

Bee, M. A., & Miller, C. T. (2016). Signaler and receiver psychology. In Psychological mechanisms in animal communication (pp. 1-16). Springer International Publishing.

Brumm, H. (2013). Introduction. In Animal Communication and Noise (pp. 187-227). Springer Berlin Heidelberg.

Brumm, H., & Zollinger, S. A. (2013). Avian vocal production in noise. In Animal Communication and Noise (pp. 187-227). Springer Berlin Heidelberg.

Farris, H. E., & Taylor, R. C. (2016). Mate searching animals as model systems for understanding perceptual grouping. In Psychological Mechanisms in Animal Communication (pp. 89-118). Springer International Publishing.

Francis, C. D. (2015). Vocal traits and diet explain avian sensitivities to anthropogenic noise. Global Change Biology, 21, 1809-1820.

Gomez, D., Théry, M., Gauthier, A. L., & Lengagne, T. (2011). Costly help of audiovisual bimodality for female mate choice in a nocturnal anuran (*Hyla arborea*). Behavioral Ecology, 22, 889-898.

Gordon, S. D., & Uetz, G. W. (2012). Environmental interference: impact of acoustic noise on seismic communication and mating success. Behavioral Ecology, 23, 707-714.

Grafe, T. U., Preininger, D., Sztatecsny, M., Kasah, R., Dehling, J. M., Proksch, S., & Hödl, W. (2012). Multimodal communication in a noisy environment: a case study of the Bornean rock frog *Staurois parvus*. PLoS One, 7, e37965.

Hage, S. R., Jiang, T., Berquist, S. W., 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.

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.

Halfwerk, W., Both, C., & Slabbekoorn, H. (2016). Noise affects nest-box choice of 2 competing songbird species, but not their reproduction. Behavioral Ecology, 27, 1592-1600.

Halfwerk, W., Dixon, M. M., Ottens, K. J., Taylor, R. C., Ryan, M. J., Page, R. A., & Jones, P. L. (2014). Risks of multimodal signaling: bat predators attend to dynamic motion in frog sexual displays. Journal of Experimental Biology, 217, 3038-3044.

Higham, J. P., & Hebets, E. A. (2013). An introduction to multimodal communication. Behavioral Ecology and Sociobiology, 67, 1381-1388.

Holt, M. M., Southall, B. L., Insley, S. J., & Schusterman, R. J. (2010). Call directionality and its behavioural significance in male northern elephant seals, *Mirounga angustirostris*. Animal Behaviour, 80, 351-361.

Lecker, C. A., Parsons, M. H., Lecker, D. R., Sarno, R. J., & Parsons, F. E. (2015). The temporal multimodal influence of optical and auditory cues on the repellent behaviour of ring-billed gulls (*Larus delewarensis*). Wildlife Research, 42, 232-240.

Maruska, K. P., Ung, U. S., & Fernald, R. D. (2012). The African cichlid fish Astatotilapia burtoni uses acoustic communication for reproduction: sound production, hearing, and behavioral significance. PLoS One, 7, e37612.

Miller, C. T., & Bee, M. A. (2012). Receiver psychology turns 20: is it time for a broader approach? Animal Behaviour, 83, 331-343.

Munoz, N. E., & Blumstein, D. T. (2012). Multisensory perception in uncertain environments. Behavioral Ecology, 23, 457-462.

Page, R. A., & Jones, P. L. (2016). Overcoming Sensory Uncertainty: Factors Affecting Foraging Decisions in Frog-Eating Bats. In Psychological Mechanisms in Animal Communication (pp. 285-312). Springer International Publishing.

Partan, S. R. (2013). Ten unanswered questions in multimodal communication. Behavioral Ecology and Sociobiology, 67, 1523-1539.

Potvin, D. A. (2017). Coping with a changing soundscape: avoidance, adjustments and adaptations. Animal Cognition, 20, 9-18.

Preininger, D., Boeckle, M., Freudmann, A., Starnberger, I., Sztatecsny, M., & Hödl, W. (2013). Multimodal signaling in the small torrent frog (*Micrixalus saxicola*) in a complex acoustic environment. Behavioral Ecology and Sociobiology, 67, 1449-1456.

Reichert, M. S., Symes, L. B., & Höbel, G. (2016). Lighting up sound preferences: cross-modal influences on the precedence effect in treefrogs. Animal Behaviour, 119, 151-159.

Rhebergen, F., Taylor, R. C., Ryan, M. J., Page, R. A., & Halfwerk, W. (2015). Multimodal cues improve prey localization under complex environmental conditions. Proceedings of the Royal Society B: Biological Sciences, 282, 20151403.

Ríos-Chelén, A. A., Lee, G. C., & Patricelli, G. L. (2015). Anthropogenic noise is associated with changes in acoustic but not visual signals in red-winged blackbirds. Behavioral Ecology and Sociobiology, 69, 1139-1151.

Römer, H. (2013). Masking by noise in acoustic insects: problems and solutions. In Animal communication and noise (pp. 33-63). Springer Berlin Heidelberg.

Rubi, T. L., & Stephens, D. W. (2016). Why Complex Signals Matter, Sometimes. In Psychological Mechanisms in Animal Communication (pp. 119-135). Springer International Publishing.

Schwartz, J. J., & Bee, M. A. (2013). Anuran acoustic signal production in noisy environments. In Animal communication and noise (pp. 91-132). Springer Berlin Heidelberg.

Swaddle, J. P., Francis, C. D., Barber, J. R., Cooper, C. B., Kyba, C. C., Dominoni, D. M., ... & Luther, D. (2015). A framework to assess evolutionary responses to anthropogenic light and sound. Trends in Ecology & Evolution, 30, 550-560.

Taylor, R. C., & Ryan, M. J. (2013). Interactions of multisensory components perceptually rescue túngara frog mating signals. Science, 341, 273-274.

Taylor, R. C., Klein, B. A., & Ryan, M. J. (2011). Inter-signal interaction and uncertain information in anuran multimodal signals. Current Zoology, 57, 153-161.

Troïanowski, M., Condette, C., Mondy, N., Dumet, A., & Lengagne, T. (2015). Traffic noise affects colouration but not calls in the European treefrog (*Hyla arborea*). Behaviour, 152, 821-836.

Troïanowski, M., Melot, G., & Lengagne, T. (2014). Multimodality: A way to cope with road traffic noise? The case of European treefrog (*Hyla arborea*). Behavioural Processes, 107, 88-93.

Uetz, G. W., Roberts, J. A., Clark, D. L., Gibson, J. S., & Gordon, S. D. (2013). Multimodal signals increase active space of communication by wolf spiders in a complex litter environment. Behavioral Ecology and Sociobiology, 67, 1471-1482.

van der Sluijs, I., Gray, S. M., Amorim, M. C. P., Barber, I., Candolin, U., Hendry, A. P., et al. (2011). Communication in troubled waters: responses of fish communication systems to changing environments. Evolutionary Ecology, 25, 623-640.

Vélez, A., Schwartz, J. J., & Bee, M. A. (2013). Anuran acoustic signal perception in noisy environments. In Animal communication and noise (pp. 133-185). Springer Berlin Heidelberg.

Weissburg, M., Smee, D. L., & Ferner, M. C. (2014). The sensory ecology of nonconsumptive predator effects. The American Naturalist, 184, 141-157.

Wiley, R. H. (2015). Noise matters: The evolution of communication. Harvard University Press. Cambridge, Massachusetts.

Wilson, A. J., Dean, M., & Higham, J. P. (2013). A game theoretic approach to multimodal communication. Behavioral Ecology and Sociobiology, 67, 1399-1415.

Cross-modal impacts

Bee, M. A., & Miller, C. T. (2016). Signaler and receiver psychology. In Psychological mechanisms in animal communication (pp. 1-16). Springer International Publishing.

Blumstein, D. T. (2014). Attention, habituation, and antipredator behaviour: implications for urban birds. Avian urban ecology: Behavioural and physiological adaptations, 41e53.

Brumm, H. (2013). Introduction. In Animal Communication and Noise (pp. 187-227). Springer Berlin Heidelberg.

Chan, A. A. Y. H., & Blumstein, D. T. (2011). Attention, noise, and implications for wildlife conservation and management. Applied Animal Behaviour Science, 131, 1-7.

Chan, A. A. Y. H., Giraldo-Perez, P., Smith, S., & Blumstein, D. T. (2010a). Anthropogenic noise affects risk assessment and attention: the distracted prey hypothesis. Biology Letters, 6, 458-461.

Chan, A. A. Y. H., Stahlman, W. D., Garlick, D., Fast, C. D., Blumstein, D. T., & Blaisdell, A. P. (2010b). Increased amplitude and duration of acoustic stimuli enhance distraction. Animal Behaviour, 80, 1075-1079.

Estramil, N., Bouton, N., Verzijden, M. N., Hofker, K., Riebel, K., & Slabbekoorn, H. (2014). Cichlids respond to conspecific sounds but females exhibit no phonotaxis without the presence of live males. Ecology of Freshwater Fish, 23, 305-312.

Francis, C. D. (2015). Vocal traits and diet explain avian sensitivities to anthropogenic noise. Global Change Biology, 21, 1809-1820.

Francis, C. D., & Barber, J. R. (2013). A framework for understanding noise impacts on wildlife: an urgent conservation priority. Frontiers in Ecology and the Environment, 11, 305-313.

Goodwin, S. E., & Podos, J. (2013). Shift of song frequencies in response to masking tones. Animal Behaviour, 85, 435-440.

Gordon, S. D., & Uetz, G. W. (2012). Environmental interference: impact of acoustic noise on seismic communication and mating success. Behavioral Ecology, 23, 707-714.

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.

Halfwerk, W., Both, C., & Slabbekoorn, H. (2016). Noise affects nest-box choice of 2 competing songbird species, but not their reproduction. Behavioral Ecology, 27, 1592-1600.

Higham, J. P., & Hebets, E. A. (2013). An introduction to multimodal communication. Behavioral Ecology and Sociobiology, 67, 1381-1388.

Kunc, H. P., McLaughlin, K. E., & Schmidt, R. (2016). Aquatic noise pollution: implications for individuals, populations, and ecosystems. Proceedings of the Royal Society of London B: Biological Sciences, 283, 20160839.

Kunc, H. P., Lyons, G. N., Sigwart, J. D., McLaughlin, K. E., & Houghton, J. D. (2014). Anthropogenic noise affects behavior across sensory modalities. The American Naturalist, 184, E93-E100.

McGregor, P. K., Horn, A. G., Leonard, M. L., & Thomsen, F. (2013). Anthropogenic noise and conservation. In Animal communication and noise (pp. 409-444). Springer Berlin Heidelberg.

McLaughlin, K. E., & Kunc, H. P. (2013). Experimentally increased noise levels change spatial and singing behaviour. Biology Letters, 9, 20120771.

