

Variation in song characteristics and responses to anthropogenic noise of Lincoln's Sparrow (*Melospiza lincolnii*) in the boreal forest

by

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## **Abstract**

The study of avian vocalizations intrigues humans in many ways, in part because song production has many similarities with human speech. Since the development of technologies to record and analyze songs, the study of avian vocalizations has provided insights into song learning and its function in animal communication. One of the initial observations was the geographic variation of songs within the same species, which led to the finding of song learning being mediated by social interactions. Past studies showed that songbirds are capable of adapting their songs both in evolutionary time and within their lifetimes. Natural conditions can also influence song features; for example, vegetation acts as a selective force shaping the acoustic features of songs. In recent years, there has been increasing awareness about the effect of anthropogenic noise on animals that rely on acoustic signals for communication. The general responses to noise described for birds in the field are a decrease of species richness close to the noise source, changes in avian assemblages, and behavioural changes in even tolerant species. The main objective of this thesis was to investigate what factors influence the persistence of a common sparrow species, the Lincoln's Sparrow (*Melospiza lincolnii*), in environments modified by industrial activities, particularly with noise. The objectives of my thesis were to: 1) quantify the geographic variation of Lincoln's Sparrow songs and the variation associated with vegetation structure; 2) determine if the occupancy of Lincoln's Sparrow differs in areas with industrial noise compared to less disturbed, quiet areas; and 3) identify which vocal traits are associated with persistence of Lincoln's Sparrow in noisy environments.

To address the first objective, I studied the geographic variation of Lincoln's Sparrow songs in natural conditions using recordings obtained with autonomous recorders units (ARUs) in

Alberta, Canada. I created a song catalogue of 74 individuals, compared syllable sharing between individuals from different locations across Alberta using spectrograms, measured acoustic features of songs, and classified shared and unshared syllables. I described the relationship between acoustic features of songs and proportion of vegetation along a spatial distance of 795.2 km. I found that Lincoln's Sparrow had songs with higher frequencies and wider bandwidths in areas with a higher proportion of open areas and deciduous forest. Unshared syllables were lower in frequency in areas with denser vegetation.

To address the second objective, I estimated the occupancy of Lincoln's Sparrow along a gradient of industrial noise created by the oil gas industry in Northern Alberta, Canada. Using ARUs, I detected the locations where the species was present. I also developed novel methods to obtain relative measurements of noise amplitude from sound files recorded by ARUs. Lincoln's Sparrow occupancy slightly decreased in the gradient of noise. Individuals seem to tolerate certain levels noise and also are attracted to the open habitats that are associated with infrastructure created by the energy sector, which typically includes combinations of remnant forest and open areas with scattered shrubs.

To address the third objective, I studied vocal responses to chronic industrial noise generated by compressor stations. I recorded 15 Lincoln's Sparrow males close to compressor stations and 15 males in quiet areas, using two methods: manual recorder and ARUs deployed on their singing perch and on the nearest shrub to the singing perch. I obtained acoustic features of 400 songs (high frequency, low frequency, bandwidth, and peak frequency), song length, singing rate, and song relative amplitude. I found that singing rate and relative amplitude of songs were higher in noisy areas. I performed a song attenuation test of a Lincoln's Sparrow song at different distances (0 - 50 m) and heights (1.5, 2.5, 3.5 m) in a noisy and a quiet area. I found increased

attenuation as distance increased relative to the control, suggesting a new selection pressure for short distance communication in noisy areas.

In conclusion, I showed for the first time high geographic variation in Lincoln's Sparrow song associated with variation in vegetation structure in natural settings. In the oil sand industries, Lincoln's Sparrow was detected in open areas that also have industrial noise, showing a tolerance to inhabit areas influenced by anthropogenic noise. This tolerance for anthropogenic noise may be facilitated by increasing the singing rate and the amplitude of their songs.

## **Preface**

This thesis is an original work by Natalie V. Sánchez. For Chapter 4, the data collected was under the University of Alberta Animal Care and Use Committee (ACUC) guidelines under the permit number: AUP00001523. The bird-banding component was under the scientific permit to capture and band migratory birds 10277 AM.

Chapter 2 of this thesis will be submitted for publication to the Journal of Field Ornithology. This article will include Branko Hilje (BH) and Erin M. Bayne (EMB) as co-authors. Natalie V. Sánchez (NVS) proposed the study, analyzed the data, and wrote the manuscript with input from EB. BH collected and analyzed additional data. All authors contributed with manuscript revisions.

Chapter 3 of this thesis will be submitted for publication to Frontiers in Ecology and Evolution, Advances in Ecoacoustics. This article will include Luis Sandoval (LS), Richard Hedley (RH), and Colleen C. St. Clair (CCSC), and Erin M. Bayne (EMB) as co-authors. For this study, Natalie V. Sánchez (NVS) proposed the focus of the manuscript, collected part of the data in the field, analyzed the occupancy and noise data, and wrote the manuscript with input from EB and CCSC. EB designed the study and provided funding. LS and NVS designed the method to measure noise and analyzed part of the noise data. RH organized and analyzed data. All the authors contributed to manuscript revisions.

Chapter 4 of this thesis will be submitted for publication to Ornithological Applications and will include Erin M. Bayne (EMB) as co-author. For this study, Natalie V. Sánchez (NVS) proposed the study, banded the birds, recorded the songs, deployed autonomous recorders, analyzed the data, and wrote the manuscript with intellectual and financial support from EB.

## Dedication

I dedicated this thesis to my Granma Carmen Porras (1930-2019) and my Grandpa Carlos Sánchez (1926-2003) who kindly taught me values and supported me through my education. To my dog Dante, he is a breath of fresh air and love in my life.

*The common organisms are the most interesting ones.*

*Los organismos comunes son los más interesantes.*

## **Acknowledgements**

I thank my supervisor Dr. Erin M. Bayne for giving me the opportunity to join his lab and pursue my dream of doing research in bioacoustics and to support me through all these years. I also appreciated the permission to continue with the graduate program from Costa Rica during this difficult time, which was fundamental to succeed in my graduate studies. I thank my two wonderful Committee Members, Dr. Colleen Cassady St. Clair and Dr. Kimberley Mathot for all the discussions about my project, new methodologies, and science. You both have been a source of inspiration to me and I look forward to continue collaborating in the future. I thank Dr. Christopher Sturdy and Dr. Ken A. Otter for being my external examiners.

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challenging time of my life as a field biologist there, but at the same time it was an incredible learning experience that I accomplished thanks to you all of you. I thank Ronena Wolach and Zachary Davis who gave me support and motivation during the online portion of the doctoral program; it was very nice to have you there virtually to overcome the challenges of teaching and writing the thesis from home.

I thank to my collaborators Luis Sandoval, Richard Hedley, and Branko Hilje. With your support and knowledge, I complemented fundamental parts of this thesis. Luis Sandoval helped me to develop a methodological approach to measure noise levels from uncalibrated recordings. Richard Hedley provided advice on data analysis and editorial comments. Branko Hilje helped me create a song catalogue for my study species, collect data, and provided editorial comments on this thesis. Daniel Mennill and Luis Esteban Vargas-Castro offered insights on syllable variation on my study species and provided thoughtful recommendations on singing behaviour and sound transmission in songbirds. Dan Mennill has also given me support to continue studying bird songs and finish this thesis. Corrina Copp facilitated access to geographic locations of the recording sites and vegetation layers from the Alberta Biodiversity Monitoring Institute. Lionel Leston provided information about GIS vegetation layers and helped with data extraction. Hannah Stormer helped obtaining the initial measurements of noise.

I want to especially thank my field assistants Natalia Liftshifz, Branko Hilje, and Cassidy Bodnar. Thanks Nata for banding birds, recording Lincoln's Sparrows, spending an entire summer season with me in Lac La Biche, and for being my friend. That was an amazing time. Branko helped me to perform the playback experiment in very noisy compressor stations and Cassidy helped me during in 2017 to deploy 100 autonomous recorders plus the mini grids in the

boreal forest. I am very thankful to Branko Hilje who started this journey with me (and Dante) and continues to support me as a trusted friend and colleague.

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Finally, I want to thank the *Melospiza lincolnii* (Lincoln's Sparrow) individuals who gave me the opportunity to learn the way they sing and live in a very remote location in the boreal forest, where I had never imagined doing what I really love, understanding the secret lives of birds and their songs.

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## Chapter 1. Introduction

### **Acoustic communication in birds and anthropogenic noise**

The signal transmission of bird songs and the environmental conditions affecting song are key factors in their cultural evolution (Morton 1975, Wiley and Richards 1982). The sounds emitted by birds are molded by structural features (vegetation type), abiotic (wind, rain, and flowing water), and biotic factors (other animal sounds) that degrade signals and affect localization ability (Catchpole and Slater 1995). For these reasons, birds have evolved vocal behaviors that maximize signal transmission in their preferred habitat, especially in mating contexts (Endler 1992, Patten et al. 2004). For songbirds, the effective transmission of song is fundamental to maintain territories, particularly during male-male interactions, and to attract potential mates (Eriksson and Wallin 1986). There is strong evidence of natural selection optimizing song characteristics to enhance transmission for the conditions the bird is most likely to live in (Catchpole and Slater 1995). Although recent evidence challenges the role of vegetation structure shaping the acoustic features of songs (Mikula et al. 2021), vegetation acting as vertical obstruction does decrease sound transmission (Boncoraglio and Saino 2007, Graham et al. 2017); thus, there is considerable value in studying song communication in different physical and acoustic contexts.

Beside the natural conditions affecting bird song transmission, the noise created by humans (cities, industry) may reduce or interfere with the acoustic signal by overlapping partially or completely with bird songs (Shannon et al. 2015, Francis et al. 2017). Over the past decade, there has been a growing awareness about the environmental effects of anthropogenic

noise on animals, especially songbirds (Knight and Swaddle 2011, Shannon et al. 2015, Buxton et al. 2019). Songbirds comprise one of the most studied groups of animals in the context of noise because their communication includes extensive acoustic signals. Most research has focused on the effects of urban noise on passerine birds (Slabbekoorn and Ripmeester 2008), with some research on chronic industrial noise and its effects on species that inhabit adjacent landscapes (Bayne et al. 2008, Francis et al. 2009, Blickley and Patricelli 2012).

In Alberta, noise generated by energy infrastructure can reduce the quality of adjacent habitats if noise alters the soundscape to the point that songbirds avoid noisy areas. Bayne et al. (2008) published the only work to date on the effects of chronic noise on multiple bird species in the oil sands region in Alberta and found that many species in noisy areas dominated by mature aspen forests were less likely to occur. Additionally, one species (the Ovenbird, *Seiurus aurocapilla*) evaluated in the same area had lower reproductive success near noisy areas (Habib et al. 2007). In general, songbird species seem to respond to noise by avoiding noisy areas, which results in declines in species richness or abundance (Reijnen et al. 1996, Forman et al. 2002, Perillo et al. 2017, Carral-Murrieta et al. 2020). However, this research also revealed that not all species are affected to the same degree. There is little information on how vegetation structure, habitat preference, morphology, and song plasticity interact to influence the transmission of songs in noisy conditions. Therefore, our understanding of the mechanisms that allow some species to persist in noisy environments remains uncertain.

It has been reported for some songbirds in urban areas that they shift the low frequency part of the song to higher frequencies, or an increase in the amplitude of their vocalizations to avoid acoustic interference with the ambient noise (Wood and Yezerinac 2006, Luther and Baptista 2010, Proppe et al. 2012). Songs with higher minimum frequencies suffer less acoustic

interference because anthropogenic noise typically occupies low frequencies on the sound spectrum (< 2 kHz) (Lohr et al. 2003). Birds that are able to do this seem to be more likely to persist in human dominated environments although there are few explicit tests (Proppe et al. 2013). Urban bird songs have higher minimum frequencies, apparently in response to higher levels of low-frequency noise in comparison with rural birds (Patricelli and Blickley 2006, Wood and Yezerinac 2006, Proppe et al. 2012). In addition, singing at higher perches is another strategy reported to avoid interference with busy roads in urban areas (Polak 2014). It is expected that birds in noisier urban environments might experience stronger selective pressure to change their songs and modify their singing behaviours than rural birds (Chilton and Lein 1996, Luther and Baptista 2010). Changes in song characteristics have not been as well addressed in the case of chronic industrial noise.

Some species that remain in the areas influenced by chronic noise seem to adjust their songs to increase transmission. However, this pattern is not consistent for all species. Two related passerine birds, Plumbeous vireo (*Vireo plumbeus*) and Grey vireo (*Vireo vicinior*) adjusted their song in two different ways; Plumbeous vireos increased their minimum frequencies, and Grey vireos increased their maximum frequencies (Francis et al. 2011). Suboscine songbirds with less plastic songs, like the Grey flycatchers (*Empidonax wrightii*) did not change their frequency while the ash-throated flycatcher (*Myiarchus cinerascens*) only had a marginal increase in their song frequency (Francis et al. 2010). Oscine birds in grasslands, responded to industrial infrastructure by changing the frequency of their songs, with Savannah Sparrow (*Passerculus sandwichensis*) increasing and Baird's Sparrow (*Ammodramus bairdii*) decreasing (Curry et al. 2018). Because songbirds' vocal adaptations are not consistent yet in the context of chronic noise, exhibiting different capacities to adjust, we still lack the knowledge to

predict which species may be able to deal with noise. Thus, we need to study what traits give an advantage in noisy conditions. In general, species capable of song learning seem to be consistent in their response to noise, shifting the lower part of their songs to increase transmission (Wood and Yezerinac 2006, Luther and Baptista 2010, Derryberry et al. 2020).

Lincoln's Sparrow (*Melospiza lincolnii*) is an ideal candidate species to examine vocal responses to chronic noise conditions. In Alberta, Lincoln's Sparrow, an oscine songbird, inhabit areas with vegetation disturbed by human activities (Figure 1.1), which in turn means they are more likely to be exposed to chronic noise (Bayne et al 2016), learn their song from conspecifics, and has a medium high complex song defined as a multi-syllabic song (1–16 variants, males can perform from 1 up to 6 song types, mean repertoire 3.7 types) with a frequency range from 1.5 to 7.5 kHz (Cicero and Benowitz-Frederick 2000). As stated above, complex songs and potential vocal plasticity might be traits that allow adaptation to noise. Given their vocal flexibility, I hypothesized Lincoln's Sparrow would be able to adjust their songs to songs that transmit better in noisy environments. I predicted an increase in the low frequency part of their songs as this pattern has been observed in similar species with high vocal plasticity (Wood and Yezerinac 2006, Derryberry 2009, Luther and Baptista 2010). Another potential adjustment might be the use of syllables with narrower bandwidth (the difference between high and low frequency). Low frequency modulated songs are better transmitted than high frequency modulated songs in forest habitats (Derryberry et al. 2018). Therefore, narrower bandwidths are expected in noisy conditions. Finally, this selection of syllables might reduce the number of syllables used in noisy areas in comparison to quiet areas, resulting in simpler songs. Changes in song characteristics are not the only way that species may react to noise. Changes in space use in noisy areas and/or

adapting behaviors to maximize sound transmission are alternative strategies that also need to be investigated.

### **Summary of thesis objectives and methodologies**

I assessed the occupancy and vocal responses of a common songbird currently dealing with chronic industrial noise, Lincoln's Sparrow, to contribute to understanding of traits that could reveal mechanisms that potentially allow species to persist in an increasingly noisy environment.

#### ***Specific objectives***

1. Describe Lincoln's Sparrows' song variation in Alberta.
2. Estimate the relative importance of vegetation and noise associated with industrial activities on the occupancy of Lincoln's Sparrow in Alberta.
3. Measure vocal behavioural responses to chronic industrial noise on Lincoln's Sparrow.

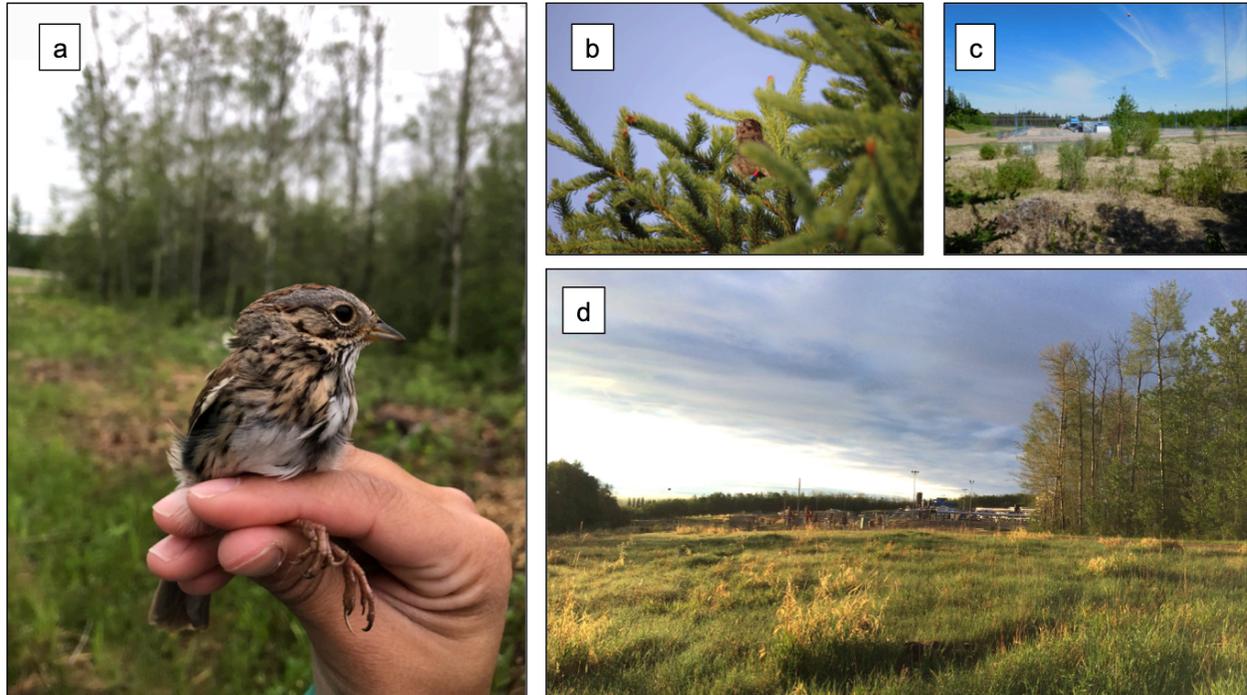
In Chapter 2, I created a catalogue of Lincoln's Sparrow songs and syllables types in Alberta generated from spectrograms (Raven Pro 1.5); songs were recorded using autonomous recording units (ARUs) in 2016 and 2017. I also measured acoustic features of songs (high frequency, low frequency, bandwidth, and length) using a power spectrum view (considering amplitude and frequency) testing for potential differences explained by vegetation type (grass, shrubs, deciduous forest, mixed-woods, and conifers) extracted from GIS layers. Finally, I compared acoustic features of shared and un-shared syllables of songs between vegetation types.