McNett, G. D., Luan, L. H., & Cocroft, R. B. (2010). Wind-induced noise alters signaler and receiver behavior in vibrational communication. Behavioral Ecology and Sociobiology, 64, 2043-2051.

Meillère, A., Brischoux, F., & Angelier, F. (2015). Impact of chronic noise exposure on antipredator behavior: an experiment in breeding house sparrows. Behavioral Ecology, 26, 569-577.

Miller, C. T., & Bee, M. A. (2012). Receiver psychology turns 20: is it time for a broader approach? Animal Behaviour, 83, 331-343.

Morris-Drake, A., Kern, J. M., & Radford, A. N. (2016). Cross-modal impacts of anthropogenic noise on information use. Current Biology, 26, R911-R912.

Munoz, N. E., & Blumstein, D. T. (2012). Multisensory perception in uncertain environments. Behavioral Ecology, 23, 457-462.

Page, R. A., & Jones, P. L. (2016). Overcoming Sensory Uncertainty: Factors Affecting Foraging Decisions in Frog-Eating Bats. In Psychological Mechanisms in Animal Communication (pp. 285-312). Springer International Publishing.

Purser, J., & Radford, A. N. (2011). Acoustic noise induces attention shifts and reduces foraging performance in three-spined sticklebacks (*Gasterosteus aculeatus*). PLoS One, 6, e17478.

Reichert, M. S., & Höbel, G. (2015). Modality interactions alter the shape of acoustic mate preference functions in gray treefrogs. Evolution, 69, 2384-2398.

Römer, H. (2013). Masking by noise in acoustic insects: problems and solutions. In Animal communication and noise (pp. 33-63). Springer Berlin Heidelberg.

Shannon, G., Angeloni, L. M., Wittemyer, G., Fristrup, K. M., & Crooks, K. R. (2014). Road traffic noise modifies behaviour of a keystone species. Animal Behaviour, 94, 135-141.

Shannon, G., Crooks, K. R., Wittemyer, G., Fristrup, K. M., & Angeloni, L. M. (2016b). Road noise causes earlier predator detection and flight response in a free-ranging mammal. Behavioral Ecology, 27, 1370-1375.

Shannon, G., McKenna, M. F., Angeloni, L. M., Crooks, K. R., Fristrup, K. M., Brown, E., *et al.* (2016a). A synthesis of two decades of research documenting the effects of noise on wildlife. Biological Reviews, 91, 982-1005.

Swaddle, J. P., Francis, C. D., Barber, J. R., Cooper, C. B., Kyba, C. C., Dominoni, D. M., ... & Luther, D. (2015). A framework to assess evolutionary responses to anthropogenic light and sound. Trends in Ecology & Evolution, 30, 550-560.

van der Sluijs, I., Gray, S. M., Amorim, M. C. P., Barber, I., Candolin, U., Hendry, A. P., *et al.* (2011). Communication in troubled waters: responses of fish communication systems to changing environments. Evolutionary Ecology, 25, 623-640.

Ware, H. E., McClure, C. J., Carlisle, J. D., & Barber, J. R. (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.

Supplemental material for: Rosa, P., and N. Koper. 2018. Integrating multiple disciplines to explain effects of anthropogenic noise on animal communication. Ecosphere 9:e02127.

APPENDIX S3.2 Estimating masking footprint of different oil-well noise on three species of grassland songbirds

MEASURING OIL-WELL NOISE

From mid-May to end of June of 2013 and 2014, I recorded noise emanating from generator-powered pumpjacks (*n* = 5; 73 dB(C) at 10 m) and screwpumps (*n* = 5; 79 dB(C) at 10 m), and quieter power-grid pumpjacks (*n* = 5; 62 dB(C) at 10 m) and screwpumps (*n* = 5; 59 dB(C) at 10 m), which were powered through connections to the provincial power grid via power distribution lines. Sound pressure levels (SPL) were measured using a Brüel and Kjær, 2250 SPL meter-frequency analyser (Brüel and Kjær, Denmark) calibrated daily using a 1 kHz a sound calibrator type 4231 (Brüel and Kjær, Denmark). Infrastructure noise measurements were taken in accordance with ISO standard calculations for single source (ISO 3746 2010; ISO 1996-2 2007; ISO 1996-1 2003). I took 6 sound measurements along a circle around the oil-well at 60° from one another, and an additional background sound sample (ISO 3746 2010). I took 30 s sound measurements for screwpumps, and pumpjack measurements varied between 10–60 s depending on the duration of their cycle which encompasses all of the noise variability produced by this oil-well type. The height of the microphone was **0.45*r*** and horizontal distance from centre of oil-well was **0.89*r*** (Equations S3.2.1–S3.2.2; ISO 3746 2010). I measured time-averaged sound metrics (i.e. L_{eq}) to characterise broadband noise in A– and C–weighting, and one-third-octave midpoint frequency band measurements in Z-weighting to analyse spectral composition. For more information on oil-well recording methods, see Rosa et al. (2015).

$$\boldsymbol{r \geq 2d_0 = 1, 2, 4, 6, 8, 10, 12, 14, \text{ or } 16} \qquad \text{(S3.2.1)}$$

$$\boldsymbol{d_0 \geq = \sqrt{(l_1/2)^2 + (l_2/2)^2 + l_3^2}} \qquad \text{(S3.2.2)}$$

$\boldsymbol{l_1}$**:** length (m)
$\boldsymbol{l_2}$**:** width (m)
$\boldsymbol{l_3}$**:** height (m)

GRASSLAND BIRD SONG FREQUENCY RANGES

From mid-May to early July in 2014, I recorded songs from three species of grassland songbirds: Baird’s Sparrow (*Ammodramus bairdii*), Chestnut-collared Longspur (*Calcarius ornatus*), and Savannah Sparrow (*Passerculus sandwichensis*) at three different study sites southeast of Brooks, Alberta, Canada (49° 0 ′ 0.004″ to 50° 53′ 56.475″ N; 110° 0′ 2.757″ W to 112° 28′ 44.473″ W) as uncompressed audio WAV files (48 kHz sampling rate, 16-bit resolution) using Zoom H4N Digital Recorders (Zoom, Japan). For each species, I calculated average peak frequency and frequency range of song vocalizations (Table S3.2.1). For additional information on song recording and measurement methods, see Curry et al. (2018).

Table S3.2.1 Song metrics of three different grassland songbirds recorded from May to July 2014, in Brooks, Alberta, Canada.

Species	Individuals recorded	Songs recorded	Average peak frequency (Hz)	Frequency range	
				Minimum (Hz)	Maximum (Hz)
Baird’s Sparrow	16	49	4978.3	3562.5	7218.8
Chestnut-collared Longspur	7	18	3546.9	2718.8	4500.0
Savannah sparrow	21	62	6796.9	3750	8437.5

ISO-PREDICTED SPATIAL PROPAGATION OF SOUND

I used predicted values of single source sound attenuation to calculate acoustic footprints of four types of oil-wells using field measurements of oil-well noise SPL, distance from infrastructure, and weather parameters obtained from Alberta Agriculture and Forestry (ACIS 2017; i.e., relative humidity barometric pressure, and temperature) averaged over the course of the 12–13 week breeding season of 2013 and 2014. To calculate predicted LZ_{eq} for each one-third-octave frequency band, the ISO-model subtracts the sum of total attenuation (A) from time-averaged SPL field measurements (LwZ; Equations S3.2.3–3.2.7; ISO 9613-2 1996; ISO 9613-1 1993).

$$\mathbf{LZ_{eq} = LwZ - A} \qquad \text{(S3.2.3)}$$

$$\mathbf{A = A_{div} + A_{atm} + Ajusted\ A_{gr}} \qquad \text{(S3.2.4)}$$

$\mathbf{A_{div}}$**:** attenuation due to geometric divergence (dB)

$$\mathbf{A_{div} = 20 \log_{10}(\mathit{d}/\mathit{d}_0) + 11} \qquad \text{(S3.2.5)}$$

$\mathbf{A_{atm}}$**:** attenuation due to atmospheric absorption (dB)

$$\mathbf{A_{atm} = \alpha \mathit{d}} \qquad \text{(S3.2.6)}$$

$\boldsymbol{\alpha}$**:** atmospheric attenuation coefficient (dB/m) based on frequency (Hz), ambient atmospheric pressure (kPa), reference atmospheric pressure (= 101.325 kPa), ambient temperature (K), reference air temperature (= 293.15 K), oxygen relaxation frequency (Hz), and nitrogen relaxation frequency (Hz).
$\boldsymbol{d}$**:** distance from source (m)

$\mathbf{A_{gr}}$**:** attenuation due to ground effect (dB)

$$\mathbf{A_{gr} = A_s + A_r + A_m} \qquad \text{(S3.2.7)}$$

$\mathbf{A_s}$**:** source region component of ground effect attenuation
$\mathbf{A_r}$**:** receiver region component of ground effect attenuation
$\mathbf{A_m}$**:** middle region component of ground effect attenuation

To estimate distance threshold values for potential occurrence of energetic and informational masking, I conducted a spectral analyses of SPL of each one-third-octave frequency bands (LZ_{eq}). As masking thresholds vary with species' vocal and hearing capacity (e.g. Okanoya and Dooling 1987), I opted for a conservative distance threshold estimate where the anthropogenic noises raise the threshold at which a signal can be detected or discriminated from background noise (Dooling and Blumenrath 2013). Both types of masking vary with best hearing capacity of different species, and thus are species-specific. Peak signal energy of the vocalization was found to be more indicative of energetic masking effects in chronic noise conditions compared to the spectral profile of the noise (Lohr et al. 2003). Hence, I used the farthest distance at which SPL within the peak frequency band (Table S3.2.2) was above ambient background noise as the threshold distance for energetic masking for each species and in the four noise conditions (see Table S3.2.3 for results).

Anthropogenic noise with lower SPL than the ambient noise or composed of even just a few frequencies bands that are still detectable can affect exposed wildlife through informational masking. Informational masking can occur in the area closest to the noise source until the last frequency is audible by the receiver (Dooling and Blumenrath 2013). Therefore, to estimate informational masking threshold values for each oil infrastructure type, I also compared time-averaged SPL value bands of midpoint frequency of oil-well noise to the SPL of ambient sound within the range of vocalization of each species. Informational masking threshold was estimated to occur within the distance at which at least 1 one-third-octave frequency band within these frequency ranges (Table S3.2.2) had a higher time-averaged SPL value than its corresponding ambient sound frequency band (see Table S3.2.3 for results).

Table S3.2.2 One-third-octave frequency bands of peak frequency and vocalization frequency range (minimum and maximum) of three different grassland songbirds recorded from May to July 2014, in Brooks, Alberta, Canada. Signal power of peak frequency and across the range of species' vocalizations was compared to power within corresponding one-third octave frequency bands of four different noise profiles.