In Chapter 3, I modeled the relative importance of disturbances created by the oil and gas industry, vegetation, and industrial noise to explain Lincoln's Sparrow occupancy in Northern

Alberta, Canada. In a systematic design of 280 ARUs deployed in three areas with high, medium, and low levels of industrial disturbances, I estimated Lincoln's Sparrow occupancy and detection probability using a detection history of 3 days of acoustic survey. To include industrial noise in the models as a predictive variable, I developed a method to extract relative amplitude values from un-calibrated recordings. This method consists of selecting areas of the power spectrum view (using Raven Pro 1.6) that does not have other bird or insect vocalizations and measures noise at 8 frequency octave bands (500, 1000, 2000, 4000, 8000, and 16000 Hz). Anthropogenic noise usually is concentrated below 2 kHz; however, masking and background noise expand to higher frequencies in the acoustic spectrum.

In Chapter 4, I addressed the vocal responses of Lincoln's Sparrow to chronic industrial noise. For this, I manually recorded Lincoln's Sparrow males singing in areas close to compressor stations in Northern Alberta, Canada. Compressor stations are part of the transportation system of oil and gas and are active year-round (producing noise that can reach 109 dB). At five compressor stations, I recorded 15 males and compared their vocal features with males recorded at least 800 m from the compressor stations in quiet areas (males were recorded haphazardly). Additional recordings were obtained using ARUs deployed on the singing perch or to the nearest shrub from the singing perch. I compared acoustic features of songs (high frequency, low frequency, bandwidth, and peak frequency), song length, singing rate, and number of song types between sites. I obtained the acoustic measurements using the power spectrum view (Raven Pro 1.6). In addition, I performed a sound attenuation test of the transmission of a Lincoln's Sparrow song at various distances (5, 10, 20, 30, 40, and 50 m) and heights (1.5, 2.5, and 3.5 m) in areas influenced by chronic noise.

I conclude my thesis by discussing the most important findings and framing them in the context of increased environmental transformations by humans. I emphasized specifically the acoustic environment, which challenges adaptations of declining wild birds.



**Figure 1.1.** a) Lincoln's Sparrow (*Melospiza lincolnii*) captured near a noisy compressor station in Northern Alberta, Canada. b) Lincoln's Sparrow (color-banded individual) singing at the top of a young spruce. c) Open areas with sparse shrubs next to a compressor station surrounded by conifers. d) Open areas and aspen forest with grass and shrubs next to a compressor station.

## Chapter 2. Geographic song variation in Lincoln's Sparrow (*Melospiza lincolnii*): Is vegetation structure shaping the acoustic features of songs?

### **Abstract**

Song variation within passerine birds has typically been explained by social interactions or local adaptations to a particular environment. In sparrows, there is evidence of songs being adapted to be more effectively transmitted and received in certain vegetation structure. For a less studied sparrow, the Lincoln's Sparrow (*Melospiza lincolnii*), we aimed to describe the variation in songs across different ecosystems using autonomous recording units deployed in Alberta, Canada. To explain differences in acoustic features across the province, we used geographic location of songs and vegetation structure. For this, we first created a song catalogue to classify song types and syllable types. Then, we measured the acoustic structure of songs and unique syllables found for each male using spectrogram and power spectra analyses. We performed multivariate analysis testing for the effect of space and vegetation on acoustic features. We identified 74 individuals, 116 song types, and 151 syllable types. We did not find evidence of geographic structure in terms of song types, with Lincoln's Sparrows having high syllable sharing across Alberta. However, individuals sang higher-frequency songs in open areas with more grass and shrubs. Finally, unique syllables were lower in frequency in coniferous forest (denser vegetation). Therefore, Lincoln's Sparrow seems to adjust their songs by vegetation type. This study is a contribution to the understanding of song variation of a common sparrow at a large geographic scale.

## **Introduction**

Songbirds have the ability to sing a variety of songs ranging from very simple to highly complex. This variation is associated with different learning capacities; species that learn songs from tutors (Marler 1970; Mennill et al. 2018) having higher song complexity than species with innate songs (Nottebohm 1969). Consequently, individuals learning songs from conspecifics tend to have a larger repertoire size, especially when the learning period is not fixed to a short stage in time (Catchpole and Slater 2008). Song variation in some species is even flexible in the sense that an adult bird can create new songs by combining syllables and elements they hear from other individuals they interact with (Brenowitz and Beecher 2005). There are advantages to sharing song among conspecifics such as greater stability in territory tenure by decreasing aggressive physical encounters with neighbours (Hughes et al. 1998; Beecher et al. 2000) and similar mating success by sharing the song of the most attractive males in the population (Krebs et al. 1978; McGregor and Krebs 1982). As distance between territories increases, song sharing tends to decrease as a result since individuals are less likely to interact (Catchpole and Slater 2008). This pattern is then observed between populations, resulting in a spatial structure of song types with fewer elements of songs shared as the distance between populations increases.

Besides social interactions drawing geographic patterns of vocal variations, territoriality and female choice regulate the amount of similarities in song structure and the acoustic properties within individuals (Baker and Cunningham 1985, Slabbekoorn and Smith 2002a, Baker 2006). Songbird species that migrate and return to similar habitats for reproduction could benefit from maintaining similar song structure as a function of the habitat they select (Slabbekoorn and Smith 2002b) and potentially adapting their song to fit that environment (Wiley and Richards 1982). Songs target a receiver, thus songbirds within the same population

should also share songs with similar acoustic structure (e.g. frequency and bandwidth) to improve transmission in that local environment (Morton 1975; Wiley and Richards 1978). Furthermore, the local characteristics of the site, such as vegetation, wind, and even new sounds and noises created by humans could alter the songs that birds will sing (Derryberry et al. 2020). As human disturbances increasingly alter the environmental conditions where birds breed, it is expected that local adaptations to particular habitats will occur, especially in songbirds with high vocal flexibility.

Sparrows are well studied in terms of song sharing both within and between populations (Baptista 1977; Stoddard et al. 1991; Bell et al. 2003). Numerous studies have also assessed if their songs are adapted to transmit in different environments (Tubaro et al. 1993; Derryberry 2009). It is also known that there is a high degree of variation in song complexity between different sparrow species. For example, in the genus *Melospiza*, the Swamp Sparrow (*Melospiza georgiana*) has a simple-syllabic song with a limited number of repeated syllables that vary relatively little over space (Marler and Pickert 1984). Conversely, the Song Sparrow (*M. melodia*) has a multi-syllabic song and individuals sing various song types with high number of different elaborated elements (Hiebert et al. 1989). On a large geographic scale, Swamp Sparrow share many syllables, because of their simple songs (Marler and Pickert 1984). In Song Sparrow, despite high song complexity, distinct songs were found in different populations (Peters et al. 2000), which means less syllable sharing. Lincoln's Sparrow (*M. lincolni*) has an intermediate repertoire size compared with their sister species. Male Lincoln's Sparrows in similar vegetation conditions shared more songs within populations than between populations in three regions of California (Cicero and Benowitz-Fredericks 2000). Clearly, variation in song complexity could lead to observation of structure patterns at different geographic scales, however, for Lincoln's

Sparrow it is unknown how its song changes (syllable sharing and acoustic structure) when populations breed in different environments at farther distances and larger geographic scales.

Our objective was to assess the relative importance of vegetation type and spatial distance as predictors of Lincoln's Sparrow song variation along a spatial distance ~ 800 km in the boreal forest and foothills regions of Alberta, Canada in different vegetation conditions. We described variation in songs, syllables, and acoustic features using data obtained with autonomous recording units (hereafter ARUs). If there is high site fidelity after breeding and low dispersal of individuals in Lincoln's Sparrow populations (Wilson et al. 2000; Vargas-Castro 2015), we expected a decrease in syllable sharing as distance between recording sites increased. Based on the acoustic adaptation hypothesis (Morton 1975; Brown and Handford 2000), we expected Lincoln's Sparrow to have lower frequency songs in dense vegetation (with leaves, branches and, tree trunks) to minimize degradation and increase transmission (Morton 1975; Marten et al. 1977; Boncoraglio and Saino 2007). We also predicted that unique syllables in Lincoln's Sparrow songs might be more adjusted to vegetation type (i.e. low-frequency in denser sites) to increase transmission of unique song features to conspecifics (Wilson and Mennill 2010, Osiejuk 2014). This study contributes to the understanding of song variation of an overlooked sparrow species.

## **Methods**

### ***Study species***

Lincoln's Sparrow (hereafter LISP) is a common North American breeding bird, which migrates during the winter to southern United States, Mexico, and Northern Central America (Sibley 2014). In Northern Alberta, LISP has a higher density in larch (*Larix laricina*) and black spruce (*Picea mariana*) forests (ABMI 2018). In subalpine and mountain regions, they are found in boggy meadows with dense shrub cover (Ammon 1995). LISP is highly territorial during the breeding season, and males sing from conspicuous perches (Ammon 1995; Cicero 1997). Cicero and Benowitz-Fredericks (2000) described the mean repertoire size for 58 individuals and found an average repertoire consisted of 3.7 song types with 2.6 variants per song, from three different populations in insular mountain meadows in California. Individuals males can be identified easily by their position in the singing perch (Cicero 1997), therefore a male singing close to a recording device is very likely to be the same individual on consecutive days.

### ***Song recording***

LISP songs were obtained from recordings of autonomous recording units (ARUs, model SM4 developed by Wildlife Acoustics) deployed from mid May to mid July 2016-2017 in Alberta, Canada (Figure 2.1) as part of a general avian monitoring program run by the Alberta Biodiversity Monitoring Institute ([www.abmi.ca](http://www.abmi.ca)). The SM4 recorders have two omni-directional microphones (SMM-A1 sensitivity:  $-4 \pm 3$  dB,  $0 \text{ dB}=1\text{V}/\text{pa}$  at 1kHz), recording in stereo format at 44.1 kHz with a 16-bit resolution in a WAV format. We used a recording scheduled synchronized at 0500 h, which matches the highest peak of vocal activity of most boreal birds.

A database where the species are identified by expert transcribers was searched to find Lincoln's Sparrow detections (1532 detections in 2016-2017). We only used those that were deemed close to the ARU by the transcribers. From this list, we selected 100 sites including 200 recordings with LISP detections. At this step, the geographic location of the site associated to each recording was unknown.

We then processed those recordings with a LISP by visually identifying individuals in the spectrogram; a song or multiple songs with similar amplitude values were assigned to an individual in a 10 min recording. We identified 74 individuals. Relative amplitude measurements were obtained with Raven Pro 1.5 (Bioacoustics Research Program 2014—The Cornell Lab of Ornithology), LISP detections in the database with songs lower than 40 dB were excluded. On three occasions, we identified two different LISP individuals in the same recording by looking at the spectrogram view where we found two different songs with varying strengths on each channel at similar times. This indicates that two birds were singing from different locations near the same ARU, therefore, these songs were included in the analysis as produced by different individuals. Visual identifications of the songs were performed with Audacity(R) recording and editing software version 2.2.1 (Audacity Team) and Raven Pro 1.5 (Bioacoustics Research Program 2014—The Cornell Lab of Ornithology).

### ***Syllable classification and analysis***

We then generated and analysed spectrograms of the recordings using Raven Pro 1.5 (Bioacoustics Research Program 2014—The Cornell Lab of Ornithology). All the spectrograms were generated with Hann window type, 700 samples, and a discrete Fourier transform (DFT)

size of 2048 samples with a temporal overlap of 75%. The Lincoln's Sparrow songs were detected visually on at least two different 10- minute recordings per location. The spectrogram was visually inspected to identify song types, song variants, and syllable types of each male.

Syllables were observed and classified based on characteristics showing a specific pattern in the frequency-time domain of the spectrogram. Each syllable belonging to a specific song was saved as an image (.jpeg). Then we created a catalogue using all the images of syllables based on visual inspection of the spectrogram. In addition, a person not familiar with the LISP songs classified the syllables, and then we compared them all with syllables in the catalogue. This approach to syllable type identification has been used in similar studies of song classification (Molles and Vehrencamp 1999; Vargas-Castro et al. 2015). We created a dissimilarity matrix after running a spectrogram correlation analysis using Raven Pro 1.5, where we compared syllables of songs that came from different individuals at different ARUs. This analysis compares the spectrographic signal (frequency and time) of each syllable against each other. The output of the test is a comparison matrix of values ranging from 1 to 0, with values close to 1 being similar syllables and close to 0, different syllables. We used a band-pass filter of 1000-8000 Hz to eliminate noise interference outside the songs' frequency range (Vargas-Castro et al. 2015). Using Non-Metric Multidimensional Scaling (vegan R package, Oksanen et al. 2016), we confirmed syllable classification in specific types for the syllables shared between males (Figure 2.2). In cases where the different observers differed in syllable classification, we discussed and achieved consensus classifying the syllables despite slight variations in their acoustic features such as frequency or length (Figure 2.3).

### *Acoustic features*

We measured the following song characteristics of LISP song: the lowest frequency of the song (Hz), highest frequency (Hz), bandwidth (Hz), bandwidth of the first syllable (Hz), maximum power (dB), length (s), and total number of syllables per song. The same spectrogram settings described for syllable classification were used for the power spectrum view generated in Raven Pro. We measured the song features mentioned above using the threshold method (Podos 1997, Ríos-Chelén et al. 2017), for three songs per song type per individual. To obtain the acoustic features of the syllables, we selected the first LISP song detected in the recording and measured the same acoustic features described above (highest and lowest frequency, bandwidth, and length). In total, we measured the acoustic features of 262 syllables.

### *Statistical analysis*

#### *Syllable sharing*

We compared the syllables per individual to assess song structure with a cluster analysis using the R package *ecodist* (Goslee and Urban 2007). The cluster analysis used all of the syllables found per song per male by finding distinct clusters groups of shared syllables. Second, to account for the fact that we may not have recorded the entire repertoire of the males, we evaluated syllable sharing only using the syllables found in the first song detected in each recording using a similarity index. We assumed the syllables in the first song represented a random sample of all the syllables possible at a population level.

The similarity index used was the Sørensen coefficient:  $(2a)/((2a+b+c))$  where a=number of syllables shared by two males, b=unique syllables of the first male, c=unique syllables of the second male. The index gives a value between 0 and 1, 1 indicating the two males share all syllables. Then, we performed a Mantel test of the dissimilarity matrix created when comparing all the syllables found in the first song for each male against the rest of the males' songs with the distance matrix of the geographic distances where the males were located (Supplementary Appendix I). The geographic distances were calculated using the R package geosphere (Karney 2013) and the Mantel's test using the R package vegan (Oksanen et al. 2016). R 4.0.4 software (R Core Team 2020) was used to perform all the analyses.

### *Acoustic features*

To test for spatial patterns in the acoustic features of LISP songs, we ran an indirect gradient analysis using latitude, longitude, and vegetation. For this, we use the R packages ecodist (Goslee and Urban 2007) and vegan (Oksanen et al. 2016). Additionally, to test for differences between geographic locations (individual breeding in Northern vs Southern latitudes), we performed a Non-Metric Multidimensional Scaling and calculated a PERMANOVA test. Northern and Central Alberta is dominated by boreal forest while the more southerly areas studied were in the mountains, foothills, parkland, and grassland ecoregions (Eberhart and Woodard 1987; Larsen 1997). Northern ARU locations (above 56°00'00") correspond to the boreal ecoregion, whereas more southerly latitudes included boreal forest and foothills (Natural Regions Committee 2006).

For the vegetation variables, we extracted the dominant vegetation type at each site (50 m buffer) from the ABMI vegetation data (wall-to-wall Vegetation Inventory 2015) using ArcGIS 10.3.1 (Environmental Systems Research Institute, Inc., Redlands, California, USA). We performed a Non-Metric Multidimensional Scaling to determine if the acoustic structure of LISP differed between vegetation types using the vegan package (Oksanen et al. 2016) and a PERMANOVA test. Additionally, we calculated the proportion of coniferous forest, deciduous forest, mixed-wood, shrubs, grass, and marsh present from the Alberta Vegetation Inventory (AVI) within each 50 m buffer around the ARU where LISP were recorded. Coniferous forest is the forest type with the highest density of trees per area in comparison to the other habitat types. We performed an indirect gradient analysis to test the effect of the proportion of forest/vegetation types present around the ARU influenced the acoustic structure variables from LISP.

Finally, we evaluated the acoustic features of the syllables in different vegetation types. We calculated a multi-way ANOVA for high frequency, low frequency, bandwidth and length of the syllables, also taking into account whether the syllables were shared or unshared by the males. To reduce the number of levels, we grouped the vegetation types into three categories: conifer, other-forest (deciduous and mixed-wood), and open areas (shrubs, grass, and marsh). We performed a post-hoc Tukey's HSD test for multiple comparisons. The data for this analysis had normally distributed residuals (Shapiro-Wilk normality test:  $W = 0.98$ ,  $P = 0.052$ ) and homogeneous variance (Levene's test:  $F_{2,256} = 2.054$ ,  $P = 0.07$ ). All the analyses were performed using R 4.0.4 software (R Core Team 2020).

## Results

### *Syllable sharing*

We identified 74 individuals and 116 song types in the dataset. Most of the males sang 1 or 2 song types per 10 min period. We also identified 7 cases of song variants for 5 males; a song variant was defined as a song that has at least three syllables repeated at the beginning and additions/deletions of syllables at the end. For males singing more than one song, the number of songs varied from 1 to 3 song types and from 1 to 3 variants. We identified 151 syllable types. The average number of syllables was 6.5 syllables  $\pm$  1.4 ( $\pm$ SD), ranging from 4 to 10 syllables in a given song (Figure 2.4).

Most of the males sang unique syllables, but they did share some syllables with other individuals (Figure 2.4). Males singing at closer locations shared from 2 to 4 syllables at the beginning of the song. Syllables shared at larger distances were located at the end of the song (i.e. syllable 16 shared by 10 males). However, we did not find evidence of clusters in terms of the number of syllables shared by the males in the study area, the dissimilarity matrix of the syllables did not have a relationship with the geographic separation of the samples (Mantel test  $r = 0.052$ ,  $P = 0.168$ ). Therefore, as samples became physically more separated their corresponding syllables did not necessarily become more dissimilar (Figure 2.5).

### *Acoustic features*

LISP song varied in their acoustic features across the latitudinal range. Latitude was better predictor than longitude of the variation of the acoustic features ( $P = 0.04$ ). Individuals singing

in the Southern locations had a larger bandwidth and the highest part of their songs was higher in frequency than in Northern locations (Figure 2.6). We also identified two different groups in terms of variation in acoustic structure for Northern and Southern individuals (PERMANOVA,  $F_{1,73} = 9.29$ ,  $P = 0.02$ ). On average, LISP singing in Northern sites has shorter bandwidth and the high frequency part of their song was lower.

We did not find associations between bandwidth, total length, or song frequencies (highest or lowest part of the song) with the dominant vegetation type (PERMANOVA,  $F_{4,73} = 0.523$ ,  $P = 0.773$ ). However, the proportion of forest was important in explaining LISP song variation. LISP songs were higher in frequency, and had wider bandwidth in deciduous and mixed-wood forest (Figure 2.7) than in conifers. Individuals singing in open habitats, such as grass-dominated areas, had songs with lower frequencies than those in deciduous and mixed-wood forest (Figure 2.7).

We found that unique syllables sang in conifers (denser vegetation) had lower frequencies in both low ( $F_{1,256} = 14.93$ ,  $P = 0.0001$ ) and high ( $F_{1,256} = 21.46$ ,  $P < 0.0001$ ) frequency parts of the songs, and lower bandwidth ( $F_{1,256} = 15.327$ ,  $P = 0.00012$ , Table 2.1, Figure 2.8). Syllable length was similar between unique and shared syllables ( $F_{1,256} = 0.260$ ,  $P = 0.611$ ). Post-hoc Tukey's HSD test with significant results are included in Table 2.1.

## **Discussion**

Lincoln's Sparrow songs were highly variable in Alberta. We found no males shared an identical song type and there were syllables unique for each male, suggesting a high level of individual variation. This variation was higher in the last part of the song as reported for other sparrows

(Podos et al. 1992; Moran et al. 2019). Typically, males sang songs with preferred syllables at the start of a song. This behaviour has been hypothesized to occur because it is crucial for species recognition (Becker 1982; Williams et al. 2013). Similar to Cicero and Benowitz-Fredericks (2000) who studied LISP in California, we found the first part of LISP song was less variable across Alberta. Additionally, males closer together geographically, shared more syllables in the first part of their song. But the number of syllables shared at this geographic scale was not sufficient to create clusters of song types. Instead, as latitude increased the presence of unique syllables made the songs increasingly different between males. This might be explained by “open-ended improvisation” (Vargas-Castro et al. 2015), which suggests that the highest individual variability will occur in the terminal elements of the song (Podos et al. 1992).

Over the 795.2 km distance we evaluated, some syllables were shared in many locations. Thus, our results suggest that space has limited effect on syllable sharing. In other words, there were not dialects at geographic and measurement scale we assessed. A song dialect is a variant song tradition shared by members of a local population of birds, within defined boundaries, (Mundinger 1982). We cannot reject the idea of dialects existing in Alberta as sampling more individuals closer together at a given site may have revealed more clustering. Cicero and Benowitz-Fredericks (2000) found a spatial structure for Lincoln’s Sparrow populations at three different locations in California, but at much shorter distances relative to our study area. They also reported that the sharing of song traditions on LISP occurred at the syllable level, with 221 syllables found (126 shared and 95 unique to a song type, Cicero and Benowitz-Fredericks 2000). For the Swamp Sparrow, it has been suggested the presence of local dialects (Mundinger 1982) occurs because of the limited number of simple syllables types used (Marler and Pickert 1984). We might expect something similar occurring since LISP did not share unique syllables

between sites and only shared simple syllables (last part of the song) as geographic distance increased, similar to the Swamp Sparrow (Liu et al. 2008). We also may not have recorded the entire repertoire of each male, which could also influence the ability to detect more localized song sharing.

In terms of acoustic structure, we found that Lincoln's Sparrows tended to have songs with higher bandwidth and higher frequencies in southern locations and in areas with more deciduous forest or mixed-wood than conifer dominated environments. However, the effect of vegetation type was weak. Therefore, we could not separate the effect of space (latitude) from vegetation. Our ARUs were systematically placed and thus sampled vegetation in proportion to its availability. Coniferous forests increase in frequency further north so more of our samples in the north came from conifer-dominated stands. Interestingly, low frequency songs were more common in areas dominated by grass (most open areas Alberta, Van Rensen et al. 2015). These findings placed within the context of the acoustic adaptation hypotheses are opposite to what is expected (low frequency songs in denser vegetation). However, in Northern locations conifer forests become increasingly open, particularly in wet areas (i.e. bogs and fens). Another possible explanation might be that these songs reflect songs adapted to earlier land covers, such as forest that used to be there but is now gone. Tubaro et al. (1993) found that the Rufous-collared Sparrow dialects changed after habitat modification over time. Thus, a similar process may occur with Lincoln's Sparrows songs but further investigation into changes in vegetation over time would be required to confirm this hypothesis.

The use of autonomous recording units to study geographic variation of songs for passerine birds has potential but also has some limitations. Very long recording periods across very large spatial extents will allow increased sharing of data to test various hypotheses about

song structure for many birds. However, the identification of individuals and determining of their complete song repertoire is a challenge. To reduce this effect, we sampled our recordings over a short period of time to maximize the chance the vocalizations came from one individual. The use of multiple recordings to increase the number of songs recorded per individual is more likely to result in incorrect identification of the singing individual and could result in assigning more song types to a single male if in fact multiple males sing within the sampling area of the ARU. In addition, there is a risk of classifying unique syllables versus shared syllables in more cases. We decided to use only one song per individual and argue it represents a random sample of the song repertoire; however higher sampling intensity and the use of rarefaction to assess if a plateau in the total number of syllables is reached at each location is recommended. This single song approach was particularly useful to describe acoustic features of songs. Comparably, the use of one song in studies of geographic variation is a method previously used in sparrows (Derryberry 2009, Shizuka et al. 2016). Doing so with banded birds to allow for individual recognition should improve our ability to determine all of the song types sang by an individual, but would come with significant increases in the costs of data collection and presumably a reduced spatial extent of study. In Chapter 4, I provide evidence that the use of ARUs can be suitable to record a more complete sample of LISP's repertoire if the singing perch is identified *a priori* to deploy the recorder.

In conclusion, Lincoln's Sparrow songs were highly variable between locations, with high syllable sharing in the last part of the song. Besides the song complexity, higher song sharing between closer individuals is expected at this geographic scale as reported for Song Sparrow (Wilson et al. 2000; Searcy et al. 2002). The effect of vegetation that was considered here had an influence on songs, lower frequency songs in open areas and lower frequency

syllables might reflect a behavioural response to song transmission that can be further investigated in mating (Slabbekoorn and Smith 2002) or predation context (Boncoraglio and Saino 2007). This study also provided insights on the use of autonomous recording units to describe song features and syllable classification, which is a valuable tool if the distance of the singing bird is close enough to obtain good quality recordings. Monitoring programs such as ABMI have tens of thousands of locations and hours where sound is recorded, providing an opportunity to explore song dialects despite some of the data being of lower quality for bird song research than achieved by more targeted recording. Finally, we showed insights in the distribution of Lincoln's Sparrow songs, which can lead to future studies in song dialects and dispersal patterns on this overlooked species.

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## Tables

**Table 2.1.** Multi-way ANOVA output of Lincoln's Sparrow acoustic features of shared and unshared (unique) syllables explained by vegetation type. The significant contrasts outputs from the post-hoc Tukey's HSD tests are included.

<b>Length</b>			
	Df	F	P-value
syllables	1	0.26	0.611
veg-type	2	0.93	0.396
syllables:veg-type	2	0.141	0.869
Total	256		

<b>Bandwidth</b>			
	Df	F	P-value
syllables	1	15.327	0.00012
veg-type	2	1.912	0.1499
syllables:veg-type	2	1.722	0.1807
Total	256		
Tukey's HSD test contrast syllables:conifer			0.0053

<b>High Frequency</b>			
	Df	F	P-value
syllables	1	21.456	<0.0001
veg-type	2	0.886	0.414
syllables:veg-type	2	0.935	0.394
Total	256		

Tukey's HSD test contrast  
syllables:conifer 0.0013

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**Low Frequency**

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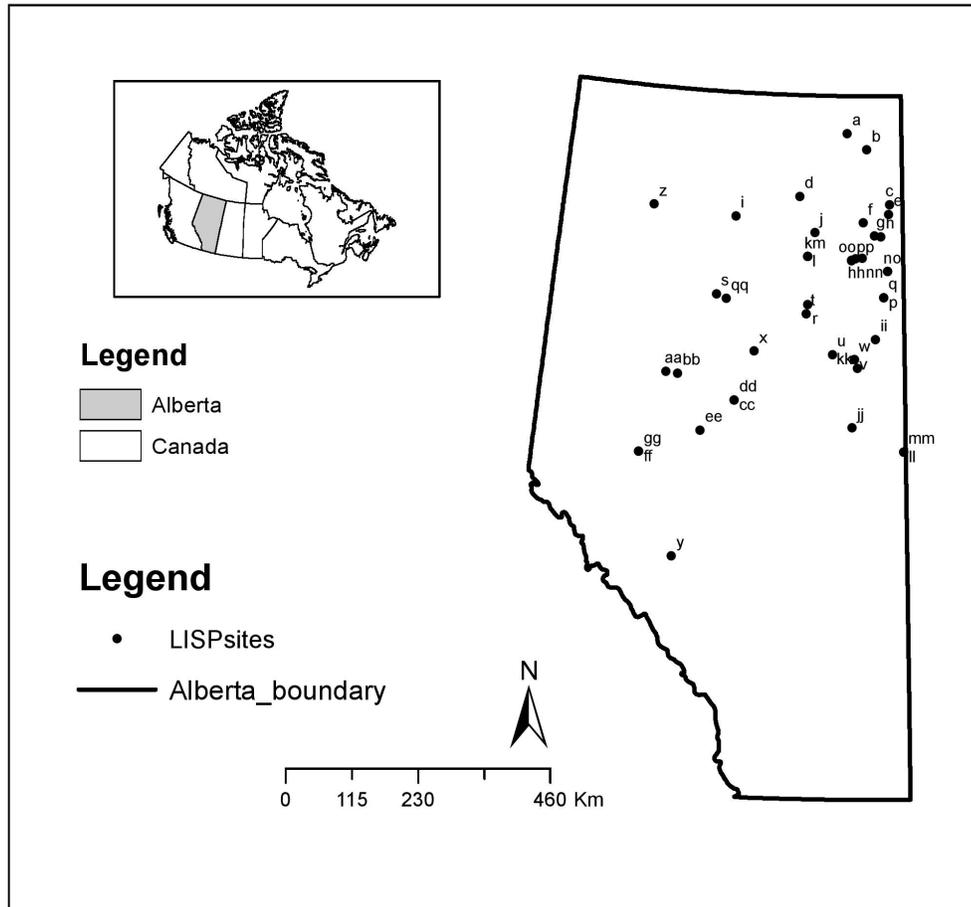
	Df	F	P-value
syllables	1	14.929	0.00014
veg-type	2	0.405	0.667
syllables:veg-type	2	0.261	0.77
Total	256		

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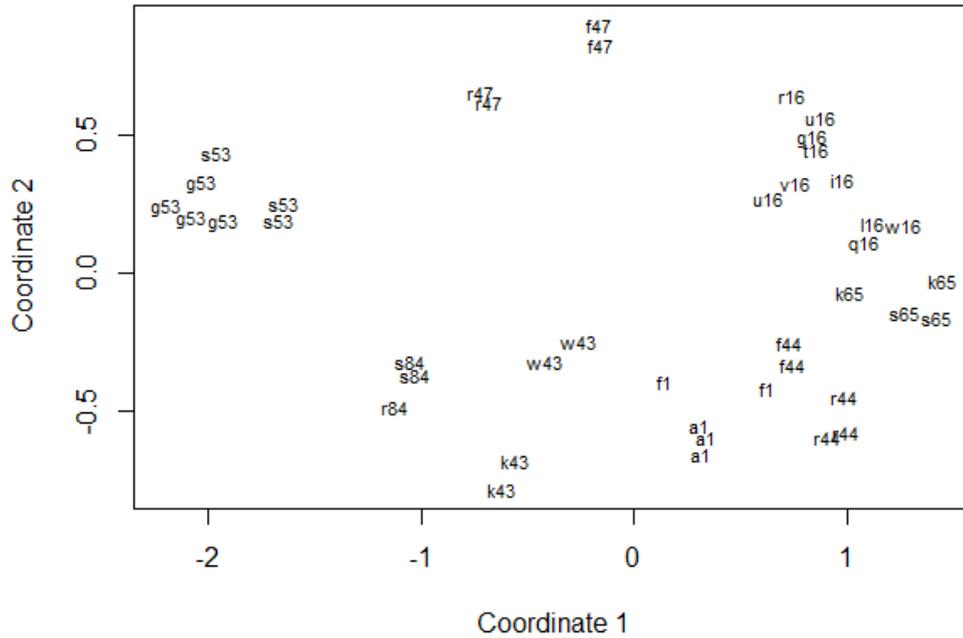
Tukey's HSD test contrast  
syllables:conifer 0.0279

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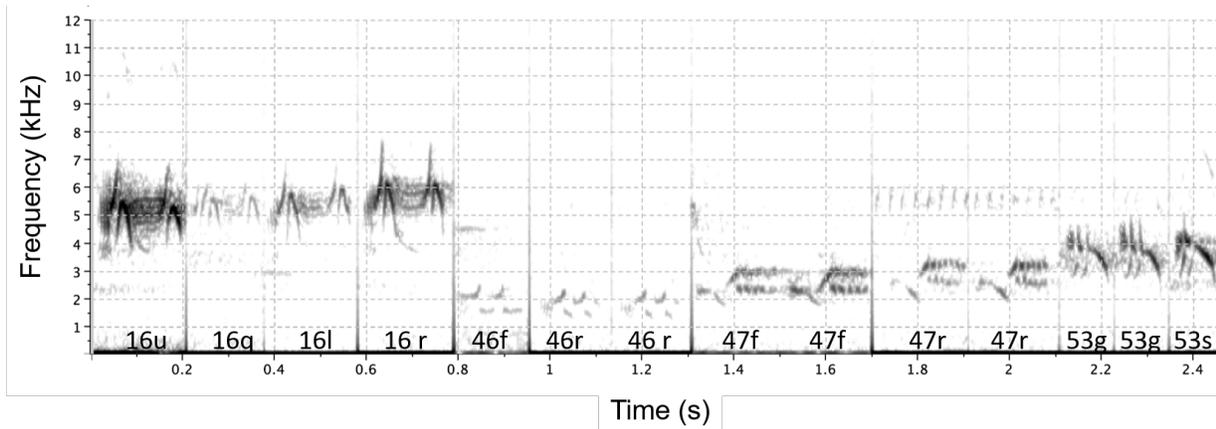
## Figures



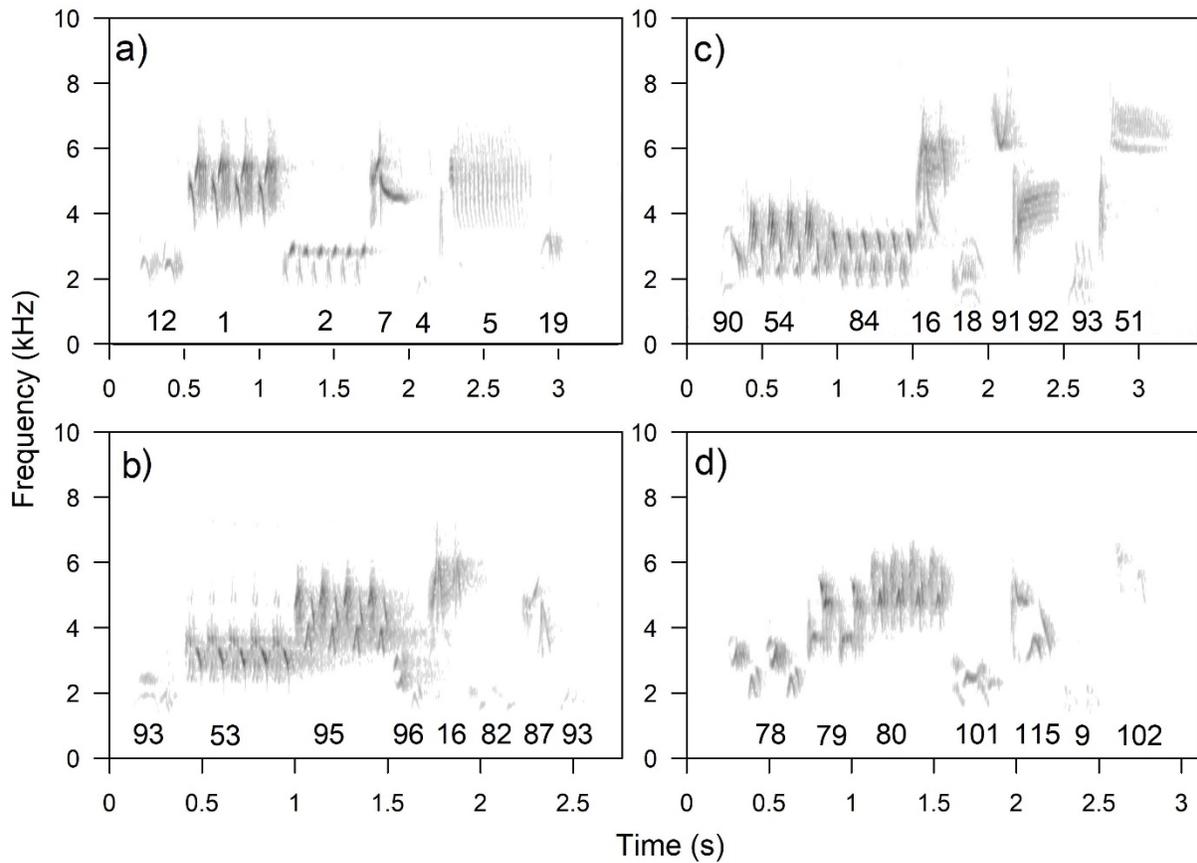
**Figure 2.1.** Lincoln's Sparrow recorded with autonomous recording units (ARUs) in Alberta, Canada. The locations correspond to Alberta Biodiversity Monitoring Institute public locations (approximate 5km buffer of the exact location). The letters indicate Lincoln's Sparrow males recorded by the ARU (N=71).