Species	Peak (Hz)	Range Minimum (Hz)	 Maximum (Hz)
Baird's Sparrow	5000	3150	8000
Chestnut-collared Longspur	3150	2500	5000
Savannah Sparrow	6300	4000	8000

Table S3.2.3 Estimated acoustic footprint of energetic and informational masking for Baird's Sparrow (a; *Ammodramus bairdii*), Chestnut-collared Longspur (b; *Calcarius ornatus*), and Savannah Sparrow (c; *Passerculus sandwichensis*) songs by four different oil-wells in Brooks, Alberta, Canada. Distance thresholds and surface areas were obtained by conducting spectral analyses of the different noise profiles. Signal-to-noise ratio within average peak frequency band was used to estimate energetic masking and signal-to-noise ratio across the frequency range was used to estimate informational masking for each species.

Power source	Oil-well type	Energetic masking Radius (m)	 Area (ha)	Informational masking Radius (m)	 Area (ha)	Increase in acoustic footprint from energetic to informational masking (%)
(a) Baird's Sparrow						
Generator-	pumpjack	105	3.5	115	4.2	20.0
powered	screwpump	155	7.5	205	13.2	76.0
Power-	pumpjack	30	0.3	60	1.1	266.7
grid	screwpump	55	1.0	65	1.3	30.0
(b) Chestnut-collared Longspur						
Generator-	pumpjack	100	3.1	115	4.2	35.5
powered	screwpump	205	13.2	295	27.3	106.8
Power-	pumpjack	60	1.1	60	1.1	0.0
grid	screwpump	60	1.1	90	2.5	127.3
(c) Savannah Sparrow						
Generator-	pumpjack	115	4.2	115	4.2	0.0
powered	screwpump	150	7.1	195	11.9	67.6
Power-	pumpjack	45	0.6	55	1.0	66.7
grid	screwpump	50	0.8	65	1.3	62.5

LITERATURE CITED

ACIS - Alberta Climate Information Service. 2017. Data provided by Alberta Agriculture and Forestry, https://agriculture.alberta.ca/acis. Accessed May 2017.

Curry, C. M., B. Antze, M. H. Warrington, P. Des Brisay, P. Rosa, and N. Koper. 2018. Ability to alter song in two grassland songbirds exposed to simulated anthropogenic noise is not related to pre-existing variability. Bioacoustics 1–26.

Dooling, R. J., and S. H. Blumenrath. 2013. Pages 229–250 *in* H. Brumm, editor. Animal communication and noise 2. Springer-Verlag, Berlin.

ISO 1996-1. 2003. Acoustics — Description, Measurement and Assessment of Environmental Noise. Part 1: Basis Quantities and Assessment Procedures. International Organization for Standardization, Geneva, Switzerland.

ISO 1996-2. 2007. Acoustics — Description, Measurement and Assessment of Environmental Noise. Part 2: Determination of Environmental Noise Levels. International Organization for Standardization, Geneva, Switzerland.

ISO 3746. 2010. Acoustics — Determination of sound power levels and sound energy levels of noise sources using sound pressure. Survey method using an enveloping measurement surface over a reflecting plane. International Organization for Standardization, Geneva, Switzerland.

ISO 9613-1. 1993. Acoustics — Attenuation of sound during propagation outdoors. Part 1: Calculation of the absorption of sound by the atmosphere. International Standards Organization, Geneva, Switzerland.

ISO 9613-2 1996. Acoustics — Attenuation of sound during propagation outdoors. Part 2: General method of calculation. International Standards Organization, Geneva, Switzerland.

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

Okanoya, K., and R. J. Dooling, 1987. Hearing in passerine and psittacine birds: A comparative study of absolute and masked auditory thresholds. Journal of Comparative Psychology 101:7–15.

Rosa, P., C. R. Swider, L. Leston, and N. Koper. 2015. Disentangling effects of noise from presence of anthropogenic infrastructure: Design and testing of system for large-scale playback experiments. Wildlife Society Bulletin 39:364–372.

*Supplemental material for: Rosa, P., and N. Koper. 2018. Integrating multiple disciplines to explain effects of anthropogenic noise on animal communication. Ecosphere 9:e02127.

APPENDIX S4.1. Extended methods and details on playback system fidelity, signal transmission interference, and spatial sound propagation of oil infrastructure

EXPERIMENTAL STUDY DESIGN AND PLAYBACK STIMULI FIDELITY

Background

Drilling operations in our study area consist of three different stages that vary in noise depending on which engines are being used. Generally, a drilling rig operates three different types of engines per rig: (1) combination building, (2) drawworks used for hoisting a wire rope that drops or lifts pipes or casing, (3) two mud pumps used to circulate the drilling fluid which powers the drill bit (Erny and Hurt 2018) The drilling stage which is the loudest of the three stages (LC_{eq}: 90.1 dB(C)) has a total of fours engines running simulateously (i.e., combination, drawworks, and two mud pumps). The casing stage produces a different type of noise, because pipes and casing are being inserted which results in unpredictable clanking noises. During the casing stage, the combination and drawworks engines are operating while the two mud pumps are idling (LC_{eq}: 90.5 dB(C)). Cementing is the quietest stage with only the combination engine operating (LC_{eq}: 88.1 dB(C)). These three different stages are cycled throughout the drilling operation and have variable durations depending on the period (or depth) of the well (Fig. S4.1.1).

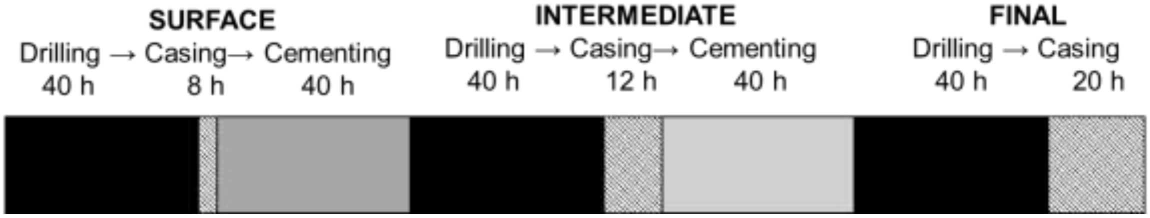


Figure S4.1.1 Duration of the three different stages that occur during the average drilling operation in our study area (i.e., drilling, casing, cementing) divided into the three different periods (i.e., surface, intermediate, and final).

Methods

In addition to chronic power-grid and generator pumpjack treatments that were in place from 2013 to 2015, I added operational drilling noise in 2014 and 2015. In 2015, I changed the location of the playback units to control for potential biases related to characteristics intrinsic to each site (e.g., vegetation, landscape-scale disturbances such as position of dugout and water sources for cattle).

Previous work demonstrated the fidelity of the playback broadcasting unit to noise from real generator and power-grid powered pumpjacks (see Rosa et al. 2015). Here, I conducted similar sound analyses on drilling rig noise by comparing broadband sound pressure level (SPL) measurements, which are indicative of noise amplitude (Huber and Runstein 2005), and SPL across individual frequency bands to compare spectral composition to that of the original noise source. I took SPL measurements along transects radiating in 4 cardinal directions using a Brüel and Kjær 2250 SPL meter/frequency analyser (Brüel and Kjær, Denmark) at three different drilling operations and the three drilling playback sites. Due to logistical constraints, I could only take measurements up to 50 m away from the active drilling rigs. I measured LC_{eq} (C-weighted time-averaged values of SPL in decibels) for broadband sound and LZ_{eq} (Z-weighted time-averaged values of SPL in decibels) for individual one-third-octave frequency bands to measure spectral composition (Rosa et al. 2015). Thirty-second measurements were taken during all three stages of drilling activity (i.e., drilling, laying casing, and waiting on cement) in winds < 7 km/hour, and background measurements were also taken (*n* = 374; Rosa et al. 2015).

To compare attenuation of broadband noise (LC_{eq}) at drilling playback broadcasting units to real drilling operations, I used generalised nonlinear mixed model (PROC NLMIXED; SAS

9.4, SAS Institute Inc. 2012) to account for repeated measures within transects and sites. As noted in Rosa et al. (2015), the inclusion of either transect or site as random variables yielded comparable results, and therefore, I opted to include transect as a random variable. The model assessed the C-weighted time-averaged value of SPL in decibels (LC_{eq}) of drilling rig noise (response variable) as a function of distance (independent variable). LC_{eq} values were log-transformed to fit a Gaussian distribution, distances were centred to reduce potential collinearity with interaction terms, a quadratic function of distance was also included in the model, and I included interaction terms between type of source (i.e., real drilling operation or broadcasting playback unit) and centred-distance and quadratic-distance.

I also compared spectral composition of noise produced during the three stages of an actual drilling rig (i.e., drilling, casing, and cementing) to the corresponding broadcast playback stimulus at 10 m from either the drilling rig or the playback infrastructure during each stage of the drilling operation. I took SPL measurements in LZ_{eq} and time-average SPL for 19 one-third-octave frequency bands that extend below and above the hearing range of birds (i.e., 315 to 20 000 Hz; Dooling 1980, 1982, 1992). For each frequency band, I took four measurements in all four cardinal directions from the drilling rig and broadcasting playback unit. Since LZ_{eq} measurements were not normally distributed, I used a Mann-Whitney U test to assess whether SPL measurements of each one-third-octave frequency band were significantly different between the real drilling rig noise and the broadcasted recording (PROC NPAR1WAY; SAS 9.4, SAS Institute Inc. 2012).

Results

Broadband noise amplitude (log-transformed LC_{eq}) significantly decreased with increased distance from the noise-producing structures ($\beta_{distance} = -3.31 \pm 0.70$ [SE], $P = 0.018$; $\beta_{distance^2} = 24.00 \pm 0.34$, $P < 0.0001$). There was no significant difference in attenuation between the broadcasting playback units and the real drilling operations ($\beta_{type} = -0.016 \pm 0.01$, $P = 0.315$; $\beta_{type\times distance} = 0.03 \pm 0.37$, $P = 0.943$; Fig. S4.1.2). Spectral composition of the broadcast drilling noise was very similar to the operational drilling noise for each stage (i.e., drilling, casing, cementing; Fig. S4.1.3). Vocal and best hearing capacity of birds ranges from approximately 1 kHz to 5 kHz, with greater acuity between 2 to 4 kHz (Dooling 1980, 1982, 1992; Dooling et al. 2000) and with a maximum capacity of ~10 kHz (Necker 2000; Beason 2004). The only difference between real and playback noises within this range was at 5000 Hz in the casing stage of a drilling rig operations; no other frequency bands or periods differed significantly between real infrastructure noise and playback recordings. Cumulatively, these results suggest that playback units were able to very accurately reproduce noise from drilling operations at broadcast sites.