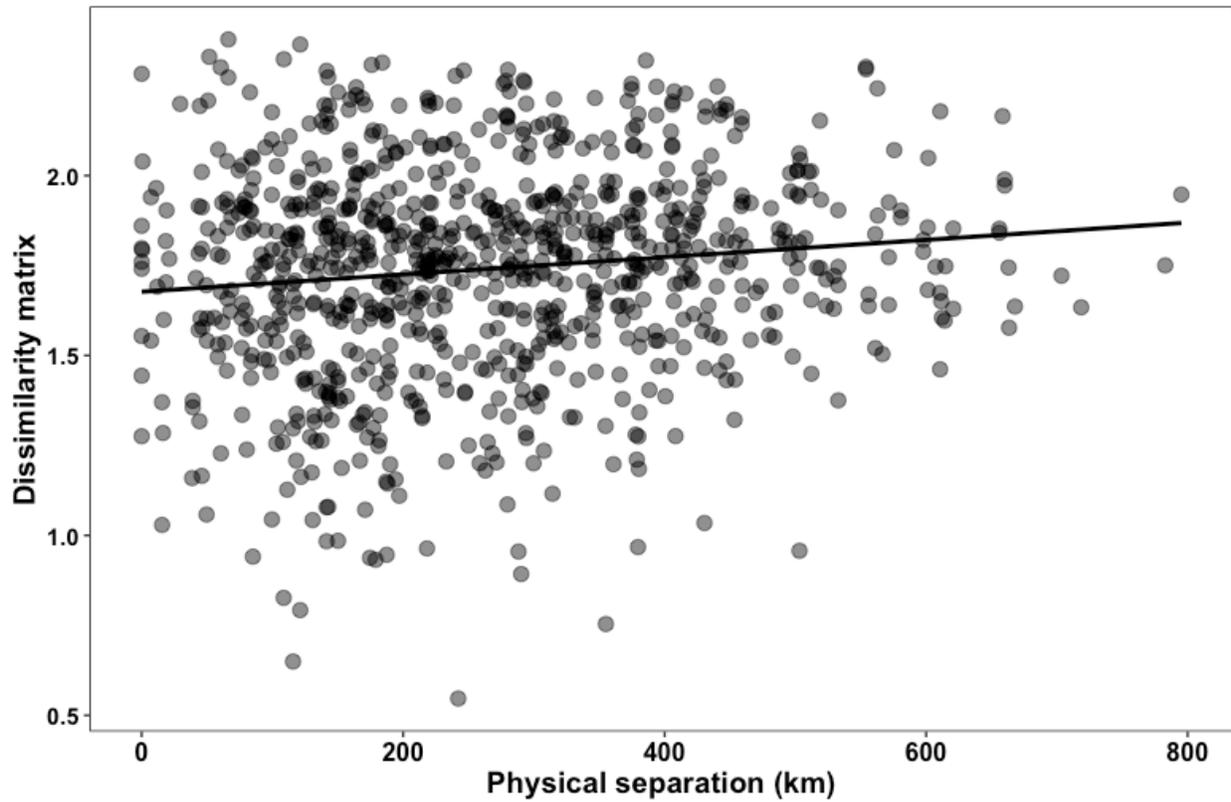
**Figure 2.2.** Non-Metric Multidimensional Scaling of the acoustic features (high frequency, low frequency, and bandwidth) of syllables classified as the same syllable by the human observers. Each letter represents a male. The numbers are a unique code for syllable types in our catalogue. For graphical representation, we only included 8 syllables from 13 males.



**Figure 2.3.** Syllables of Lincoln’s Sparrow songs classified as the same syllable in our catalogue. Each letter represents a male. The numbers are a unique code for syllable types.

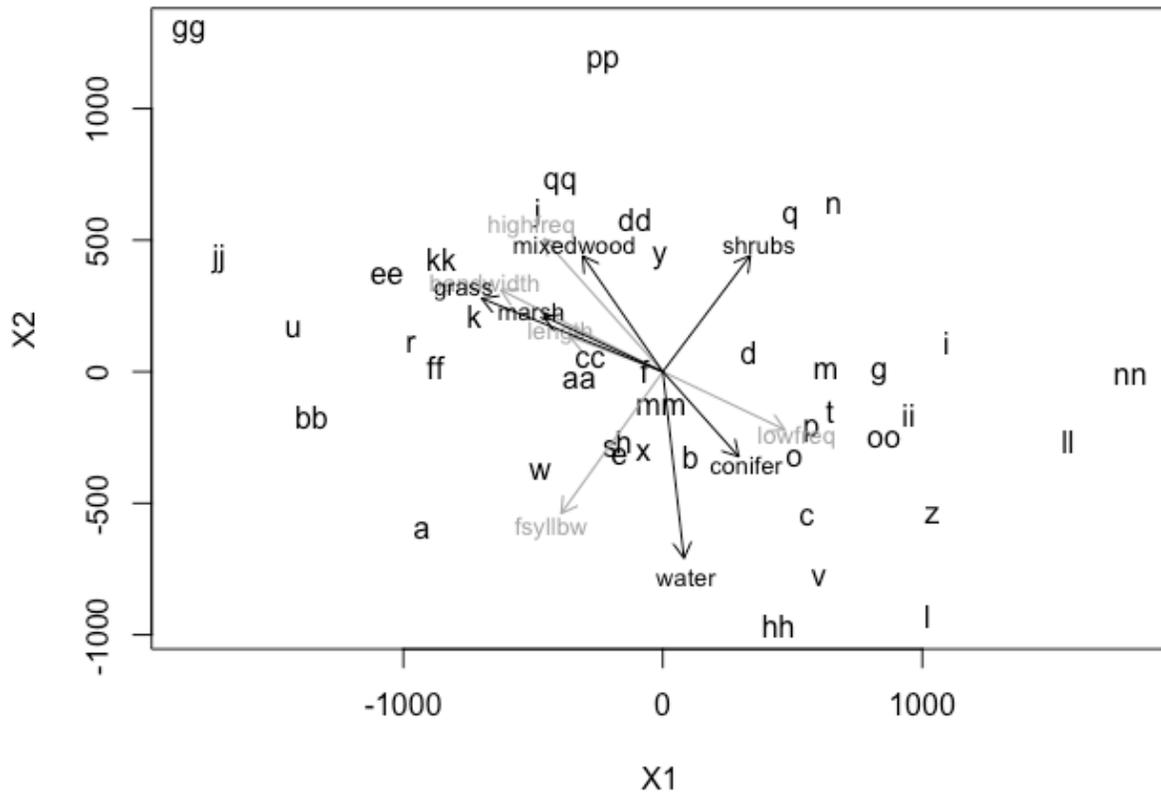


**Figure 2.4.** Four Lincoln’s Sparrow song types of four different males (a-d). Male a is located in the northern edge of the study area, males b-c are located in the middle, and male d is southerly. Each song has unique syllables and some shared syllables (16-93), which are numbered in our syllable catalogue.

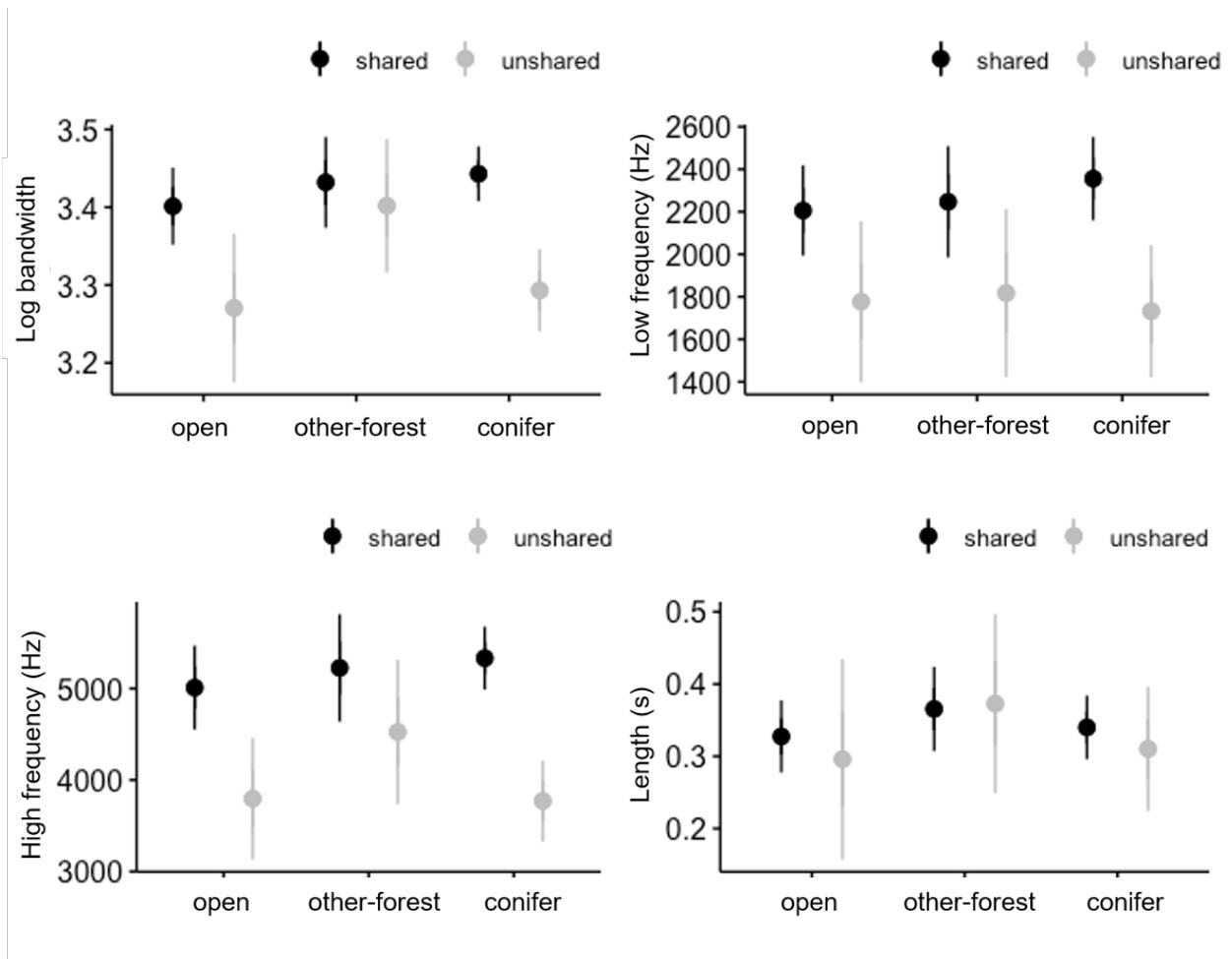


**Figure 2.5.** Pairwise comparison of the dissimilarity matrix (Sorensen similarity index of the syllables) and the geographic distance (Latitude, Longitude) of the samples (recordings of Lincoln’s Sparrow males’ songs) with a regression line.





**Figure 2.7.** Indirect gradient analysis of Lincoln’s Sparrow song features explained by proportion of vegetation type in a 50 m buffer (black arrows). Song features (gray arrows): bandwidth, highest frequency, lowest frequency, total length, and bandwidth of the first syllable. Vegetation type: conifers, deciduous, shrubs, grass, mixed-wood, and marsh. The tips of the arrows indicate higher values of the variable.



**Figure 2.8.** Acoustic features of Lincoln's Sparrow shared and unshared (unique) syllables sang in three vegetation categories. Error bars are 95 % CI.

## Chapter 3. Relative importance of vegetation change versus noise caused by industrial development on Lincoln's Sparrow occupancy

### **Abstract**

Anthropogenic noise is creating a new acoustic environment that could be detrimental for animals that communicate using acoustic signals. Most of the studies on the effects of noise in wildlife come from traffic noise in cities and less is known about the effects of noise created by industry in otherwise natural settings. Songbirds inhabiting areas far from the cities but still influenced by industries in remote locations could be affected by noise but also may be impacted by the change in vegetation conditions related to industrial development. We focused on describing the relative importance of industrial noise (compressor stations, facilities, and transportation) on occupancy of Lincoln's Sparrow (*Melospiza lincolnii*) relative to the habitat change caused by site clearing and edge effects. We chose this species based on its flexibility to breed in different habitats of varying seral stages in the boreal forest: open areas (shrubs and grass) associated with conifer forests and/or deciduous forests. To test the influence of industrial noise, we selected three areas in Northern Alberta with high, medium, and low industrial development and varying road density. At each area, we deployed in a systematic arrangement autonomous recording units (280 units in total, separated by 600 m) to obtain the detection history of the focal species across 3 consecutive days. For the noise measurements, we developed a method that used the relative noise values extracted from the recordings of 8 frequency-octave bands. Then, we divided the noise measurements in three types: noise with the highest energy in the low part of the spectrum (mean 0.5 – 1 kHz), masking noise (mean 2 – 8 kHz), and noise

containing all frequency octave bands (mean 0.5 – 16 kHz). We found variation in responses to noise type, vegetation, and proportion of disturbances. Masking industrial noise had a slight negative effect on Lincoln's Sparrow occupancy. However, it preferred open areas with shrubs and grass and higher proportion of sites with industrial activities. Although vegetation is usually one of the main considerations to evaluate habitat use, the acoustic environment in industrial sites seems to influence areas that will be occupied by songbirds in human-altered wildlands.

## **Introduction**

The study of anthropogenic noise impacts on bird species richness, productivity, and abundance has primarily focused on the influence of traffic and ambient noise in urban environments (Reijnen et al. 1996, Stone 2000). In general, species richness and densities of breeding birds decrease close to roads with high traffic volume or in noisy parts of cities (Reijnen et al. 1996, Forman et al. 2002, Perillo et al. 2017, Carral-Murrieta et al. 2020). Other kinds of noise might similarly degrade the quality of habitat for songbirds (Bayne et al. 2008, Francis et al. 2009, Nenninger and Koper 2018).

Certain types of anthropogenic noise are more likely to overlap spatially and temporally with the morning singing times of songbirds. Whereas urban and traffic noise are intermittent with variation through time, industrial noise typically produces constant noise. For example, in the boreal forest of Canada, compressor stations and processing facilities from the oilsands industry creates constant noise (Northrup and Wittemyer 2013, Nenninger and Koper 2018) adjacent to breeding bird habitat. Many forms of chronic industrial noise are low frequency (0-2.5 kHz) with high amplitude levels (75-90 dB at the source), reaching 105 dB at the largest

industrial facilities (MacDonald et al. 1996). Despite the potential for a large effect of such noise in natural areas, chronic noise from compressor stations and processing facilities in conjunction with the vehicle traffic to maintain these types of equipment has been less studied than intermittent traffic noise in urban environments (Francis 2015, Halfwerk and Slabbekoorn 2015, Shannon et al. 2016).

The limited comparisons of birds in quiet areas versus noisy areas created by industrial development in wilderness areas have shown species-specific responses. Previous work in Alberta's boreal forest found lower densities for all birds combined, lower densities for some common species, and reduced occupancy rates for a number of species close to noisy compressor stations relative to silent well sites with similar vegetation disturbance (Bayne et al. 2008). However, not all species showed negative effects and some showed trends towards being more abundant near noisy compressor stations (Bayne et al. 2008). Similarly, bird assemblages in noisy areas of New Mexico differed in comparison with quiet sites, which were associated with high acoustic masking of certain species close to generators (Francis et al. 2009). A major difference was that the western scrub-jay (*Aphelocoma californica*), a nest predator, decreased in sites with anthropogenic noise. In turn, lower predation rates for other bird species were observed in noisy areas suggesting a potential benefit of noise for some species (Francis et al. 2009, Francis et al. 2012). For secondary cavity-nesting birds, some species had higher occupancy close to noisy generators, while others had lower occupancies (Kleist et al. 2017). Clearly, more studies are needed to understand why species react differently to intermittent and chronic noise in otherwise natural ecosystems, and why some species do or do not react to noise (Francis and Barber 2013).

The habitat requirements of a species is one potential source of variation that may influence how noise impacts birds. It is well documented that vegetation type influences habitat selection by birds (MacArthur et al. 1962, MacArthur 1964). Most of the species in Bayne et al. (2008) that were more sensitive to industrial noise tended to prefer mature forest (Bayne et al. 2008). Whether species that use early seral habitat and prefer edges react to noise is not as well understood. If the human disturbance that creates noise also changes vegetation structure and composition (i.e. through edge effects and creating new early seral vegetation patches), then responses to noise may be confounded by the presence of more suitable habitat closer to noisy areas. Thus, similarly to cities, noisy areas in remote locations may attract more tolerant species (or “urban exploiters”). Sensitive species that cannot use disturbed or edge vegetation may simply be filtered out by loss of habitat rather than these species avoiding noisy areas per se (Blair 1996, Cardoso et al. 2018). In the boreal forest near industrial facilities associated with oil and gas extraction, there is considerable variation in the state of the vegetation related to natural processes as well as human disturbances which make it possible to separate the relative importance of habitat change versus noise (Venier and Pearce 2007, Venier et al. 2014, Dabros et al. 2018).

A fundamental challenge in summarizing studies that purport to study how birds respond to noise, is few studies directly quantify noise (i.e. Bayne et al. 2008). Instead, surrogate variables (i.e. distance to noise source, noisy vs quiet, traffic volume) are often used. Quantification of noise measurements are needed to separate the relative importance of noise relative to changes in habitat conditions caused by the disturbances that create noise. At the same time, there are many ways to measure noise and there has been very limited assessment of how birds react to different ways of quantifying noise (Scobie et al. 2016).

An additional factor that is rarely addressed in noise impact studies is the possibility that vegetation conditions interact with noise transmission by altering sound absorption (Martens and Michelson 1981). Low-frequency sounds can transmit farther distances in open areas, while denser vegetation can provide a vertical obstruction to the sound waves that can mitigate the distance anthropogenic noise travels (Truax 1978; Rossing and Fletcher 2004). Whether different vertical obstructions related to vegetation type make the surrounding habitat more or less suitable for some songbird species because of differences in the way noise transmits in different vegetation types remains poorly studied.