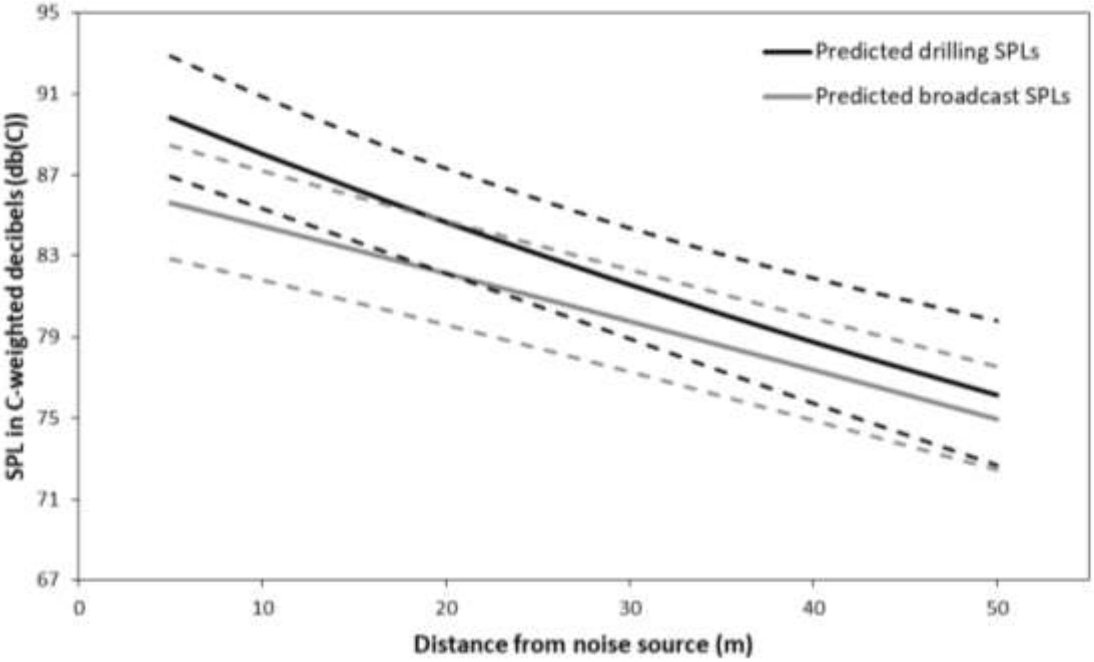


Figure S4.1.2 Predicted sound pressure levels (C-weighted time-averaged value of SPL, in decibels; LC_{eq}) and 95% confidence intervals with increasing distance (m) from three drilling rig operations (black) and corresponding broadcasting playback units (grey) in Alberta, Canada, 2014.

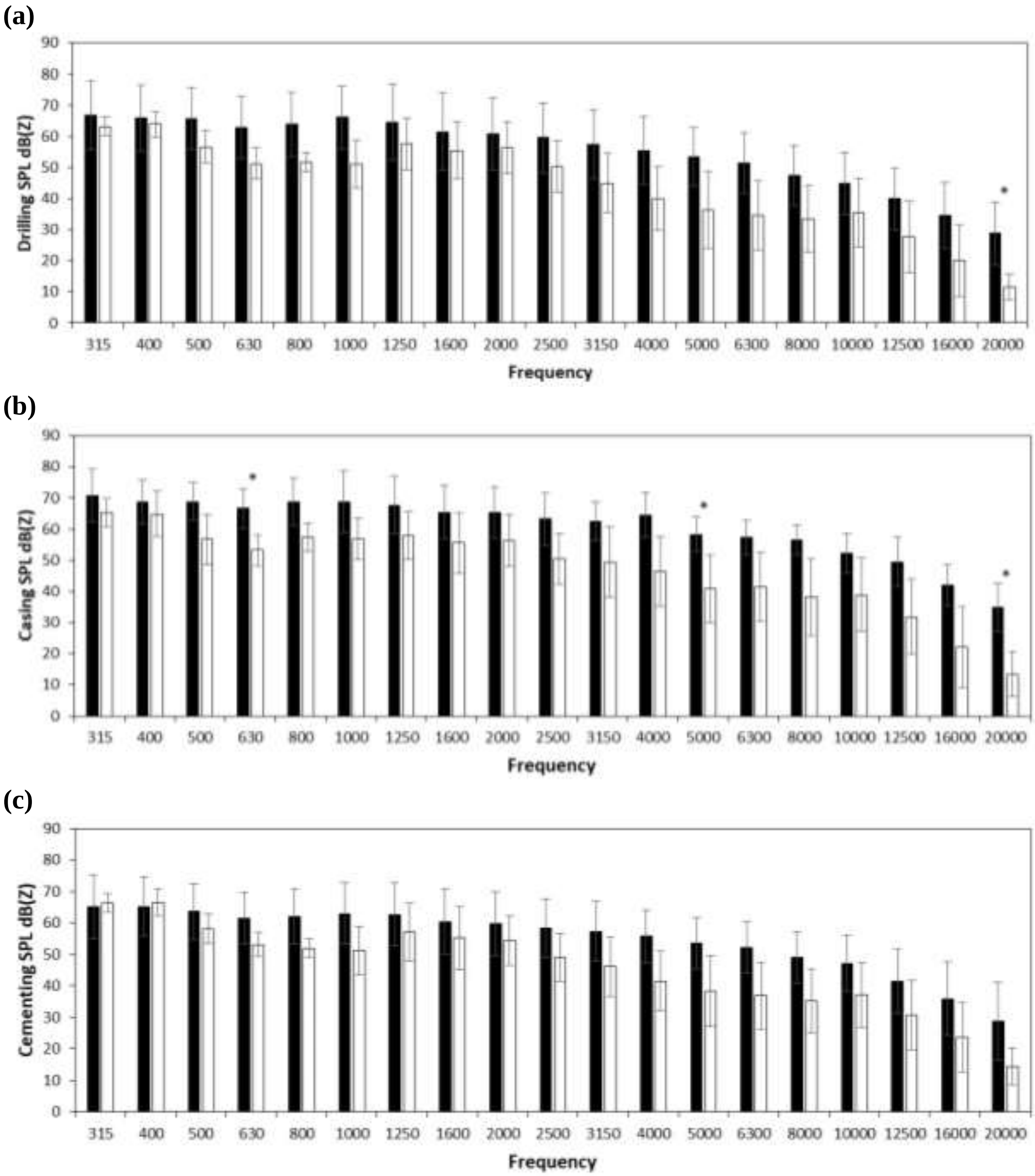


Figure S4.1.3 Average sound pressure levels (SPL; Z-weighted time-averaged value of SPL, in decibels; LZ_{eq}) of midpoint frequencies of one-third-octave frequency bands from 315 Hz to 20 000 Hz, measured during the three different stages of a drilling operations (black bars): drilling (a), casing (b), and cementing (c), and its corresponding broadcast playback stimulus (white bars). Asterisks denote significant differences in SPLs ($P < 0.05$), and error bars show standard error of the mean.

INTERFERENCE OF NOISE WITH SONG TRANSMISSION

Song analysis methods

To estimate the distance at which different noise profiles have the potential to hinder communication for each species, I estimated the farthest distance at which SPL (sound pressure level) within the peak song frequency band was above ambient background noise. From mid-May to early July in 2014 at three different study sites, I recorded songs from two species of grassland songbirds: Chestnut-collared Longspur (*Calcarius ornatus*) and Savannah Sparrow (*Passerculus sandwichensis*) as uncompressed audio WAV files (48 kHz sampling rate, 16-bit resolution) using Zoom H4N Digital Recorders (Zoom, Japan). For Sprague's Pipit (*Anthus spragueii*) and Vesper Sparrow (*Pooecetes gramineus*), I took measurements from three different highly rated song recordings (i.e., rated 'A' or loud and clear) from Xeno-canto (Sprague's Pipit: XC13750, XC18641, XC18646; Vesper Sparrow: XC186417, XC186419, XC186844; https://www.xeno-canto.org) taken in Grasslands National Park (49.1238° N, 107.4470° W). For each species, I calculated average peak frequency of song vocalisations and frequency range in Raven Pro 1.5 Beta (Bioacoustics Research Program 2014; see Curry et al. 2018 for additional details on song recording and measurement methods).

Noise analysis methods

From mid-May to end of June of 2013 and 2014, I measured noise characteristics from three types of common oil infrastructures in the study area: (1) generator-powered pumpjacks (*n* = 5; 73 dB(C) at 10 m), (2) power-grid pumpjacks (*n* = 5; 62 dB(C) at 10 m), and (3) drilling rigs (*n* = 5; 88 dB(C) at 10 m). Using ISO standard protocols and calculations for single noise sources (ISO 1996-1 2003; ISO 1996-2 2007; ISO 3746 2010), I measured 6 points at 60° intervals along a circle around the oil infrastructure units and took background ambient noise measures at each sample site (ISO 3746 2010). Based on these field sound measurements and ISO models, I predicted values of surface areas impacted by the different noise sources based on field measures of noise amplitude, distance from infrastructure and weather parameters (i.e., relative humidity barometric pressure, and temperature) averaged over the course of the 12–13 week breeding season of 2013 and 2014 (ACIS 2017).

Overlap between one-third-octave frequency bands of peak song frequency and corresponding noise in the same frequency is an appropriate predictor of potential interference with signal transmission in a laboratory setting (Lohr et al. 2003). Hence, surface area at which noise within peak frequency of species' vocalisation exceeds ambient noise corresponds to energetic masking, thus potentially preventing signal transmission (Dooling & Blumenrath 2013). Additionally, the area where noise was audible to birds, which may result in informational masking (distraction; e.g., Chan and Blumstein 2011) (audible range: Dooling 1980, 1982, 1992) was estimated as the distance at which at least 1 one-third-octave frequency band within the audible frequency range had higher time-averaged SPL value than its corresponding ambient sound frequency band.

Results

Acoustic footprint of different noise types, and thus their potential to interfere with communication events, differed depending on species' peak frequency and frequency range (Table S4.1.1, see Fig. 4.2). Although drilling rigs were always audible further from the infrastructure than operational oil wells, energetic masking from wells sometimes covered a greater area than did noise from drilling rigs, due to differences in their frequency spectra.

Table S4.1.1 ISO-prediced noise interference in signal transmission of four grassland songbird species. Energetic masking occurs where noise is greater within the species peak frequency, thus potentially preventing signal transmission. Surface area where noise is audible within the species vocalisation frequency range can lead to interference in signal transmission and reception (informational masking; see Fig. 4.2).

			Energetic masking		Audible within frequency range	
Peak frequency (Hz)	Frequency range (Hz)	Oil infrastructure type	Radius (m)	Area (ha)	Radius (m)	Area (ha)
(a) Chesnut-collared Longspur						
3150	2500 – 5000	Drilling rig	165	8.6	235	17.4
		Generator pumpjack	100	3.1	115	4.2
		Power-grid pumpjack	60	1.1	60	1.1
(b) Savannah Sparrow						
6300	4000 – 8000	Drilling rig	105	3.5	150	7.1
		Generator pumpjack	115	4.2	115	4.2
		Power-grid pumpjack	45	0.6	55	1.0
(c) Sprague's Pipit						
5000	2000 – 8000	Drilling rig	105	3.5	325	33.2
		Generator pumpjack	105	3.5	205	13.2
		Power-grid pumpjack	30	0.3	60	1.1
(d) Vesper Sparrow						
3150	2000 – 8000	Drilling rig	165	8.6	325	33.2
		Generator pumpjack	100	3.1	205	13.2
		Power-grid pumpjack	60	1.1	60	1.1

LITERATURE CITED

ACIS - Alberta Climate Information Service. 2017. Data provided by Alberta Agriculture and Forestry, https://agriculture.alberta.ca/acis. Accessed May 2017.

Beason, C. R. 2004. What can birds hear? U.S. Department of Agriculture National Wildlife Research Center-Staff Publications 78:92–96.

Bioacoustics Research Program. 2014. Raven Pro: Interactive Sound Analysis Software (Version 1.5). Cornell Laboratory of Ornithology, Ithaca, NY, USA.

Chan, A. A. Y. H., and D. T. Blumstein. 2011. Attention, noise, and implications for wildlife conservation and management. Applied Animal Behaviour Science 131:1–7.

Curry, C. M., B. Antze, M. H. Warrington, P. Des Brisay, P. Rosa, and N. Koper. 2018. Ability to alter song in two grassland songbirds exposed to simulated anthropogenic noise is not related to pre-existing variability. Bioacoustics 1–26.

Dooling, R. J. 1980. Behavior and psychophysics of hearing in birds. Pages 261–288 *in* A. N. Popper, and R. R. Fay, editors. Comparative studies of hearing in vertebrate. Springer-Verlag, NY, USA.

Dooling, R. J. 1982. Auditory perception in birds. Pages 95–130 *in* D. E. Kroodsma, editor. Acoustic communication in Birds (Vol. 1): Production, perception, and design features of sounds. Academic Press, NY, USA.

Dooling, R. J. 1992. Hearing in birds. Pages 545–559 *in* D. B. Webster, R. R. Fay, and A. N. Popper, editors. The evolutionary biology of hearing. Springer-Verlag, NY, USA.

Dooling, R. J., and S. H. Blumenrath. 2013. Avian sound perception in noise. Pages 229–250 *in* H. Brumm, editor. Animal communication and noise 2. Springer-Verlag, Berlin.

Dooling, R. J., B. Lohr, and M. L. Dent. 2000. Hearing in birds and reptiles. Pages 308–359 *in* R. R. Fay, and A. N. Popper. Comparative hearing: birds and reptiles. Springer-Verlag, NY, USA.

Erny, B, & Hurt, J. (Eds.). 2018. Oil and gas well drilling and serving eTool. Occupational Safety and Health Administration, United States Departement of Labor, https://www.osha.gov/SLTC/etools/oilandgas/index.html. Accessed January 16, 2019.

Huber, D. M., and R. E. Runstein. 2005. Modern recording techniques, 6th edition. Elsevier, Burlington, MA, USA.

ISO 1996-1. 2003. Acoustics — Description, Measurement and Assessment of Environmental Noise. Part 1: Basis Quantities and Assessment Procedures. International Organization for Standardization, Geneva, Switzerland.

ISO 1996-2. 2007. Acoustics — Description, Measurement and Assessment of Environmental Noise. Part 2: Determination of Environmental Noise Levels. International Organization for Standardization, Geneva, Switzerland.

ISO 3746. 2010. Acoustics — Determination of sound power levels and sound energy levels of noise sources using sound pressure. Survey method using an enveloping measurement surface over a reflecting plane. International Organization for Standardization, Geneva, Switzerland.

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

Necker, R. 2000. The avian ear and hearing. Pages 21–38 *in* G. C. Whinow, editor. Sturkie's avian physiology, 5th edition, Academic Press, NY, USA.

Rosa, P., C. R. Swider, L. Leston, and N. Koper. 2015. Disentangling effects of noise from presence of anthropogenic infrastructure: design and testing of system for large-scale playback experiments. Wildlife Society Bulletin 39:364–372.

SAS Institute, Inc. 2012. SAS Statistical Software. Version 9.4. SAS Institute, Cary, North Carolina, USA.

APPENDIX S4.2. Extended abundance, nesting success, nestling measurements, and clutch size methods and results: anthropogenic noise and infrastructure decouple habitat use from habitat quality in grassland songbirds

METHODS

Field surveys

Avian abundance transects – Two observers conducted two transect surveys per site simultaneously and spent a total of 40 min per transect recording bird observations (including distance and direction from observer to estimate location of observation and sex and behaviour whenever possible). Along the 400-m transect, observers moved at a steady pace, taking 5 min to walk 50 m while noting species observed within 100 m on either side of the transect line (Fig. S4.2.1). Starting point order was alternated to control for potential observer bias such as under-estimating abundance near the end of transects, which is a potential subconscious response of observers to avoid recounting birds. Observers were trained and tested in bird identification (i.e., sight and sound), distance estimations, and field methods prior to conducting surveys.

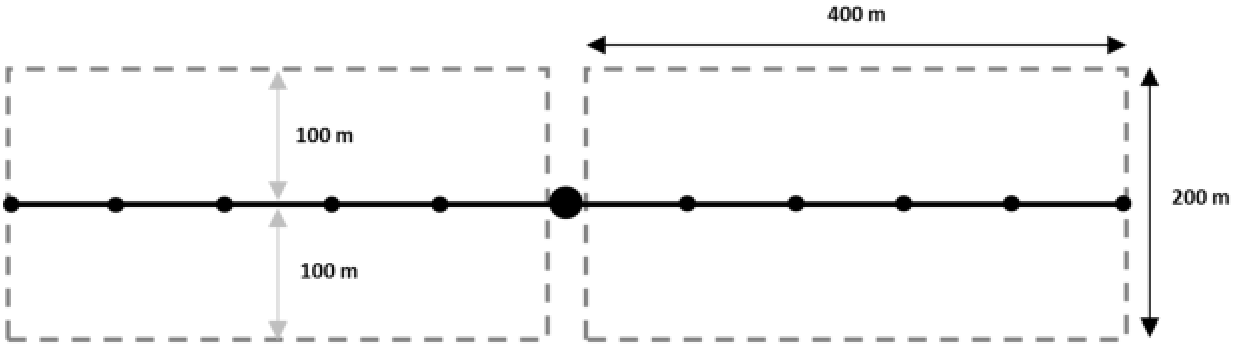


Figure S4.2.1 Area surveyed by observers along two 400-m transects lines (black lines) radiating away from the playback unit or centre-point of control sites (large circle). Transects were generally directed East and West and covered a 400 m × 200 m surface per transect.

Nest searching and monitoring – In 2013, rope-drag surveys were conducted of two plots (400 m × 400 m; 32 ha) in each site, each radiating away from the infrastructure or the centre-point of the control site. In 2014, four plots were surveyed in all four cardinal directions (i.e., two plots 200 m × 400 m and two plots 200 m × 300 m, to eliminate overlap of plots; 28-ha) and in 2015, the four plots were increased in surface area (i.e., two plots 400 m × 400 m and two plots 400 m × 300 m; 56 ha) to increase sample sizes. Surveys were conducted on foot to minimize ecological impacts on prairies.

Clutch size consisted of the final number of eggs laid by the female. If nests were found after hatching, I used number of nestlings as an estimate of clutch size. To avoid confounding the physiological effects of noise with those related to brood parasitism, I did not measure nestlings or count clutch sizes from nests that had been parasitized by Brown-headed Cowbirds (*Molothrus ater*).

Vegetation along transects and at nests – In 2013 and 2015, 12 1-m^2 vegetation plots were surveyed along each abundance transect line at 1, 5, 10, 20, 50, 100, 150, 200, 250, 300, 350, and 400 m from the playback unit or centre-point of control sites. In 2014, 19 vegetation plots were surveyed at 5, 10, 15, 25, 50, 75, 100, 125, 150, 175, 200, 225, 250, 275, 300, 235, 350, 375, 400 m. The middle of the vegetation quadrat was centred at the nest cup for nest vegetation surveys. Four sub-quadrats per plot were delimited by placing two metre sticks on the ground in the shape of a cross intersecting at 50 cm, within which vegetation cover and composition was visually estimated. To measure height, density, and litter depth, a 6.3-mm dowel marked in 1-cm intervals (Wiens pole) was placed in the centre of the quadrat and at the four extremities of the metre sticks oriented in cardinal directions, at which I measured height and litter depth, and counted numbers of stems of vegetation touching the pole.

Nestling measurements – I took morphometric measurements of 5-day-old nestling Savannah Sparrows (*n* = 650 from 182 nests) and Chestnut-collared Longspurs (*n* = 219 from 61 nests). I measured nestlings at approximately day 5 (mean age = 5.04; SD ± 0.43) to minimise the risk of parents abandoning young nestlings or causing older nestlings to force fledge. Age of nestlings was estimated based on several developmental stages such as opening of eyes, feather tracts, and presence of pin-feathers (Jongsomjit et al. 2007). Nestlings were weighed individually in holding bags using a Pesola micro-line spring scale (model #20030; 30 g capacity × 0.25 g resolution; ± 0.3% accuracy). I also measured the length of the left tarsometatarsal bone (i.e., tarsus length) from the notch of the intertarsal joint to the top of the bent foot using a SPI dial calliper (model #31-415-3; 0.1 mm graduation; ±0.0015 mm accuracy). Measurements were taken as quickly as possible (mean handling time = 10.83 min; SD ± 4.23) at approximately 20 m from the nest to minimise disturbance of vegetation or attracting predators.

DATA ANALYSES

I used an information theoretic approach to determine which environmental variables improved relative fit and should be included in final models to control for effects of temporal factors, such as year and time of year, and vegetation factors, such as vegetation height and density. As each species has different habitat preferences, I used AIC (Akaike's Information Criterion; Akaike 1974) to select the appropriate variables to include in models for each species.

I adopted a frequentist approach (i.e., null hypothesis significance testing) to test hypotheses regarding effects of noise, as that was the focus of my study design (see Mundry 2011). I used an alpha value of 0.10 to reduce the chance of Type II errors (i.e., failure to detect an effect when there is one), which is a source of significant concern in conservation biology

(Taylor and Gerrodette 1993). I compared the three noise treatments (playbacks of recordings of chronic generator and power-grid pumpjacks, and intermittent drilling rigs), to both control and infrastructure-only treatments to control for potential effects related to the physical presence of the playback unit. I modelled effects of noise at both a local scale, which included distance from playback units or centre-points and an interaction with treatment, and at the site-scale (i.e., 64.7-ha; treatment variable only), which is representative of the scale at which management occurs.