Lincoln's Sparrow (*Melospiza lincolnii*) is a common songbird that breeds in many different vegetation types in Alberta's boreal forest (ABMI Species webpage 2020). Previous work suggests they are more likely to be found near relatively quiet pipelines and well sites with disturbed vegetation than mature forest (Bayne et al. 2016). Studying a species that prefers disturbed areas provides a unique way to test the importance of noise because we know their habitat requirements are met in areas where industrial development is occurring. We had four primary objectives: 1) develop a cost-effective way of quantifying noise levels that could be used to statistically separate the effects of noise from vegetation disturbance caused by energy development; 2) determine how vegetation structure influences noise transmission in the boreal forest; 3) assess if occupancy of Lincoln's Sparrow was influenced by noise, vegetation disturbance, or both; and 4) test if different ways of quantifying noise altered our conclusions.

## **Methods**

### ***Study area***

The data was collected in June 2015 using autonomous recording units (ARUs) deployed at different areas of disturbances created by the oil sands industry in Northern Alberta, Canada. According to the Alberta Biodiversity Monitoring Institute (ABMI) human footprint classification system ([www.abmi.ca](http://www.abmi.ca)), these areas vary considerably in levels of human footprint with some areas including industrial infrastructure such as processing facilities and compressor stations. All sites included roads, well sites (active and abandoned), and seismic lines (Dabros et al. 2018).

In the sampling design, we selected three large areas in which to sample a gradient of industrial disturbances. We defined site as an area of multiple ARUs (98, 83, and 99) and a station as one ARU deployed within the site. ARUs were located 600 m apart from the adjacent recorder, comprising an area of 3600 ha (Figure 3.1). The ARUs were originally laid out in systematic grids of 100 but in some cases ARUs failed to record. These areas comprised a systematic design that was random in location with respect to roads and distance to various noise sources.

### ***Acoustic survey***

The vocalizations of the study species were collected with SM2 and SM3 recorders (Wildlife Acoustics) with two omni-directional microphones (SMM-A1 sensitivity:  $-4 \pm 3$  dB, 0 dB=1V/pa at 1kHz). Previous to the deployment, we tested the microphone sensitivity using an Extech 94 dB sound calibrator. All ARUs had microphones with gain gaps between the left and right less

than 4 dB (Lankau 2015). We stored all the recordings on SD cards in stereo format (WAV) at a sampling rate of 44.1 kHz and 16-bit resolution. We defined the recording time to be 10 min long at dawn (0500 h), which matches the highest peak of vocal activity of most boreal birds. We screwed ARUs to trees at 1.5 m height, facing North (to protect the unit from direct sun as much as possible), for 3 to 4 consecutive days from late May to early July in 2015 (range = May 25 – July 6). Most of the acoustic data analyzed were from recordings collected in June, which correspond to the breeding season of the study species.

A group of 5 expert transcribers in songs and calls of Alberta birds identified the songs and calls in each 10 min recordings for three days of the acoustic surveys. We saved all detections including location of the site, weather (presence of rain or wind), and industrial noise classified from low to high, in a database. Constant industrial noise has an acoustic signature that can be identified by ear or by viewing spectrograms (Lankau et al. 2015). The transcribers classified the recordings without industrial noise as 0 (no industrial noise audible), 1 (light industrial noise with a constant line under 1000 Hz), 2 (moderate industrial noise with a constant line up to 1500 Hz), and 3 (heavy industrial noise with a constant line up to 2000 Hz) (Lankau et al. 2015, Shonfield and Bayne 2017). When cars passed by occasionally during the survey, transcribers assigned a value for the noise level they produced. We excluded windy and rainy recordings. This classification index provided a reference of noisy and quiet stations at each site at which we then measured actual noise levels.

## Site variables

### *Quantitative noise measurements*

We defined industrial noise as the sounds generated by industrial equipment, such as machinery, trucks, wells, and compressor stations. This type of noise is concentrated in the low frequencies of the acoustic spectrum at less than 2000 Hz (Nemeth & Brumm 2010, Luther and Gentry 2013). We obtained noise measurements in two different ways. First, we used Raven Pro 1.6 (Cornell Lab of Ornithology 2019) to extract noise values manually at each recording by NVS, measuring 1 sec sections in the power spectra window of the recordings (Hann window type, 700 samples, and a discrete Fourier transform size of 2048 samples with a temporal overlap of 50%), without bird vocalizations, at the beginning (within minute 0-1) and the end (within minute 9-10) of each 10 min recording. From each 1 sec section of the recording, we extracted the relative values of amplitude (average amplitude in FSdB, Raven Pro user manual) for six 1/3-frequency octave bands (500, 1000, 2000, 4000, 8000, 16000 Hz). We defined the low and high frequency limits for each 1/3-frequency octave band following values reported in the literature (Sueur 2008).

Given that we had recordings for three consecutive days at the same ARU stations, and the majority of industrial noise is constant, we argued noise levels would be similar between days. We tested this assumption by analyzing the three days noise level for five stations that were randomly selected at each site with a repeated measurement ANOVA. Average noise levels did not vary between days ( $F=0.344$ ;  $df_{2,267}$ ;  $P=0.709$ ; Supplementary materials 1). Consequently, in the following analysis, we only included the average noise level obtained as

described above from the six frequency octave bands, extracted from the recording on a single day (selected randomly).

Our second measure of ambient noise employed the Sound Level Analysis tool available in Kaleidoscope Pro (version 5.2; Wildlife Acoustics Inc., Concord, MA, USA). This was used to obtain measurements of nineteen 1/3 frequency octave bands (from 19.7 Hz to 2000 Hz). These are the same octave-bands settings used by Marín-Gómez et al. (2020) to assess the effects of anthropogenic noise on occupancy by owls. For the noise extraction procedure, we included all the 10 min recordings analyzed in the acoustic survey. To validate this automated measure of noise; we performed a correlation analysis of the average noise of 500 Hz and 1000 Hz octave bands obtained with Raven Pro and Kaleidoscope Pro. We found a positive correlation in both cases, 500 Hz ( $r = 0.81$ ,  $p < 0.0001$ ) and 1000 Hz ( $r = 0.83$ ,  $p < 0.0001$ ) (Figure 3.2).

Given the strong correlation in our two noise metrics, we decided to only use the noise values obtained with Raven Pro in our analyses since we are more confident those values did not include biotic sounds. It is important to clarify that the ARUs and the microphones were not calibrated to obtain absolute measurements of amplitude, thus noise levels should be viewed as relative amplitude values where the noisy sites had the highest noise values and were closer to 0 while quieter places had more negative values.

We classified the noise measurements from RavenPro into three noise types: 1) noiseLOW measured low frequency sounds with concentrated energy in 500 Hz and 1000 Hz frequency octave bands; 2) noiseHIGH was defined as the average values of relative decibels from 2000 Hz to 8000 Hz, which is more likely to directly interfere with communication by masking bird songs in the maximum peak of hearing of most passerine birds (Okanoya and Dooling 1988, Dooling et al. 1992); and finally, 3) noiseALL included all frequency octave

bands (measurements from 500 Hz to 16 000 Hz). This last measurement can be interpreted as a measurement of background noise since it includes all of the frequency octave bands.

### ***Vegetation***

At each station, we calculated the proportion of vegetation within a 150 m radius buffer from the Alberta Vegetation Inventory (AVI). We extracted proportion of conifers, deciduous forest, mixed-wood, grass, and shrubs. When assessing if noise transmission was influenced by vegetation conditions, we grouped plant species into three categories as follows: 1) high density **conifer** stands dominated by black spruce (*Picea mariana*); 2) medium density deciduous forest dominated by trembling aspen (*Populus tremuloides*) or mixed-woods of trembling aspen and white spruce (*P. glauca*) (hereafter **mixedwoods**); and 3) **open** areas containing shrubs and grass. We used ArcGIS 10.6.1 (Environmental Systems Research Institute, Inc., Redlands, California, USA) to calculate the buffer and to extract the proportion of vegetation.

We extracted the proportion of the 150 m radius buffer that was conifers and mixedwoods by age class (0-19, 20-40, 41-100, and more than 100 years old). Class 20-40 years did not have any values in the three study areas. Therefore, we collapsed 0-19 to 20-40 to a new category 0-40. Then, we created a new categorical variable called “age” with three levels: **young** forest (0-40 y), **mature** (40-100 y), and **old** forest (more than 100 y). Each ARU was placed in an age class based on the age class most common in the buffer. Human disturbance variables were extracted from a 150 m buffer (around each station) using the Human Footprint Inventory GIS layer ([www.abmi.ca](http://www.abmi.ca)).

## *Statistical analysis*

### *Factors influencing noise levels*

Our sites were selected based on the amount of energy sector disturbance visible from satellite imagery. Thus, we did not know prior to ARU deployment if noise levels actually differed between sites. To test if our designations of low, moderate, and high footprint sites actually had different noise levels, we used an ANOVA to test if the average noise levels were significantly different between sites (each ARU was treated as a replicate). We ran three separate ANOVAs using noiseALL, noiseLOW, and noiseHIGH as the response variable. In addition, we tested whether the noise measurements using all the frequency octave-bands had differences in relative amplitude between the sites. In other words, we compared the average noise measurements (response variable) between the three sites (fixed effect), using all the frequency octave bands measurements (obtained with Raven Pro) with a Generalized Linear Mixed Model (GLMM).

We then assessed whether the various noise metrics were correlated with different types of energy sector footprint. Using generalized linear models with a Gaussian distribution and identity link, we tested 5 hypotheses about what the various noise metrics were measuring: 1) they described general noise in the environment caused by nuisance factors that vary in some unknown way as a function of forest composition (conifer, mixedwood, open) and age (young, mature, old) but not energy sector footprint (hereafter vegetation); 2) they were correlated with the proportion of total energy footprint within a 150m buffer with no designation of the type of noise that each footprint is likely to create; 3) they were correlated with footprint that are more likely to produce chronic noise sources like oilsands processing facilities, compressor stations, and active wells (hereafter chronic noise footprint); 4) they were correlated with footprint like roads, abandoned wells, pipelines, and seismic lines that are used to access the energy network

via trucks and off-highway vehicles (hereafter intermittent noise footprint); 5) if both chronic or intermittent noise footprint contributed to our noise measurement in an additive way; and 6) if chronic versus intermittent noise contributed to noise measurements in an interactive way.

Natural variation in environment was controlled for in all models.

### *Occupancy models*

We estimated the factors influencing Lincoln's Sparrow occupancy using the single-season occupancy model framework (MacKenzie et al. 2002). The model estimates the occupancy ( $\psi$ ) and the detection probability ( $p$ ) based on the detection history of singing birds of three consecutive days recorded per station. We generated 42 models that allowed us to test the following hypotheses/ questions: a) any variation in Lincoln's Sparrow occurrence was simply due to detection error caused by time of sampling (day of year, hereafter date); b) natural vegetation conditions are the primary driver of occupancy; c) any type of energy development (proportion of area disturbed by abandoned well, active well, facility, road, seismic line, and pipeline) creates altered habitat conditions that influence Lincoln's Sparrow occupancy; d) linear features (proportion of area disturbed roads, seismic lines, and pipelines) create edge habitat preferred by Lincoln's Sparrow; e) polygonal features (active well, abandoned well, facility) create early seral open habitat preferred by Lincoln's Sparrow; and f) both linear and polygonal features create habitat for Lincoln's Sparrow but at different rates.

To these six basic model structures, we added the three different noise measurements noiseLOW, noiseHIGH, and noiseALL to see if we observed different responses on the occupancy side of the equation (24 models). Finally, we evaluated whether the three noise metrics influenced detection across all models under the premise that noise may influence our ability to observe Lincoln's Sparrow, even when present, because of reduced ability to aurally

detect them because of the noise. This resulted in 42 models being compared. Day of year (hereafter DOY) was included on the detection side of all models. Time of day was controlled by design. The models were ranked using Akaike Information Criteria (AIC, Burnham and Anderson 2002). All the occupancy models and model selection analyses were performed with the software RStudio (version 1.4.1106) and the R package “unmarked” (Fiske and Chandler 2011).

## Results

### *Noise levels*

We analyzed recordings from 280 stations at sites that we *a priori* ranked as having high, moderate, and low levels of energy footprint. There were significant differences in average noise for NoiseALL ( $F_{2,277} = 36.9, P < 0.0001$ ), NoiseLOW ( $F_{2,277} = 44.5, P < 0.0001$ ), and NoiseHIGH ( $F_{2,277} = 15.9, P < 0.0001$ ) between sites. Post-hoc Tukey’s test found that the low footprint site had significantly lower noise levels than the moderate ( $P < 0.001$ ) or high footprint site ( $P < 0.001$ ). Moderate and high footprint sites were not significantly different ( $P = 0.98$ ) (Figure 3.3a). The linear regression of the log transformed relative amplitude values including all the frequency octave bands also showed differences between the slope of the high site with the low site and the intermediate site with the low site (Table 3.1, Figure 3.4).

The three noise metrics were correlated. The correlation coefficient ( $r$ ) for the three noise metrics was: noiseALL vs noiseLOW = 0.95, noiseALL vs noiseHIGH = 0.88, and noiseLOW vs noiseHIGH = 0.71. The model that best predicted all three noise measurements was the Chronic Noise footprint \* Intermittent Noise footprint + vegetation variables (Table 3.2). The AIC weight for this model was 0.99 for all three noise metrics.

Given the correlation between noise metrics it was not surprising that the same model was selected as having the best fit, but there were some distinct differences in beta estimates (Table 3.3). Across all models, age of forest showed the same effect on noise level with the lowest noise level in mature forests. Based on 95% confidence intervals this was lower than old forests, which had intermediate noise levels. Young forest had the highest noise levels and the 95% CI did not overlap with mature but did overlap with old (Figure 3.3b).

For noiseLOW, conifer and mixedwood had beta values that included zero based on 95% CI, while the open habitat had the loudest noiseLOW scores (Figure 3.5). For noiseALL, conifer had beta values that included zero indicating no change in noiseALL controlling for other variables. noiseALL increased as mixedwood increased but not as steeply as in open vegetation (Figure 3.5, Figure 3.6). noiseHIGH showed a very different pattern. Conifer and open had 95% CI that included zero while there was an increase in noiseHIGH as mixedwood increased (Figure 3.5).

In all models, the predicted noise level was best fit by the models that had an interaction between chronic noise footprint and intermittent noise footprint. The patterns were the same across all noise metrics. When the proportion of chronic noise footprint increased and intermittent noise footprint was low, noise was the highest and the rate of change in noise the steepest. As the amount of intermittent noise footprint increased, the slope between chronic noise footprint and noise level became shallower although the overall noise level increased (Figure 3.7).

### ***Occupancy models***

Lincoln's Sparrow was detected at 123 of 280 stations (at 55 of 98, 45 of 83, and 23 of 99 stations grouped as sites: high, moderate, and low industrial sites, respectively); the naïve occupancy estimate was 0.48. Along the noise gradient Lincoln's Sparrow occupancy was best explained by proportion of total disturbances, proportion of open areas, and masking noise level (noiseHIGH) in the range 2000 – 8000 Hz frequency octave bands (Table 3.4, Table 3.5). Lincoln's Sparrow had higher occupancy in sites with a greater proportion of regenerating vegetation such as grass and shrubs and less conifer forest (Figure 3.8). Masking noise (noiseHIGH) only had a slight negative effect on Lincoln's Sparrow occupancy with an increasingly large confidence interval as noiseHIGH increased (Figure 3.8).

Variation in occupancy was observed within the three noise measurements. For noiseLOW frequency octave bands (500 and 1000 Hz) and noiseALL, predicted occupancy was positive as noise increase and it changed to neutral when we included vegetation and footprint as predictors. A different pattern was observed using masking noise (2000 – 8000 Hz; noiseHIGH), as it changed from slight positive to neutral with vegetation, and to negative when we included vegetation and footprint as predictors (Table 3.5, Figure 3.9).

### **Discussion**

In recent years, wildlife responses to noise have been an area of active investigation with the main focus being urban environments (Francis and Barber 2013, Shannon et al. 2016, Ciach and Fröhlich 2017); yet industrial sites and the noise associated with their activities remain understudied (Habib et al. 2007, Francis et al. 2011c). Our approach to directly measuring noise

and a disturbance tolerant species capable of living in noisy areas provided a novel test of the effects of noise on birds and some of the factors that influence variation in noise levels in wilderness areas undergoing energy development. Testing the effect of infrastructure and vegetation on industrial noise levels recorded with ARUs, in a remote area of Alberta, Canada, with boreal forest coverage dominating the landscape, we found that industrial activities, specifically facilities (including compressor stations) and certain roads, increased the levels of noise in the environment.

The idea that the energy industry and the noise generated by its activities have negative effects on songbird occupancy comes primarily from studies that compared noisy to non-noisy areas (Bayne et al. 2008, Francis et al. 2011a). A potential drawback of a dichotomous approach is the lack of continuous variation in levels of noise. Intermediate levels of noise may be less detrimental than an extreme noisy vs. non-noisy contrast. In this study, we had 280 ARU stations describing a gradient of industrial noise levels due to variation in noise levels at different sources as well as distance to that noise source. Similarly, Marín-Gómez et al. (2020) studied the variation of occupancy for an owl species in a gradient of noise in an urban area, and found that levels of -60 dB and -40 dB (relative amplitude levels at the frequency octave bands under 2000 Hz) influenced occupancy but below -60 dB there was no effect. Here, we assessed three different quantitative measurements of noise that were not previously considered as explanatory predictors of bird occupancy inhabiting the boreal forest in the context of industrial noise. Frequency octave bands from 2000 Hz to 8000 Hz and low frequency octave bands (500 and 1000 Hz) concentrated the higher levels of energy (from -60 dB to -40 dB), which were also the ones predicting changes in occupancy by our study species.

### ***Measuring noise and factors that influence noise levels***

Regardless of potential limitations of using ARUs to measure noise levels we did find strong relationships between energy sector footprint and our noise metrics. The large sample size allowed us to test numerous hypotheses about how noise may spread in complex environments with relationships somewhat dependent on the metric of noise used. There are numerous processes affecting sound propagation, such as attenuation and reverberation due to vertical objects (Wiley and Richards 1978, 1982, Naguib and Wiley 2001). Here, the proportion of open areas was positively associated with higher noise levels recorded at a given ARU. *A priori* we expected that open habitats might have higher noise levels because of fewer obstructions. Sound propagates spherically, and energy decreases with square of distance from the source (6 dB for each doubling of distance), but when sound encounters dense trees there is often a greater decrease (as high as 5-10 dB) for each doubling of distance (Naguib and Wiley 2001). Why proportion conifers or proportion mixedwood were not important predictors is not entirely clear. While there is often an inverse correlation between the proportion conifer or proportion mixedwood with proportion open, that correlation was not strong in our study area ( $r = -0.04$ ,  $r = -0.12$ ). Based on previous work, we assumed the dense conifers would have the greatest sound absorption, which we did not observe. Conifer forests do vary in density, with low density stands being common in very wet areas. Interestingly, mixedwood was positive related with the noiseHIGH metric; this may be spurious if there were some locations where particularly high frequency noises were by chance found in mixedwoods. Further assessments of noise propagation are needed to more completely understand the role of vegetation structure on the cumulative effects of noise in industrial areas.