Avian abundance

I used generalised linear mixed models (GLMMs; PROC GLIMMIX; SAS 9.4, SAS Institute Inc. 2012) to determine which vegetation and temporal variables to include in bird abundance models. GLMMs allow the inclusion of random effects to control for repeated measures (e.g., Venables and Ripley 2002; e.g., site, plot) and fixed effects that are of specific interest in the study design (e.g., treatments; Bolker et al. 2008). They are also an appropriate tool to model non-normal distributions (Littell et al. 2006, Bolker et al. 2008) such as count data (Quinn and Keough 2002) and to simultaneously manage categorical data such as treatments and continuous data such as distances of bird from noise source (Littell et al. 2006).

Preliminary analyses – I determined the appropriate distribution for each species abundance by running generalised linear models (PROC GENMOD; SAS 9.4, SAS Institute Inc. 2012) and evaluating Q-Q plots and $\chi 2$/df ratio to assess distribution fit. Accordingly, I used a zero-inflated Poisson distribution to model Chestnut-collared Longspur (*Calcarius ornatus*) abundance, a Poisson distribution for Sprague's Pipit (*Anthus spragueii*), a negative binomial distribution for Savannah Sparrow (*Passerculus sandwichensis*), and a binomial distribution for Vesper Sparrow (*Pooecetes gramineus*) to assess probability of occurrence (i.e., presence or absence) due to low abundance of the latter species.

For each species, I ran a suite of models describing effects of temporal factors, and vegetation cover, structure and composition on abundance (Table S4.2.1) to determine which biologically important variables should be included in subsequent noise and infrastructure models. I used AIC to compare fit of each model when including different random variables to determine how much of the correlation in the data was due to repeated measures from within: (1) the same site, (2) the same plot, (3) the same site and plot (e.g., site/plot(site)), and (4) compared to models with no random variables. To avoid over-parameterisation, I first ran a suite of vegetation cover models (Table S4.2.2). The vegetation cover models within 2 AIC units of the best-fitting one were then included into the nuisance variables models (i.e., temporal, vegetation structure and cover variables, Table S4.2.3; Arnold 2010). For example, vegetation cover models within 2 AIC units of the best-fitting one for Chestnut-collared Longspur were: $C_{g + e}$, C_e, and $C_{w + e}$. Hence, for temporal-vegetation model 9 in Table S4.2.3 (i.e., horizontal vegetation structure [H] + vegetation cover [C]), I ran H + $C_{g + e}$, H + C_e, and H + $C_{w + e}$. For each species, this procedure was repeated for all temporal-vegetation models that included vegetation cover (C; i.e., models 4, 7, 9, 10, 12, 13, 14, and 15 in Table S4.2.3). Afterwards, I compared fit of all temporal-vegetation models (Ludlow et al. 2014; models within 2 AIC units of best-fit model reported in Table S4.2.4 for each species). After I selected the temporal and vegetation variables that improved model fit, I added these to my hypothesis testing model, which included included treatment for the site-scale models, while local-scale models included distance from the playback unit (or centre-point of control sites) and its interaction with treatment.

Table S4.2.1 List of temporal, vegetation structure, and cover variables and models considered in abundance analyses.

Models	Parameters
Temporal (T):	Year
	Julian date of survey
Horizontal vegetation structure (H):	Density of live grass
	Density of dead grass
Vertical vegetation structure (V):	Height
	Litter depth
Vegetation cover (C):	
Grass (C_g):	Percentage of bare ground
	Percentage of live grass
	Percentage of dead grass
Other (C_o):	Percentage of forbs
	Percentage of lichen/moss
	Percentage of shrubs
Animal waste (C_w):	Percentage of waste
Exotic (C_e):	Percentage of exotic

Table S4.2.2 Model suite of vegetation cover (C) variables considered for inclusion in abundance analyses.

Models	**Parameters**
1. Grass (C_g):	Percentages of bare ground + live grass + dead grass
2. Other (C_o):	Percentages of forbs + lichen/moss + shrubs
3. Animal waste (C_w):	Percentage of waste
4. Exotic cover (C_e):	Percentage of exotic
5. Grass and other (C_{g+o}):	Percentages of bare ground + live grass + dead grass + forbs + lichen/moss + shrubs
6. Grass and animal waste (C_{g+w}):	Percentages of bare ground + live grass + dead grass + waste
7. Grass and exotic (C_{g+e}):	Percentages of bare ground + live grass + dead grass + exotic
8. Other and animal waste (C_{o+w}):	Percentages of forbs + lichen/moss + shrubs + waste
9. Other and exotic (C_{o+e}):	Percentages of forbs + lichen/moss + shrubs + exotic
10. Animal waste and exotic (C_{w+e}):	Percentages of animal waste + exotic
11. Grass, other, and animal waste (C_{g+o+w}):	Percentages of bare ground + live grass + dead grass + forbs + lichen/moss + shrubs + waste
12. Grass, other, and exotic (C_{g+o+e}):	Percentages of bare ground + live grass + dead grass + forbs + lichen/moss + exotic
13. Grass, animal waste, and exotic (C_{g+w+e}):	Percentages of bare ground + live grass + dead grass + waste + exotic
14. Other, animal waste, and exotic (C_{o+w+e}):	Percentages of forbs + lichen/moss + shrubs + waste + exotic
15. Grass, other, animal waste, and exotic ($C_{g+o+w+e}$):	Percentages of bare ground + live grass + dead grass + forbs + lichen/moss + shrubs + waste + exotic

Table S4.2.3 Model suite of temporal, vegetation structure and vegetation cover variables considered for inclusion in abundance analyses.

Models	**Parameters**
1. Temporal (T):	Year + julian date of survey
2. Horizontal vegetation structure (H):	Densities of live grass + dead grass
3. Vertical vegetation structure (V):	Height + litter depth
4. Vegetation cover (C):	Best-fit cover model
5. Temporal and horizontal (T + H):	Year + julian date of survey + densities of live grass + dead grass
6. Temporal and vertical (T + V):	Year + julian date of survey + height + litter depth
7. Temporal and cover (T + C):	Year + julian date of survey + best-fit cover model
8. Horizontal and vertical (H + V):	Densities of live grass + dead grass + height + litter depth
9. Horizontal and cover (H + C):	Densities of live grass + dead grass + best-fit cover model
10. Vertical and cover (V + C):	Height + litter depth + best-fit cover model
11. Temporal, horizontal, and vertical (T + H + V):	Year + julian date of survey + densities of live grass + dead grass + height + litter depth
12. Temporal, horizontal, and cover (T + H + C):	Year + julian date of survey + densities of live grass + dead grass + best-fit cover model
13. Temporal, vertical, and cover (T + V + C):	Year + julian date of survey + height + litter depth + best-fit cover model
14. Horizontal, vertical, and cover (H + V + C):	Densities of live grass + dead grass + height + litter depth + best-fit cover model
15. Temporal, horizontal, vertical, and cover (T + H + V + C):	Year + julian date of survey + densities of live grass + dead grass + height + litter depth + best-fit cover model

Table S4.2.4 Vegetation and temporal variables included in abundance models in addition to treatment, distance to infrastructure or the control centre, and their interaction (variables referenced in Table S4.2.1).

Species	Variables inlcuded	Random effect	AIC
Chestnut-collared Longspur	**H + $C_{g + e}$**	**site**	**2484.28**
	H + C_{e}	site	2484.47
	H + $C_{w + e}$	site	2485.04
Savannah Sparrow	**T + C_{e}**	**site**	**5119.78**
	T + $C_{w + e}$	site	5121.59
Sprague's Pipit	**H + C_{g}**	**site**	**3190.31**
	H + $C_{g + e}$	site	3191.93
	H + $C_{g + w}$	site	3192.1
Vesper Sparrow	**T + C_{g}**	**site**	**969.44**
	T + $C_{g + w}$	site	971.3

Nesting success

To assess effects of noise and infrastructure on nesting success of grassland songbirds, I used the logistic-exposure method (Shaffer 2004). Assumptions of the logistic-exposure method are that nest completions or failures are independent of each other and that daily survival rates (DSR) among nest-days that have identical predictor variable values are homogenous (Shaffer 2004). A nest was considered successful when a minimum of one juvenile was thought to have fledged the nest (Jones and Geupel 2007).

To facilitate interpretation of results, parameter estimates and their confidence intervals (CI) were converted to odds ratios (i.e., inverse transformation of logit, Shaffer and Thompson 2007). If the odds ratio was > 1, then the odds of nesting success increased [odds ratio] times by 1 unit increase of the predictor variable. If the odds ratio was between 0 and 1, then as the predictor variable increases by 1 unit, the odds of nesting success decreased by [(1-odds ratio) x 100].

Preliminary analyses – I ran preliminary logistic-exposure models (PROC NLMIXED; SAS Institute, Inc. 2012) to determine which combination of variables (i.e., percent noise exposure during nesting period, nest stage, temporal factors including estimated nest initiation date and year, and vegetation structure and cover; Table S4.2.5) should be included in the treatment models (or hypothesis testing models). The temporal models included linear and quadratic effects of nest age and Julian date of nest initiation, and linear effects of year (Dinsmore et al. 2002, Ludlow et al. 2014). Due to the negligible presence of exotic vegetation at nests, vegetation models focused on vegetation structure and cover (Table S4.2.6; e.g., Davis and Duncan 1999, Madden et al. 2000, Ranellucci *et al.* 2012). I compared best-fit temporal, vegetation, and combined temporal-vegetation models (Ludlow et al. 2014) for each species (Table S4.2.7). Temporal variables did not improve model fit, so I only included vegetation variables in the final models. To control for repeated measures from the same nest and site, I compared preliminary models that included nest and site as random effects to models with no random variable. Using AIC, I determined that including either random effect did not improve fit, and thus used nesting success models without random effects. Once I selected the necessary vegetation variables, I added the selected terms to my hypothesis testing model, which included included treatment for the site-scale models, while local-scale models included distance from the playback unit (or centre-point of control sites) and its interaction with treatment.

Table S4.2.5 List of temporal and vegetation variable models considered in nest survival analyses.

Models	Parameters
Temporal: Where nest stage: 0 = nest only 1 = eggs 2 = young nestlings < 6 days old 3 = older nestlings ≥ 6 days old	Year Nest stage Nest stage^2 Julian date of nest initiation Julian date of nest initiation^2
Vegetation:	Average density Height Litter depth Percent cover

Table S4.2.6 Vegetation variable combinations compared for nesting success analyses.

Models
1. Average density
2. Height
3. Litter depth
4. Percent cover
5. Average density + height
6. Average density + litter depth
7. Average density + percent cover
8. Height + litter depth
9. Height + percent cover
10. Litter depth + percent cover
11. Average density + height + litter depth
12. Average density + height + percent cover
13. Average density + litter depth + percent cover
14. Height + litter depth + percent cover
15. Average density + height + litter depth + percent cover

Table S4.2.7 Vegetation models within 2 AIC of best-fitting model (bold) for nest survival analyses of four focal species.

Species	**Variables**	**AIC**
Chestnut-collared Longspur	**Average density**	**332.6**
	Average density + litter depth	333.3
	Litter depth	334.4
	Average density + height	334.5
	Average density + percent cover	334.5
Savannah Sparrow	**Height**	**1292.3**
	Average density + height	1293
	Average density	1293.5
	Height + litter depth	1293.6
	Average density + height + litter depth	1293.7
	Height + percent cover	1293.8
Sprague’s Pipit	**Height**	**116**
	Percent cover	117.7
	Height + litter depth	117.8
	Average density + height	117.9
	Height + percent cover	117.9
Vesper Sparrow	**Litter depth + percent cover**	**136.8**
	Litter depth	137.6
	Height + litter depth + percent cover	138.6
	Average density + litter depth + percent cover	138.7

Nestling body condition and clutch size

Body condition index – Scaled mass index (SMI), which scales body mass by a linear morphometric measurement, such as tarsus length, has been shown to be more predictive of energy reserves and more representative of relative size of individuals compared to ordinary least square residuals, or simply using size or weight alone (Peig and Green 2009, 2010). SMI was calculated for each individual as follows:

$$SMI_i = M_i \left[\frac{L_0}{L_i}\right]^{b_{SMA}}$$

where, for each species, M_i is the body mass of individual$_i$ nestling, L_i is individual$_i$ body length measure (i.e., tarsus length), L_0 is the arithmetic mean of tarsus length (Savannah Sparrow: L_0 = 14.32 mm, n = 650; Chestnut-collared Longspur: L_0 = 14.11 mm, n = 219), and b_{SMA} is the slope estimate (b) of a standardized major axis (SMA) regression of log-body mass on log-tarsus length (Savannah Sparrow: b_{SMA} = 1.592; Chestnut-collard Longspur: b_{SMA} = 1.644).

I used generalised linear mixed models (GLMMs) in SAS 9.4 (PROC GLIMMIX; SAS Institute, Inc. 2012) to assess effects of noise and infrastructure on nestling body condition. For all models, distributions of residuals did not differ from normality (Gaussian distribution and identity link function in SAS 9.4). Fixed effects included in models were treatment, and age of nestlings when measured and year, as preliminary models suggested significant effects of year and age on body condition. I included nest as a random variable to control for the lack of independence among nestling measurements within nests. Site-scale models included treatment, while local-scale models included log-transformed distance from the playback unit (or centre-point of control sites) and its interaction with treatment.

Clutch size – I used GLMMs to model effects of noise on clutch size at both the site and local scale. Both models included treatment as a fixed effect, and age and date to control for temporal variation in clutch size throughout the breeding season. Site was included as a random variable to account for repeated sampling from same sites over multiple years. Site-scale models included treatment, while local-scale models included log-transformed distance from the playback unit (or centre-point of control sites) and its interaction with treatment.

RESULTS

Avian abundance

I found significant effects of noise and infrastructure on relative abundance at both the local (Table S4.2.8; Fig. S4.2.2) and site (Table S4.2.9) scales for Savannah Sparrow and Vesper Sparrow, but only found found local-scale effects for Chestnut-collared Longspur and Sprague's Pipit. Additional details are in the main text of the paper (see Fig. 4.3).

Table S4.2.8 Parameter estimates (β), standard error (SE), and *P*-values for local-scale significant effects of playback treatment and distance to unit/centre on relative abundance (*P* < 0.1) of (a) Chestnut-collared Longspur, (b) Savannah Sparrow, (c) Sprague's Pipit, and (d) Vesper Sparrow from 2013 to 2015, in Brooks, Alberta, Canada. Only significant effects are shown, relative to infrastructure-only and control treatments as reference categories (see Fig. 4.3).

Reference category	**Effects**	**β**	**SE**	***P*-value**
(a) Chestnut-collared Longspur				
Infrastructure-only	*Intercept*	*2.0705*	*0.5548*	*0.0012*
	Drilling	-1.3298	0.5665	0.0194
	Power-grid	-1.2852	0.6355	0.0438
	Drilling × distance	0.00571	0.001969	0.004
	Power-grid × distance	0.003927	0.002148	0.0683
Control	*Intercept*	*1.6056*	*0.4855*	*0.0034*
	Drilling	-0.8981	0.5035	0.0753
	Drilling × distance	0.004288	0.001707	0.0124
(b) Savannah Sparrow				
Infrastructure-only	*Intercept*	*-3.1171*	*0.3306*	*< 0.0001*
	Drilling	-0.3372	0.173	0.0514
Control	*Intercept*	*-3.0061*	*0.2999*	*< 0.0001*
	Drilling	-0.4537	0.1457	0.0019
	Distance	-0.00051	0.000292	0.0817
(c) Sprague's Pipit				
Infrastructure-only	*Intercept*	*-1.1859*	*0.3014*	*0.0006*
	Control	0.741	0.2855	0.0095
	Distance	0.001511	0.000832	0.0695
	Control × distance	-0.00193	0.000937	0.04
Control	*Intercept*	*-0.445*	*0.2185*	*0.052*
	Drilling	-1.235	0.2592	< 0.0001
	Power-grid	-0.6474	0.2708	0.017
	Infrastructure-only	-0.7406	0.2854	0.0096
	Drilling × distance	0.002662	0.000802	0.0009
	Power-grid × distance	0.00157	0.000889	0.0775
	Infrastructure-only × distance	0.001917	0.000936	0.0408
(d) Vesper Sparrow				
Infrastructure-only	*Intercept*	*1.1047*	*1.5027*	*0.4669*
	Control	-2.1667	0.9225	0.019
	Drilling × distance	0.004898	0.002493	0.0496
	Control × distance	0.005611	0.002778	0.0436
Control	*Intercept*	*-1.0899*	*1.4282*	*0.4502*
	Drilling	1.8262	0.8477	0.0314
	Infrastructure-only	2.2108	0.9233	0.0168
	Infrastructure-only × distance	-0.00571	0.002781	0.0402

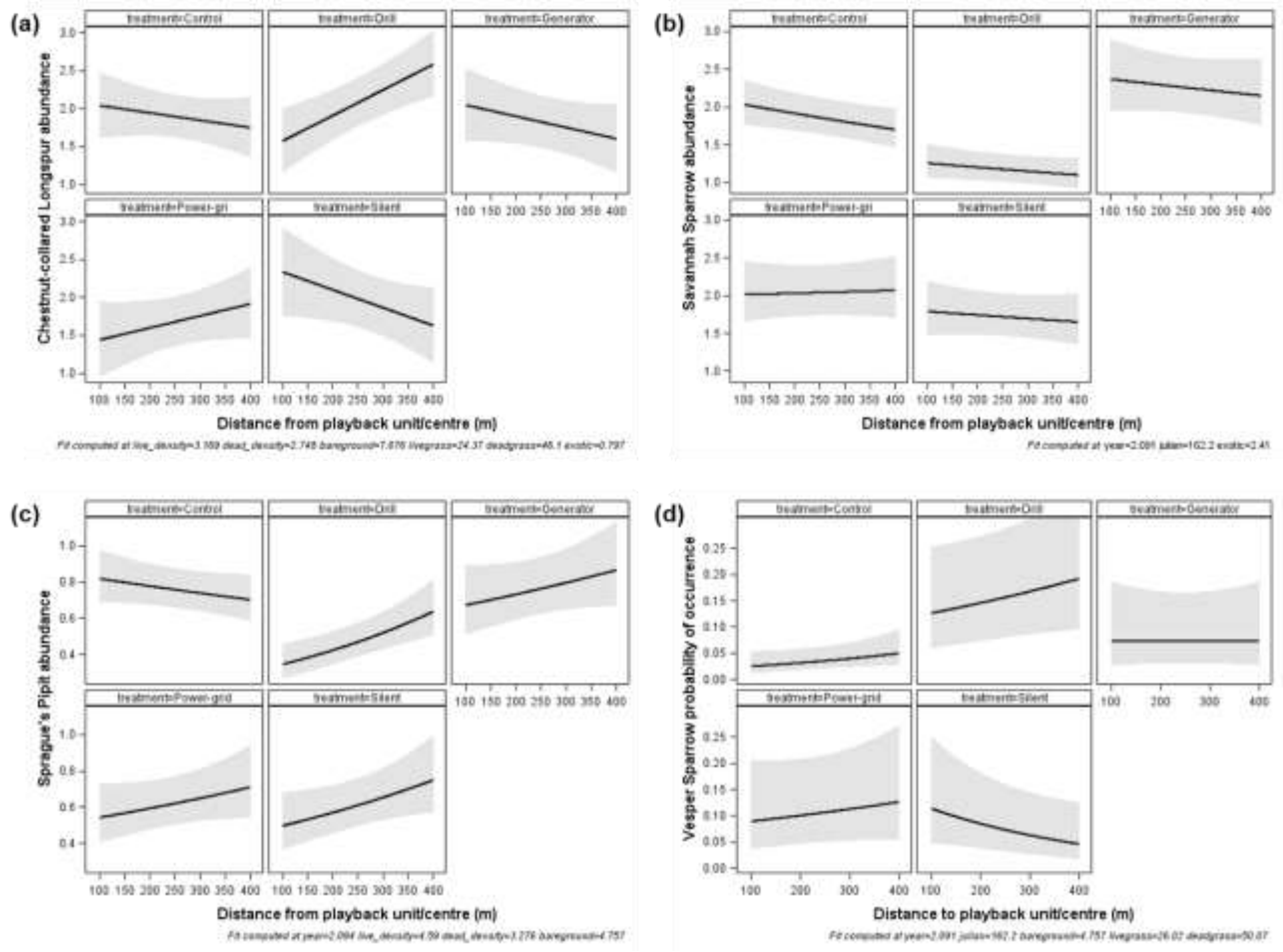


Figure S4.2.2 Local-scale effects of treatments on relative abundance of four grassland songbird species: (a) Chestnut-collared Longspur, (b) Savannah Sparrow, (c) Sprague's Pipit, and (d) Vesper Sparrow. 90% confidence intervals are shown (see Fig. 4.3). Here, "silent" treatment refers to infrastructure-only treatment.