The use of various noise metrics to evaluate occupancy responses was key to understanding at which frequencies in the acoustic spectrum, noise is causing the strongest effect. Testing multiple noise models, we observed different effects on Lincoln's Sparrow occupancy. Controlling for vegetation and energy footprint was fundamental to understand the impacts of noise. While Lincoln's Sparrow can clearly be found in areas with noise, they do not seem to prefer it per se rather they prefer habitat which tends to be closer to noise sources. Our noise metrics obtained from ARUs (un-calibrated recordings) can benefit the study of noise in the wild since it allows for comparisons in a diverse of spatial settings and more importantly capturing the noise variation in the environment. In this study, we used mostly Wildlife Acoustic SM2 recorders, which reduced the variation between measurements. With the improvements of recording devices (specially microphones), less of the noise is going to be attributable to the device, which will benefit how we obtain noise metrics and the conclusions that we can draw in conjunction with additional habitat predictors. Future studies measuring noise on ARUs need to make sure to report the model of ARU and settings used so that we can compare these types of noise measurements across studies.

The interaction between chronic noise and intermittent noise for the three noise metrics shows the complexity of measuring noise along an industrial gradient. High chronic noise was driven by the presence of large industrial facilities, active wells, and compressor stations. Thus, the noise received by the ARU is more likely to be a function of relatively few noise sources. As proportion of intermittent noise went up, total noise increased even with low footprint from chronic noise sources. Interestingly, at high levels of chronic noise, intermittent noise from roads did not add much to the total noise levels we observed. One reason for this could be that our method of measuring noise level was not able to properly measure the cumulative effects of

noise (Sueur 2018). The major highway and multi-lane gravel roads that take workers from the highway to the oilsands facilities generated much of the intermittent noise in our study area. However, the closer one gets to oilsands facilities the slower traffic is because of safety concerns. Traffic speed is an important predictor of noise level. While not reported here, we also modeled the distance to facilities and roads as noise predictors but these models did not fit as well as the proportion metrics, suggesting a cumulative noise effect is occurring.

### ***Lincoln's Sparrow Response***

Generally, songbirds with low-frequency songs are less abundant in noisy sites than those with higher frequency vocalizations (Proppe et al. 2013, Francis et al. 2015). This is why most studies that have assessed noise have focused on low-frequency anthropogenic noise. Therefore, we expected that Lincoln's Sparrow would occupy sites with moderate-high levels of noise because their songs are generally less masked above 2000 Hz. In addition, sparrows have shown acoustic flexibility in their songs that may allow them to better adjust to anthropogenic noise by altering their vocalizations (Wood & Yezerinac 2006, Gentry et al. 2017). We did find that Lincoln's Sparrow occupancy increased with noise if we consider noiseLOW or noiseALL alone as predictors. This indicates the Lincoln's Sparrow can live in noisy areas and if there are negative effects on their communication, they have adapted to these conditions sufficiently to use suitable but noisy habitat. However, the best fitting occupancy model indicated they were in these areas because the footprint and natural variation made for good habitat rather than some benefit of noise per se. The weak pattern of a negative response in occupancy to high frequency industrial noise (noiseHIGH) warrants further investigation but suggests that noise may have impacts even on species highly tolerant to human disturbance.

A fundamental question is whether the noise levels we monitored were sufficient to create any issues in Lincoln's Sparrow communication or whether they adapted their songs to be able to communicate in areas with noise. Lincoln's Sparrow songs can be masked by the noise as there is an overlap in the low frequency syllables of their song with industrial noise under 2000 Hz, with syllables ranging between 1.5 kHz up to 8 kHz (Cicero and Benowitz-Fredericks 2000, Sockman 2009). Therefore, acoustic flexibility of Lincoln's Sparrow song features can be a possible adaptation to live in noisy areas, as described for other sparrow species exposed to similar industrial noise (Curry et al. 2018). However, in other work (Chapter 4) we showed that Lincoln's Sparrow did not shift the minimum frequency of their song. Alternative strategies to deal with noise can be further investigated on Lincoln's Sparrow singing behaviour, since there is evidence that responses to noise in songbirds are related to vocal flexibility (Slabberkoorn & Peet 2003, Cardoso 2014, Roca et al. 2016).

This study is the first to use of multiple measurements of noise describing occupancy of a wild songbird in the context of chronic industrial noise. Important to emphasize is that the measurement of noise at multiple octave-bands resulted in a non-biased method to characterize the noise in the industrial gradient, giving a quantitative description of noise variation rather than a categorical human judgment. This method can be used to test if noise may influence communication in songbirds such as song transmission experiments that test for masking and song degradation for species exposed to noise. Masking noise and song degradation continue to be an understudied field in the context of chronic industrial noise. Finally, we found a relatively neutral effect of noise on Lincoln's Sparrow occupancy in a gradient of industrial noise; however, effective communication, reproductive success, and stress caused by chronic noise have not been evaluated. For terrestrial passerines and especially for Neotropical migrants who

find new conditions for reproduction every year in Northern Latitudes, understanding the multiple environmental factors that could diminish quality of breeding territories requires attention for conservation actions.

### **Acknowledgments**

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## Tables

**Table 3.1.** Post-hoc comparisons of testing for differences between average measurements of frequency octave bands between sites (high, moderate, and low levels of footprint).

	$\beta$	SE	df	t-value	p-value
high-moderate	-4.96	0.25	1084	0.71	0.479652
moderate-low	-4.46	0.25	1090	4.02	0.000061
high-low	-1.98	0.13	1180	4.83	0.000002

**Table 3.2.** Results from AIC comparisons of generalized linear models that predict how the three noise metrics respond to various models of vegetation conditions (vegetation = conifer, mixedwood, and open as continuous variables, and age class as categorical variable) and type of energy footprint (chronic noise footprint = facilities + active well + road; or intermittent noise footprint = abandoned well + seismic line + pipeline). nPars = number of parameters

<b>Models</b>	nPars	AIC	AIC	AIC
		noise ALL	noise LOW	noise HIGH
Chronic * Intermittent + Vegetation	9	1482.3	1880.4	1390.1
Chronic + Intermittent + Vegetation	8	1502.1	1896.6	1406.5
Chronic + Vegetation	7	1504.5	1902.0	1405.0
Intermittent + Vegetation	7	1563.9	1949.9	1458.6
Energy + Vegetation	7	1502.1	1895.0	1410.2
Vegetation	6	1567.8	1956.8	1457.9

**Table 3.3.** Model parameters from the best-fitting models that predict the three different noise metrics as a function of vegetation and energy footprint variables. 95% CI are shown in brackets.

	<b>noiseALL</b>	<b>noiseLOW</b>	<b>noiseHIGH</b>
Conifer	0.40 (-2.10,2.87)	0.88 (-4.16,5.92)	0.20 (-1.90,2.30)
Mixedwood	1.81 (0.05,3.56)	2.05 (-1.53,5.62)	2.26 (0.77,3.74)
Open	2.82 (0.14,5.50)	7.99 (2.53,13.44)	0.32 (-1.95,2.59)
Young Vs Mature	-1.12 (-2.18,-0.06)	-2.26 (-4.42,-0.09)	-0.83 (-1.72,0.08)
Young Vs Old	0.38 (-1.03,1.80)	0.98 (-1.91,3.87)	0.04 (-1.16,1.24)
ChronicFoot	11.05 (8.84,13.26)	20.61 (16.12,25.10)	8.52 (6.65,10.39)
IntermFoot	12.16 (6.87,17.45)	26.17 (15.40,36.93)	7.09 (2.61,11.58)
Chronic*Interm	-40.49 (-57.44,-23.53)	-75.06 (-109.59,-	-31.48 (-45.86,-17.10)
Constant	-74.10 (-75.27,-72.92)	-69.14 (-71.55, -66.73)	-77.17 (-78.18,-76.17)

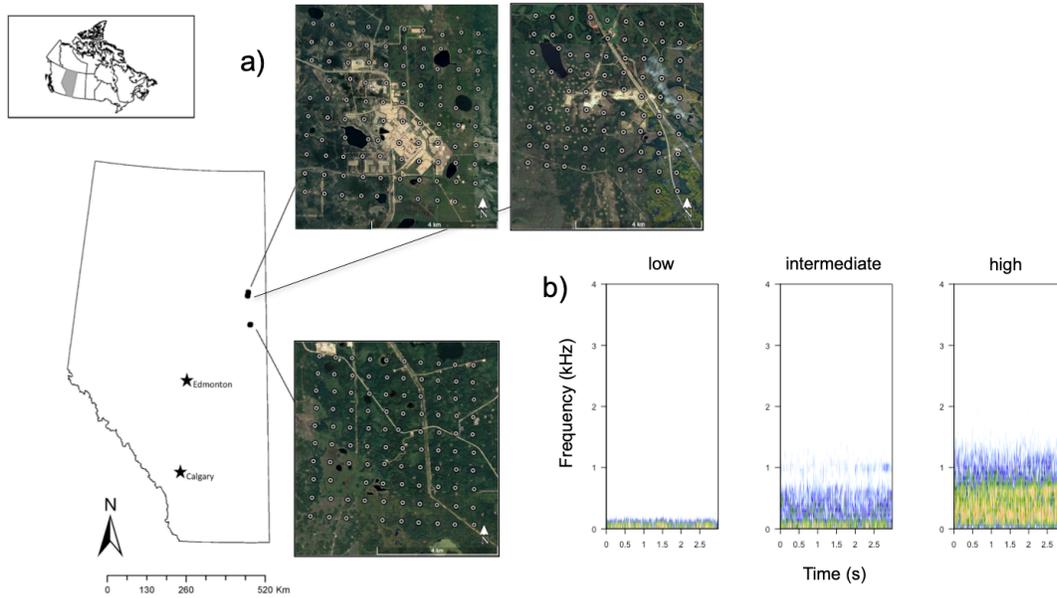
**Table 3.4.** Occupancy and detection probability models (AIC values) explaining Lincoln’s Sparrow variation. Lowest AIC value is in bold. Noise variables included: noiseLOW (average 500 Hz-1000 Hz frequency octave bands), noiseHIGH (average 2000 Hz-8000 Hz frequency octave bands), and noiseALL (average 500 Hz-16000 Hz frequency octave bands). Date of Year (DOY) was included in the detection side for all the models. Vegetation (Veg = conifers, mixedwood, open, age) and energy footprint variables (linear features = pipelines, seismic lines, roads; polygonal features= well sites, facilities, compressor stations) are included as explanatory predictors of habitat preference. The best-fitted occupancy model is in bold.

psi (occupancy)	p (detection)	NO noise	+noiseALL	+noiseLOW	+noiseHIGH
No Control Variables	DOY	832.577	823.597	818.518	831.002
Veg	DOY	806.22	805.088	800.969	808.221
Veg+Footprint	DOY	784.065	785.9411	784.538	<b>783.587</b>
Veg+Linear	DOY	801.990	802.658	800.0418	803.895
Veg+Polygon	DOY	785.686	786.806	784.473	786.177
Veg+Polygon+Linear	DOY	790.293	792.042	790.151	789.483
No Control Variable	DOY+NOISE	832.577	825.297	821.794	831.2069
Veg	DOY+NOISE	806.22	803.757	802.126	807.0216
Veg+Footprint	DOY+NOISE	784.065	785.721	784.552	785.745
Veg+Linear	DOY+NOISE	801.990	799.646	798.101	802.793
Veg+Polygon	DOY+NOISE	785.686	787.592	786.971	787.361
Veg+Polygon+Linear	DOY+NOISE	790.293	791.357	790.499	792.146

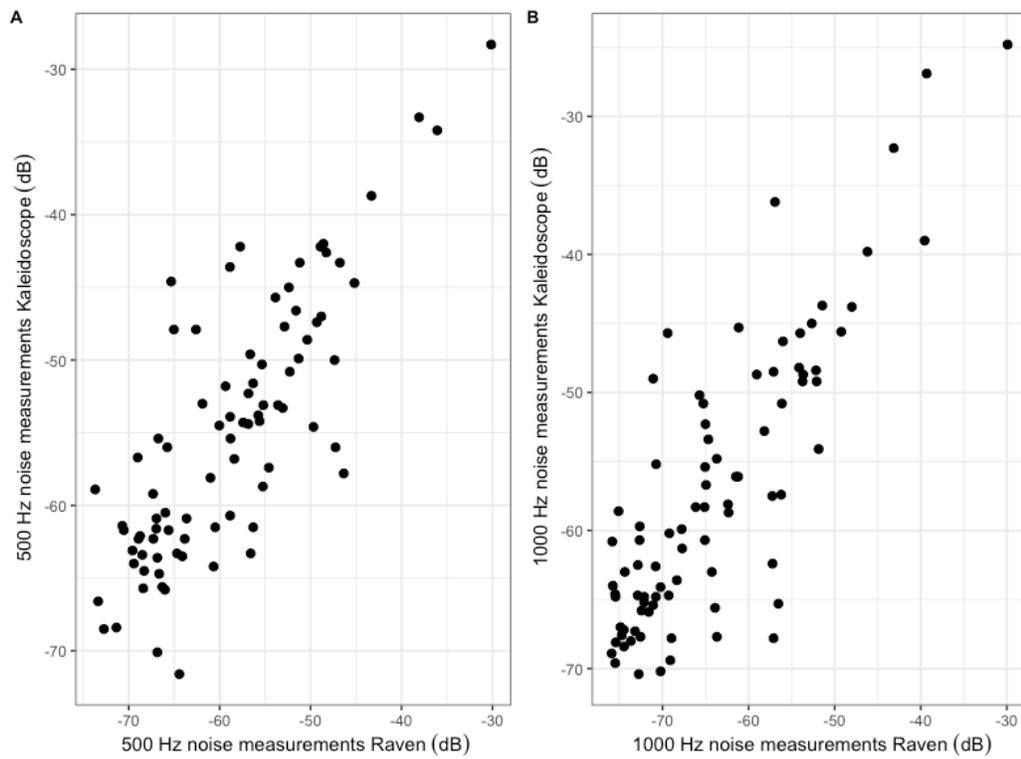
**Table 3.5.** Beta estimates of best occupancy model for Lincoln’s Sparrow including the three different noise metrics.

	Parameters	NoiseALL	noiseLOW	noiseHIGH
Psi	conifer	-0.33 (0.95)	-0.32 (0.95)	-0.36 (0.96)
	open	5.30 (2.20)	5.49 (2.20)	5.48 (2.39)
	mixedwood	-0.67 (0.68)	-0.72(0.68)	-0.35 (0.67)
	old	0.19 (0.48)	0.11 (0.48)	0.32 (0.47)
	young	1.21 (0.44)	1.21 (0.44)	1.28 (0.44)
	footprint	3.98 (1.16)	3.82 (1.15)	4.08 (1.04)
p	DOY	0.003 (0.01)	0.003 (0.1)	0.005 (0.1)

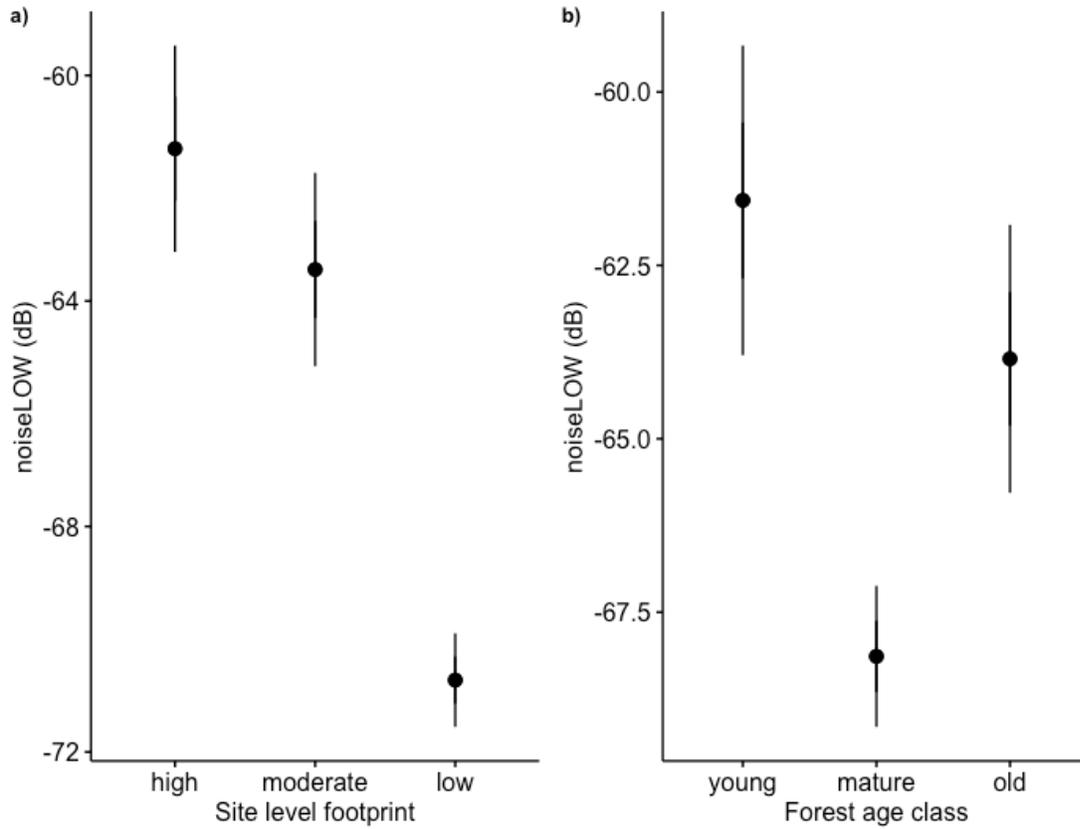
## Figures



**Figure 3.1.** a) Sample design. Autonomous recording units deployed 600 m apart in three areas of industrial disturbances in Northern Alberta, Canada. Upper areas correspond to high and medium industrial footprint level. Lower area corresponds to low industrial footprint. b) Spectrograms of noise variation at a specific station in the low, intermediate and high industrial footprint areas.



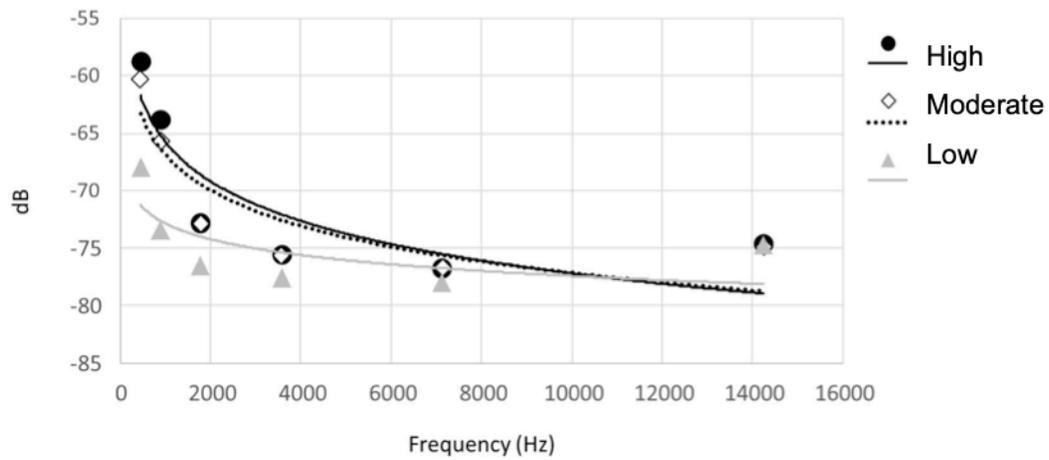
**Figure 3.2.** Correlation between noise measurements (relative amplitude) obtained with Raven Pro and Kaleidoscope Pro at A) 500 Hz and B) 1000 Hz frequency octave bands. N= 283 stations.



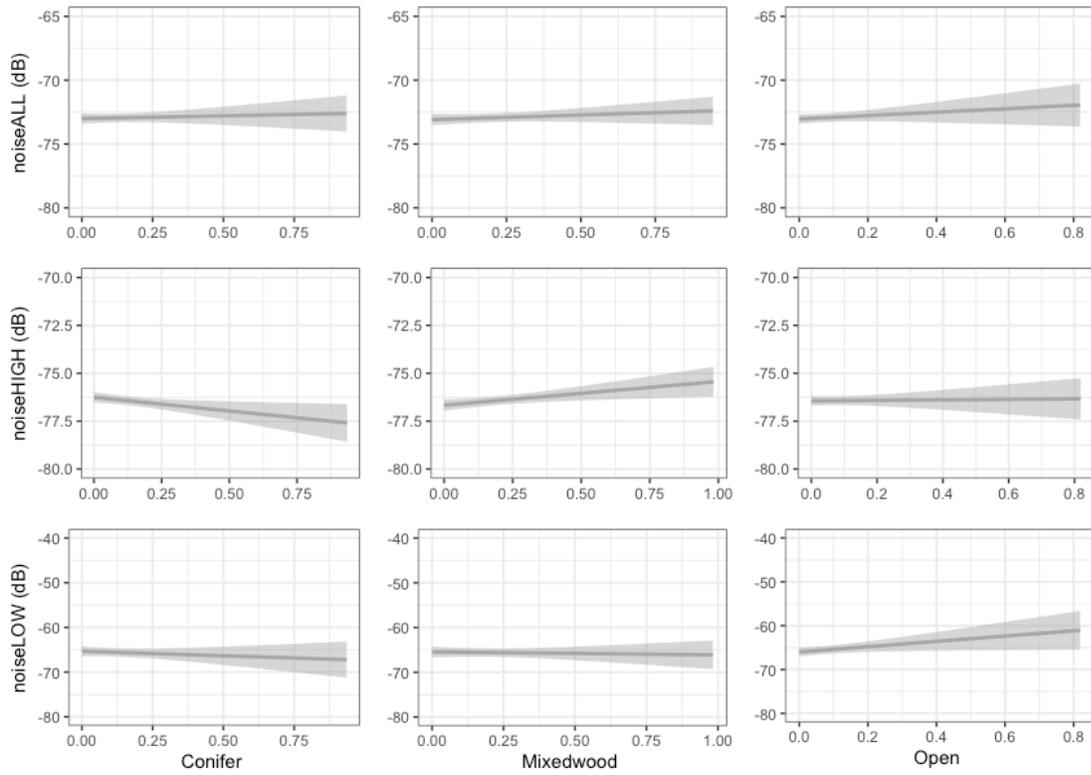
**Figure 3.3.** a) Predicted noise level for noiseLOW at the high, moderate, and low footprint sites.

b) Predicted average noise levels for noiseLOW in young, mature, and old forest ARU locations.

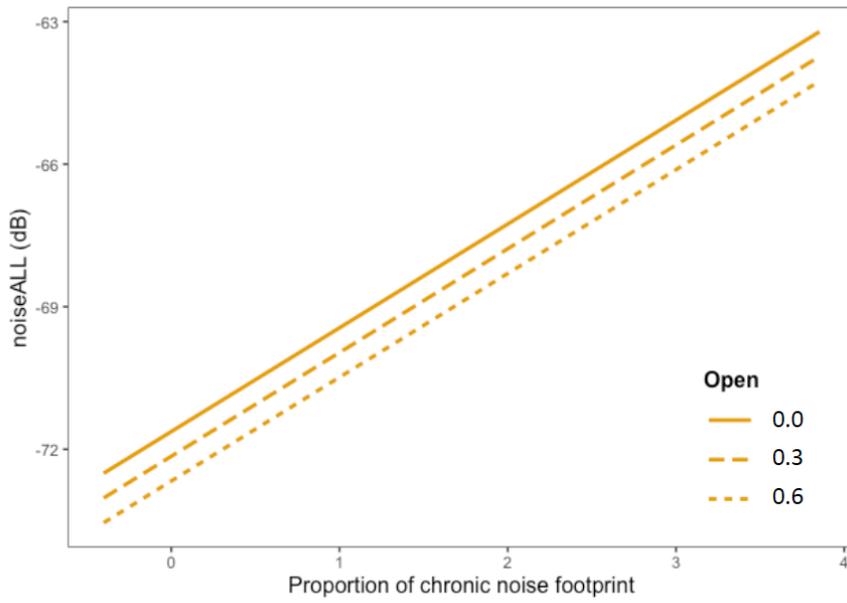
Error bars are 95% CI.



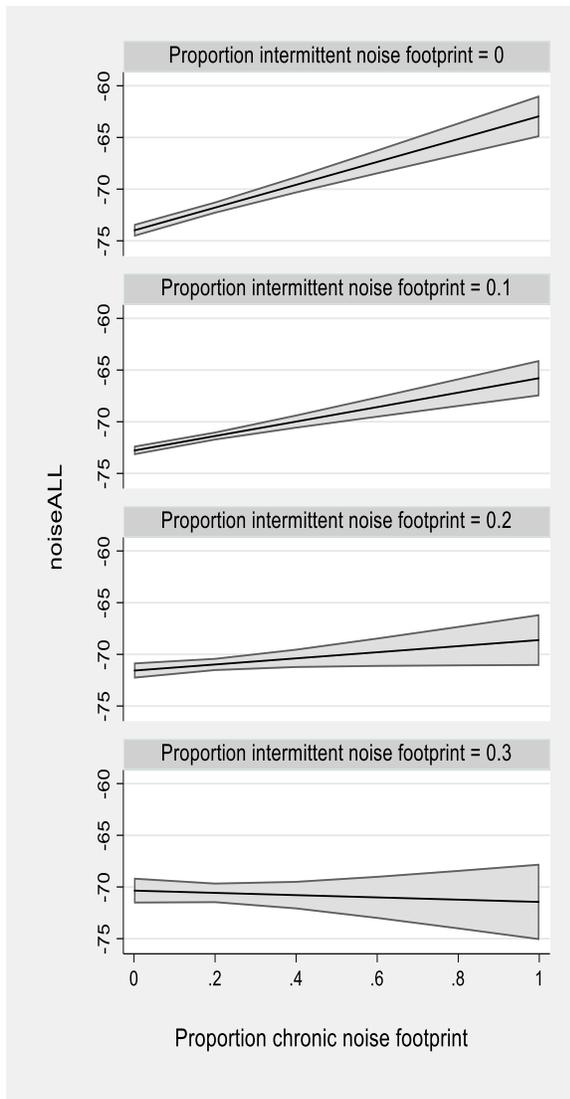
**Figure 3.4.** Relative measurements of sound amplitude measured from recordings for the six frequency octave bands per site using Raven Pro software. Sites are represented by symbols and fitted lines. High industrial footprint = black dots and line, moderate footprint = hollow diamonds and dotted line, low footprint = gray triangles and line.



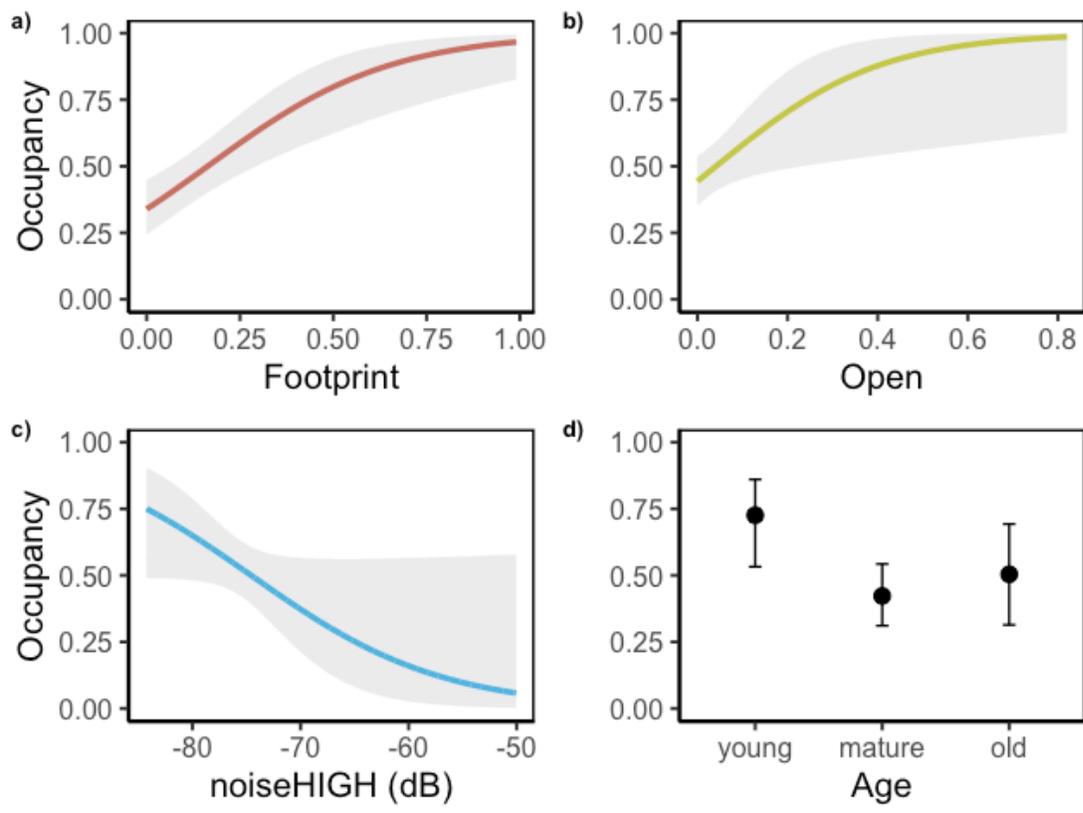
**Figure 3.5.** Predicted noise levels from the three noise metrics with increasing proportions of conifer, mixedwood, and open habitats. Error bands are 95% confidence intervals.



**Figure 3.6.** Graphical representation of model predictions of the relationship between noiseALL and proportion of energy footprint though to create chronic noise as influenced by proportion of open habitat.

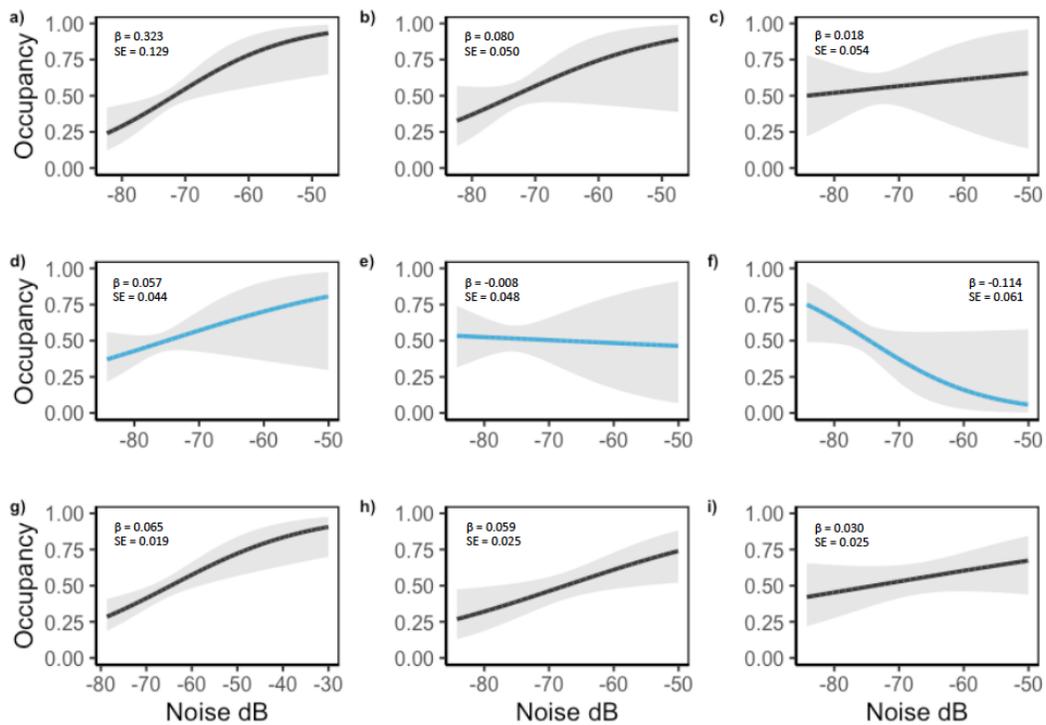


**Figure 3.7.** Change in noiseALL as a function of proportion of footprint thought to produce chronic noise. Top panel shows that relationship between proportion of footprint thought to create chronic noise and the noiseALL metric when the proportion of footprint thought to create intermittent noise was set to 0. The proportion of footprint though to create intermittent noise increases in the lower panels.



**Figure 3.8.** Lincoln's Sparrow occupancy predicted values (95% CI, gray shade) explained by a) proportion of footprint, b) proportion of open areas (grass and shrubs), c) industrial noise values (average dB from 2000 Hz to 8000 Hz frequency octave bands), and d) forest age class.

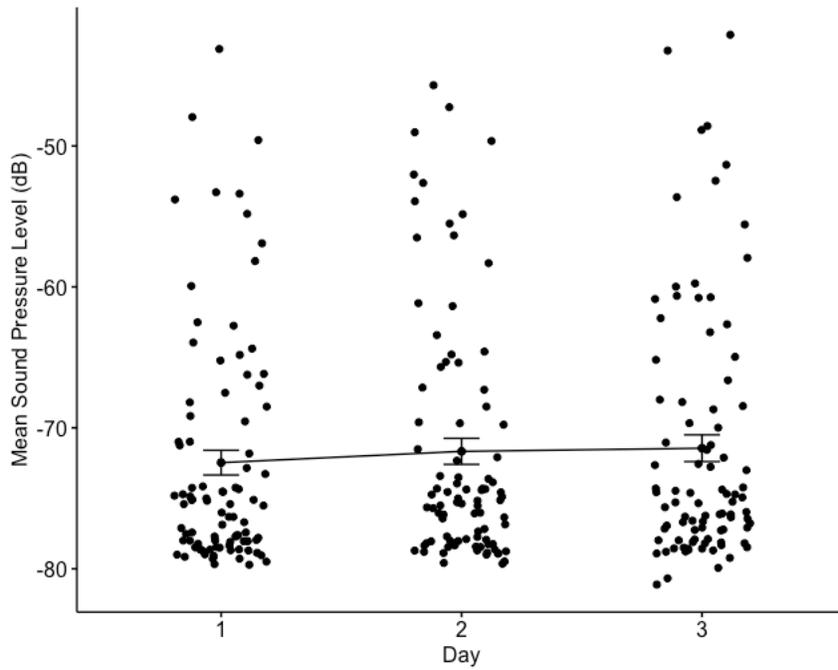
Confidence intervals for noise are shown in Figure 3.9



**Figure 3.9.** Lincoln's Sparrow occupancy predicted values (95% CI, gray shade) changed with noiseALL as unique predictor, noiseALL + vegetation, and noiseALL + vegetation + proportion of footprint (a-c). noiseHIGH as unique predictor, noiseHIGH + vegetation, and noiseHIGH + vegetation + proportion of footprint (d-f). noiseLOW as unique predictor, noiseLOW + vegetation, and noiseLOW + vegetation + proportion of footprint (g-i).

## Supplementary materials

**Supplementary material 1.** Plot of means showing the mean relative amplitude (sound pressure level) of six 1/3 octave bands (500 Hz, 1000Hz, 2000 Hz, 4000 Hz, 8000 Hz, and 16000 Hz) obtained from five randomly selected recording stations (three days at each station) for the three Big Grids.