Table S4.2.9 Parameter estimates (β), standard error (SE), and *P*-values for site-scale significant effects of playback treatment and distance to unit/centre on relative abundance ($P < 0.1$) of (a) Chestnut-collared Longspur, (b) Savannah Sparrow, (c) Sprague's Pipit, and (d) Vesper Sparrow from 2013 to 2015, in Brooks, Alberta, Canada. Only significant effects are shown, relative to infrastructure-only and control treatments as reference categories. If there were no significant effects, the lowest *P*-value is indicated.

Reference category	**Effects**	**β**	**SE**	***P*-value**
(a) Chestnut-collared Longspur				
Infrastructure-only	*Intercept*	*0.3803*	*0.2061*	*0.0792*
	All treatments			≥ 0.4374
Control	*Intercept*	*0.3552*	*0.1837*	*0.0668*
	All treatments	-0.8981	0.5035	≥ 0.4531
(b) Savannah Sparrow				
Infrastructure-only	*Intercept*	*-1.24*	*0.3306*	*0.0002*
	Drilling	-0.2374	0.079	0.0027
Control	*Intercept*	*-1.2659*	*0.2758*	< *0.0001*
	Drilling	-0.2117	0.0795	0.0079
(c) Sprague's Pipit				
Infrastructure-only	*Intercept*	*0.1601*	*0.1728*	*0.3626*
	All treatments			≥ 0.5164
Control	*Intercept*	*-0.445*	*0.2185*	*0.052*
	All treatments			≥ 0.3575
(d) Vesper Sparrow				
Infrastructure-only	*Intercept*	*0.4976*	*1.1575*	*0.6802*
	Control	-1.0956	0.2922	0.0002
Control	*Intercept*	*-0.598*	*1.128*	*0.6124*
	Drilling	1.5543	0.2627	< 0.0001
	Generator	1.0193	0.29	0.0005
	Power-grid	1.2262	0.2898	< 0.0001
	Infrastructure-only	1.0956	0.2922	0.0002

Nesting success

I found no significant effects of distance or its interaction with treatment on nesting success of Chestnut-collared Longspur ($P \geq 0.12$) or Savannah Sparrow ($P \geq 0.24$). Local-scale models that included distance to infrastructure did not converge for Sprague's Pipits or Vesper Sparrows, for which I had fewer nests. I found site-scale effects of noise on nesting success of

Savannah Sparrow and Sprague's Pipit, and effects of playback infrastructure on nesting success of Sprague's Pipit and Vesper Sparrow (Table S4.2.10). Additional results are in the main text (see Fig. 4.4).

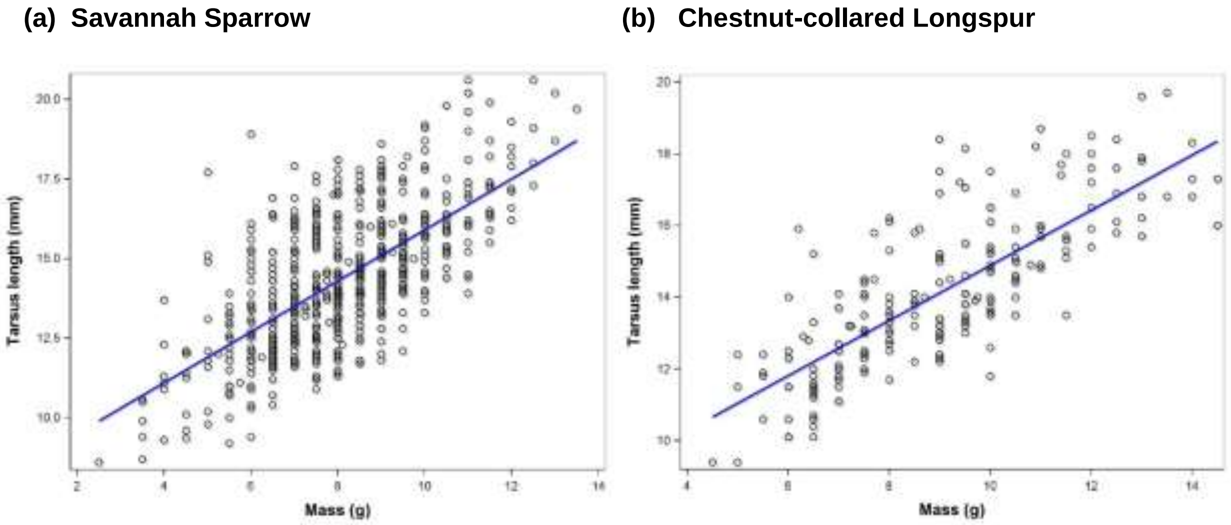
Table S4.2.10 Parameter estimates (β), standard error (SE), and *P*-values for site-scale significant effects of playback treatment and distance to unit/centre on relative abundance ($P < 0.1$) of (a) Chestnut-collared Longspur, (b) Savannah Sparrow, (c) Sprague's Pipit, and (d) Vesper Sparrow from 2013 to 2015, in Brooks, Alberta, Canada. Only significant effects are shown, relative to infrastructure-only and control treatments as reference categories (see Fig. 4.4).

Reference category	**Effects**	**β**	**SE**	***P*-value**
(a) Chestnut-collared Longspur				
Infrastructure-only	*Intercept*	*3.5289*	*0.4641*	*< 0.0001*
Control	*Intercept*	*3.6208*	*0.4421*	*< 0.0001*
(b) Savannah Sparrow				
Infrastructure-only	*Intercept*	*3.8824*	*0.2967*	*< 0.0001*
	Drilling	-0.5822	0.2162	0.0071
Control	*Intercept*	*3.6715*	*0.2967*	*< 0.0001*
	Drilling	-0.3712	0.2162	0.0861
(c) Sprague's Pipit				
Infrastructure-only	*Intercept*	*7.2879*	*0.9704*	*< 0.0001*
	Drilling	-2.0139	0.4598	< 0.0001
	Control	-1.4395	0.7088	0.0435
Control	*Intercept*	*4.9301*	*0.9704*	*< 0.0001*
	Generator	-1.8307	0.8477	0.0319
	Power-grid	1.705	0.8914	0.0571
(d) Vesper Sparrow				
Infrastructure-only	*Intercept*	*-4.6844*	*2.8086*	*0.0965*
	Drilling	1.9802	0.8794	0. 0252
	Generator	3.0796	1.5861	0.0532
	Control	2.2795	1.0747	0.0348
Control	*Intercept*	*-2.4048*	*2.8733*	*0.4034*
	Infrastructure-only	-2.2795	1.0747	0.0348

Nestling body condition and clutch size

Savannah Sparrows produced larger nestlings in treatment types in which they had higher abundances, while reproductive output of Chestnut-collared Longspurs was lower at sites they selected for breeding. Further results for nestling body condition and clutch size are in the main text.

Nestling body mass and tarsus length were positively correlated in Savannah Sparrow ($R = 0.672$, $P < 0.001$) and Chestnut-collared Longspur ($R = 0.785$, $P < 0.001$; Fig. S4.2.3).


(a) Savannah Sparrow

(b) Chestnut-collared Longspur

Figure S4.2.3 Regression of body mass by tarsus length of Savannah Sparrow (*Passerculus sandwichensis*; $n = 650$; $R = 0.672$; $P < 0.001$; a) and Chestnut-collared Longspur (*Calcarius ornatus*; $n = 219$; $R = 0.785$; $P < 0.001$; b) nestlings measured during three breeding seasons from 2013 to 2015 in Brooks, Alberta, Canada.

LITERATURE CITED

Akaike, H. 1974. A new look at the statistical model identification. IEEE Transactions on Automatic Control 19:716–723.

Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's information criterion. The Journal of Wildlife Management 74:1175–1178.

Bolker, B. M., M. E. Brooks, C. J. Clark, S. W. Geange, J. R. Poulsen, M. H. H. Stevens, and J. S. S. White. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology & Evolution 24:127–135.

Davis, S. K., and D. C. Duncan. 1999. Grassland songbird occurrence in native and crested wheatgrass pastures of southern Saskatchewan. Studies in Avian Biology 19:211–218.

Dinsmore, S. J., G. C. White, and F. L. Knopf. 2002. Advanced techniques for modeling avian nest survival. Ecology 83:3476–3488.

Jones, S. L., and G. R. Geupel. 2007. Beyond Mayfield: Measurements of nest-survival data. Studies in Avian Biology No. 34, Cooper Ornithological Society, Camarillo, CA.

Jongsomjit, D., S. L. Jones, T. Gardali, G. R. Geupel, and P. J. Gouse. 2007. A guide to nestling development and aging in altricial passerines. USDI, Fish and Wildlife Service, Biological Technical Publication FWS/BTP-R6008-2007. Washington, D.C.

Littell, R. C., G. A. Milliken, W.W. Stroup, R. D. Wolfinger, and O. Schabenberger. 2006. SAS for mixed models. SAS Institute Inc., Cary, NC, USA.

Ludlow, S. M., R. M. Brigham, and S. K. Davis. 2014. Nesting ecology of grassland songbirds: effects of predation, parasitism, and weather. The Wilson Journal of Ornithology 126:686–699.

Madden, E. M., R. K. Murphy, A. J. Hansen, and L. Murray. 2000. Models for guiding management of prairie bird habitat in northwestern North Dakota. The American Midland Naturalist 144:377–392.

Mundry, R. 2011. Issues in information theory-based statistical inference—a commentary from a frequentist's perspective. Behavioral Ecology and Sociobiology 65:57–68.

Peig, J. and A. J. Green. 2009. New perspectives for estimating body condition from mass/length data: the scaled mass index as an alternative method. Oikos 118:1883–1891.

Peig, J. and A. J. Green. 2010. The paradigm of body condition: a critical reappraisal of current methods based on mass and length. Functional Ecology 24:1323–1332.

Quinn, G. P., and M. J. Keough. 2002. Experimental design and data analysis for biologists. Cambridge University Press, New York, NY, USA.

Ranellucci, C. L., N. Koper, and D. C. Henderson. 2012. Twice-over rotational grazing and its impacts on grassland songbird abundance and habitat structure. Rangeland Ecology & Management 65:109–118.

SAS Institute, Inc. 2012. SAS Statistical Software. Version 9.4. SAS Institute, Cary, North Carolina, USA.

Shaffer, T. L. 2004. A unified approach to analyzing nest success. The Auk 121:526–540.

Shaffer, T. L., and Thompson, F.R. (2007). Making meaningful estimates of nest survival with model-based methods. Studies in Avian Biology 34, 84–95.

Taylor, B. L., and T. Gerrodette. 1993. The uses of statistical power in conservation biology: the Vaquita and Northern Spotted Owl. Conservation Biology 7:489–500.

Venables W. N., and B. D. Ripley. 2002. Random and mixed effects. Pages 271 – 300 *in* W. N. Venables, and B. D. Ripley, editors. Modern applied statistics with S. Statistics and Computing. Springer, New York, NY, USA.