## Chapter 4. Vocal responses of Lincoln's Sparrow to chronic industrial noise

### **Abstract**

Animal communication is effective when the transmission of the signal reaches the receiver and produces a behavioural response. Currently, the increase in anthropogenic noise is interfering with animal communication, especially for species that rely on acoustic cues. Songbirds are the most studied group regarding adaptations to deal with anthropogenic noise. The most common adaptation bird species show to anthropogenic noise is shifting the low frequency parts of their songs. However, not all the species exhibit this type of response. We compared the vocal features of Lincoln's Sparrow males breeding in noisy areas (close to compressor stations) and quiet areas in Northern Alberta, Canada. We predicted an increase in low frequency parts of their song and therefore reduced bandwidth. We also played a song to test the effect of distance (5, 10, 20, 30, 40, and 50 m) and height (1.5, 2.5, and 3.5 m) on song transmission close to compressor stations and a control quiet area to determine if behavioural adaptations allow songs to transmit more effectively. We did not find differences in low frequency, high frequency, peak frequency, or bandwidth of Lincoln Sparrow's songs between quiet and noisy areas. However, we found that birds singing in areas close to compressor stations had higher amplitude songs ( $7.67 \pm SE = 2.82$ ,  $P = 0.01$ ) and higher singing rate than birds singing in quiet areas ( $1.66 \pm SE = 0.28$ ,  $P = 0.0001$ ). Distance had an effect on song transmission in the noisy versus the quiet areas, as signal to noise ratio decreased substantially at 20 m in noisy areas but far less in controls. Height did not interact with distance and had no effect on signal to noise ratio. Thus, the two vocal behaviours used by Lincoln's Sparrows at areas influenced by noise from compressor stations were singing more songs and singing at higher volume. We greater variation in song types in

quiet areas. Singing rate could compensate for limited song transmission and higher amplitudes by increasing the likelihood of being heard by conspecifics or could reflect a difference in singing behavior related to breeding status. We found evidence of song adaptation by Lincoln's Sparrow to deal with anthropogenic noise, but whether it is enough to facilitate the long distance communication used to attract females and in male-male interactions remains unknown.

## **Introduction**

Anthropogenic noise continues to increase as part of urbanization and industrial development. A growing awareness is developing that anthropogenic noise causes habitat degradation for species that rely on acoustic signals for communication. The first report of a songbird species changing its song in urban environments for (Great tits, *Parus major*) was published in 2003 (Slabbekoorn and Peet 2003), and since then several other studies have found that songbirds are influenced by noise and in some cases adapt by varying their songs (Slabbekoorn & Ripmeester 2008, Francis et al. 2015, Shannon et al. 2016, Berger-Tal et al. 2019). Most of the studies on songbird vocal responses to noise in the field come from comparisons of birds in urban and non-urban habitats. Changes in singing behaviour in noisy areas that have been observed in birds include an increase in the low frequency part of songs (Dowling et al. 2012), increasing volume of the vocalization (Nemeth and Brumm 2010, Nemeth et al. 2013), or singing earlier in urban areas relative to rural areas (Fuller et al. 2007, Nordt and Klenke 2013, Gil et al. 2015).

Noise sources vary in both intensity and timing, creating different acoustic contexts for birds. In cities, urban noise is intermittent, especially when it is associated with roads. The time of the day and number of cars passing along a road have a strong influence on temporal variation

of noise (Fuller et al. 2007). Conversely, industrial noise tends to be chronic and often at higher amplitude levels than traffic. Chronic industrial noise produced by machinery, generators, compressor stations, and facilities are commonly associated with energy development (Francis et al. 2009, Blickley et al. 2012, Warrington et al. 2018). Therefore, songbirds singing in noisy industrial areas may be more likely to modify their vocal behaviour by changing song characteristics rather than timing of singing if song adjustments are needed to live in noisy places.

In the context of chronic noise, vocal responses reported in birds encompass different strategies. Based on results from urban noise, one documented response is an increase in the low frequency part of songs to avoid masking by anthropogenic noise (Slabbekoorn and Peet 2003, Roca et al. 2016) that concentrates the higher energy, usually below ~2kHz (Can et al. 2010, Gentry and Luther 2017). This type of vocal shift has been reported for Plumbeous Vireo (*Vireo plumbeus*) and Gray Vireo (*Vireo vicinior*) in sites with chronic noise produced by compressor stations (Francis et al. 2011a). Although the expected response is an increase in average song frequency in territories close to active oil drilling machinery, Savannah Sparrow (*Passerculus sandwichensis*) increased, and Baird's Sparrow (*Centronyx bairdii*) decreased their average song frequency (Curry et al. 2018). Other variations in response to noise have been recently documented, particularly for birds that seem to have vocal limitations compared to oscines (Gentry and Luther 2017). This is the case of two sub-oscine flycatchers, Ash-throated flycatcher (*Myiarchus cinerascens*) slightly increased while Grey flycatcher (*Empidonax wrightii*) did not change their songs close compressor stations (Francis et al. 2011b). For birds that seem to tolerate noise, the investigation on what are the strategies that are most effective to communicate in noisy acoustic environments are still required.

Adapting songs to allow for communication in noisy environments likely depends on a bird's vocal capacities. Songbirds reproduce the songs they learned in early periods in life, while others continue learning in subsequent years giving them the ability to better adapt in evolutionary time and potentially within the life time of an individual (Catchpole and Slater 2008). For those species that learn songs from tutors, the time of social interactions with conspecifics influence the songs that an individual will sing as an adult (Marler 1970, Beecher and Burt 2004, Mennill et al. 2018). For example, sparrows learn songs the year they were born and the next year when they establish territories (Baptista and Morton 1988). There are studies reporting shifts in song frequencies at noisy sites in sparrow species in urban areas (Wood and Yezerinac 2006, Luther et al. 2016) and in areas influenced by chronic industrial noise (Curry et al. 2018, Warrington et al. 2018). However, the responses to chronic noise were not consistent among the various sparrow species. Since the vocal learning period is variable in passerines, the time birds learn their songs can be associated with the number of songs that they can learn and produce (Marler 1970). This variation in song production or plasticity (Snell-Rood 2013) gives them the possibility to adjust acoustic features, song syntax, length, and timing to adapt to novel acoustic environments.

Anthropogenic noise is thought to affect birds primarily because it decreases signal transmission. According to the acoustic adaptation hypothesis, birds adjust their songs to reduce signal degradation depending on the environment (Morton 1975). Acoustic signals degraded over space, can be absorbed by vegetation, and attenuate as distance from the signaler increase (Morton 1975, Wiley and Richards 1978, Wiley and Richards 1982). In dense vegetation, song degradation increases with distance (Brown and Handford 2003, Barker et al. 2009), and songs transmit better at higher heights (Barker and Mennill 2009). In noisy areas, the high amplitudes

of noise concentrated at lower frequencies could reduce signal transmission of songs due to masking (Klump 1996, Patricelli and Blickley 2006). Additional signaling behaviours to increase signal transmission by songbirds in noisy environments include increased syllable spacing (Potvin et al. 2011) or increased singing rate (Brumm and Slater 2006). However, studies evaluating changes in signal transmission related to anthropogenic noise have been predominantly evaluating responses in urban conditions settings (Grabarczyk and Gill 2019, Grabarczyk et al. 2020) whereas chronic industrial settings remain less studied (Antze and Koper 2018).

In this study, we evaluated the vocal responses and singing behavior of a common sparrow species, the Lincoln's Sparrow (*Melospiza lincolni*), in response to chronic industrial noise in Northern Alberta, Canada. We tested two hypotheses regarding the responses to deal with noise: 1) Lincoln's Sparrow would alter its song frequency in noisy areas to avoid masking noise (noise below 2000 Hz where the higher energy is concentrated). For this, we compared the acoustic features of Lincoln's Sparrow songs close to noisy compressor stations and in quiet areas. We measured minimum frequency, maximum frequency, bandwidth, and peak frequency. 2) Lincoln's Sparrow would alter the song allocation to increase signal transmission by increasing song amplitude or singing rate. To evaluate song allocation, we measured singing behaviours of individuals such as amplitude, number of songs, and singing rate between noisy and quiet areas. We predicted a shift in the Lincoln's Sparrow song, singing high frequency and louder vocalizations in noisy areas. Additionally, we tested song attenuation of Lincoln's Sparrow at various distances and heights to evaluate patterns of song transmission in areas influenced by high levels of noise. We provide evidence for the vocal adaptations of a sparrow species with medium-high song plasticity in the context of chronic industrial noise.

## **Methods**

### ***Study species***

Lincoln's Sparrow (*Melospiza lincolni*) is a common species that inhabits the northeastern boreal forest of Canada during the breeding season. It occupies edges of shrubby meadows, bogs, or other sparse canopy forests with dense shrub cover. Perching sites in natural conditions can be variable, with males singing at the top of small shrubs or trees (Cicero 1997). Lincoln's Sparrow is more abundant than other species of birds near well sites and pipelines (Bayne et al. 2016) and has higher occupancy rates in areas with larger energy sector footprints (Chapter 3). Wellpads are cleared areas that regenerate after oil exploration connected to pipelines for oil transportation but have no chronic noise. Selection for areas near well pads and pipelines suggests that that Lincoln's Sparrow is capable of living in disturbed landscapes.

Vocal features of Lincoln's Sparrow songs, such as wide bandwidth and high frequency (frequency range 1.5-7.5 kHz), could also reflect preferences to breed in open areas with scattered shrubs and reflect adaptations to communicate in open habitats. These traits and the medium repertoire size make Lincoln's Sparrow a suitable species for studying specific vocal responses to chronic noise.

### ***Study area***

In May 2018, we selected 5 active compressor stations (noise levels can reach 109 dB) located in Northern Alberta to record breeding male Lincoln's Sparrows singing in their surroundings.

Compressor stations were located in Lac La Biche County (54°53' 44.41" N, 111°49' 17.09" W) and the distance between them ranged from 8 km to 52.5 km. A compressor station forms part of the system of roads, pipelines, wells, and other facilities created to extract and transport oil and gas located in open areas with small shrubs and grass (Bayne et al. 2008). In our study area, the forest near by the compressor stations was mostly aspen dominated (*Populus* spp.) with sparse conifers.

### ***Bird banding and song recording***

From late May to mid-July, we started bird banding and recording of Lincoln's Sparrows in quiet areas and noisy (compressor stations) locations (Figure 4.1). We started with observations of the singing locations and fly paths of each individual for 20 min with the goal of determining preferred song perches. The height of each song perch was measured at this time. Overall, we followed 30 males (15 in controls and 15 in noisy areas). We then set up two or three mist nets (6 meters long, 2.6 m height, mesh size 32 mm) to capture the focal bird at a subset of locations (15 males and 2 females in areas closer to the compressor station). Birds were banded it with color-rings in a sequence of unique combination of colors and a metal band with a unique number. This allowed us to confirm the ID of the bird when we recorded its songs and more importantly, to confirm that the same individual used the singing perch the following day. Most birds were recorded within 10 - 15 min of banding as well as the following day for the same period of time. Males in quiet areas were recorded at least 800 m away from the compressor stations. Based on our observation of banded birds, we were confident that singing perches of individuals could be accurately identified even without banding. Previous observations of individual males from other

studies also suggest that individuals show strong fidelity to singing perches (Cicero and Benowitz-Fredericks 2000).

We recorded Lincoln's Sparrows' songs using a Marantz PMD661 digital recorder, a Sennheiser ME66/K6 microphone, and a parabola. The files were saved in a .wav format with a 44.1 kHz sampling rate, 16 bit resolution, and the manual recording level control was set to 5 before starting recording. The recording period was from 0400 h to 0700 h. Lincoln's Sparrows start singing earlier than other boreal birds and have the ability to sing on colder mornings (Beaulieu and Sockman 2012). When recording the males, we stayed about 5 m away. In all the recording sessions, we identified the singing male and our presence did not seem to discourage the male from singing. In addition to the recordings obtained manually, we deployed two Autonomous Recording Units (ARUs), one in the tree where the bird was singing and a second recorder on the nearest tree or shrub (2 -3 m away). The ARUs recorded the songs of the bird for two or three consecutive days from 0400 h to 0700 h continuously. We used SM4 recorders (Wildlife Acoustics). The SM4 recorders have two omni-directional microphones (SMM-A2 sensitivity:  $-9 \pm 4$  dB,  $0$  dB=1V/pa at 1kHz), recording in stereo format at 44.1 kHz with a 16-bit resolution in a WAV format. With the recordings from the ARUs we increased the recording effort and the number of songs recorded per male.

### *Acoustic features*

We extracted acoustic measurements of individuals singing close to compressor stations and in quiet areas. Using the threshold method (Podos 1997, Ríos-Chelén et al. 2017), we defined the lower frequency part of the song, the higher frequency part, the bandwidth, and the peak

frequency. The threshold used was -25.5 dB from the highest dB levels recorded per song; this threshold included the lower frequency syllables observed in Lincoln's Sparrow songs. The threshold method is recommended for non-calibrated recorders and when there is a combination of recorders used to collect acoustic data (Zollinger et al. 2012). Relative amplitude measurements, average decibels and decibels at the peak frequency were extracted. We obtained these measurements selecting the songs in the power spectrum view with a window size = 700 and overlap = 50. We analyzed 400 songs from 15 males singing close to compressor stations and 15 males singing in quiet areas (50.25% manual recordings and 49.75% ARU recordings). All the acoustic measurements were obtained with Raven Pro (Center for Conservation Bioacoustics 2019).

We also tested whether there was a difference in the number of songs sung in areas close to compressor stations versus quiet areas. We defined singing rate as the number of songs in a 3-minute interval, counting from the first song recorded until 3 minutes had elapsed (30% manual recordings and 70% ARU recordings). In addition, we counted the number of variants of a song and song types that an individual male sang in noisy and quiet areas using the same dataset.

### ***Song attenuation test***

To test the effect of distance and height on Lincoln's Sparrow song transmission, we performed a sound attenuation test around a compressor station and in a control area. In the noisy area, we established four transects; two in front and two on the side of the noise source, oriented parallel and perpendicular to the noise source (Supplementary materials 1). Transects represent potential Lincoln's Sparrow territories located in the vicinity of the noise source. Each transect had 6

distances with respect to the speaker (distance 0), starting at 5m, and then from 10 m to 50 m in increments of 10 m. Heights of the speaker and the recorder also varied according to observation of males perching mean height in the field (noise = 2.80 m, 95% CI = 2.52, 3.07; quiet = 1.54 m, 95 % CI = 1.22, 1.85) (Figure 4.3). We defined three heights: 1.5 m, 2.5 m, 3.5 m for both, the speaker and recorder, and an additional combination: 3.5 m height for the speaker and 1.5 m height for the recorder (exploring an alternative position of the receiver).

We recorded the Lincoln's Sparrow song played in the experiment using a Marantz PMD661 digital recorder connected to a Sennheiser ME66/K6 microphone in a WAV format, 44.1 kHz sampling rate, 16 bit resolution, and the manual recorder level fixed at 5. We used a FOXPRO FX5 speaker to playback the song. In all the trials, the volume of the song was set at 80 dB SPL, which was previously measured in the laboratory with a Sper Scientific 840018 sound level pen (detecting the song at 1 m from the speaker). The control and noisy sites were sampled on different days within a half-hour period. Differences in temperature were observed between the noisy and quiet area but the temperature did not vary significantly over the experiment at each location. We did not observe or hear any Lincoln's Sparrow individuals during the period of the experiment. The sound attenuation test in the control area was done using only a 1.5 m height.

The response variable was the Signal to Noise Ratio (SNR) obtained using the Inband Power (dB) measurement of the song offered in the software Raven Pro (Center for Conservation Bioacoustics 2019). Following Raven Pro 1.6.1 protocol, Inband Power measurements were transformed to linear units. SNR is the amount of energy in the signal relative to the background noise and was calculated subtracting the noise (adjacent section of the spectrum view without any song) of the signal of interest (song). The song used in this experiment is a song that

contains commonly used syllables, average length, two trills (syllable repetition), a high frequency syllable and a low frequency syllable, with an acoustic structure typically observed in multiple individuals (Figure 4.2). We also extracted the SNR for a trill (repetition of syllables at a high frequency) and for the lowest frequency syllable in the song to test the effect of noise on syllable transmission.

### ***Statistical Analysis***

#### *Acoustic features*

We used Linear Mixed Models (LMMs) to test differences in acoustic features of Lincoln's Sparrow songs in noisy and quiet areas (fixed effect). Individual bird was defined as the random effect in all models. We tested the effect of noise on the high frequency part of the song, low frequency part of the song, peak frequency, and bandwidth (response variables). We tested the effect of treatment noise and quiet locations on singing rate (response variable) and number of song types (response variable). In addition, we evaluated the potential differences in song amplitude (measured as average decibels and decibels at the peak frequency, response variables) in noisy and quiet areas using LMM. Using the R package "car" we obtained P-values using the function "Anova" to report the effect of a given variable (analysis of deviance) for each model. We implemented the LMMs with the R package "nlme" using RStudio 1.4.1106 (RStudio Team 2020) and R version 4.0.4 (R Core Team 2021), and reported the estimates of the models as the effect size.

### *Song attenuation test*

We constructed LMMs to test the effect of distance and height on song transmission in an area with noise produced by a compressor station. The location of each transect was the random effect included in all the models. The transect location varied in two directions (parallel and perpendicular) in relation to the sound source of the compressor station (in front and one side). These locations and the control site simulated the location of Lincoln's Sparrow territories. For this analysis, we measured the SNR for 102 songs, 102 trills, and 102 low frequency syllables. We constructed three LMMs for each response variable: song, trill, and low syllable. LMMs included distance, distance and height, and the interaction of distance and height. Lastly, we tested the effect of distance on SNR of the song in the noisy area versus the control site (height was held constant at 1.5 m). P-values indicate the effect of a variable (analysis of deviance) obtained with the function "Anova" of the R package "car" (Fox et al. 2011). Models were implemented using the R package "nlme" (Pinheiro et al. 2018). The response variables were log-transformed to obtain normality and homogeneity of variance of the residuals. Effect side plots were obtained with the R package "sjPlots" (Lüdecke 2021). All statistical analyses were conducted in RStudio 1.4.1106 (RStudio Team 2020) and R version 4.0.4 (R Core Team 2021).

### **Results**

Comparing Lincoln's Sparrow song features in noisy and quiet areas, we found that songs had similar acoustic characteristics when measuring frequency (Figure 4.4, Table 1). Bandwidth and the higher frequency part of the song had higher variation in quiet areas than in noisy areas but did not differ on average (Figure 4.4). Song length did not vary between noisy and quiet sites

(effect size = 0.109, SE = 0.07,  $p = 0.148$ ). We found that values were higher in noisy conditions than in quiet areas for each of relative amplitude measurements of songs: average decibels (effect size = 7.67, SE = 2.82,  $p = 0.01$ ; Figure 4.5) and decibels at the peak frequency (effect size = 6.66, SE = 2.76,  $p = 0.02$ ; Figure 4.5). Singing rate was higher in noisy than quiet areas ( $X^2 = 24.425$ ,  $df = 1$ ,  $p < 0.001$ ) as measured by songs per minute (effect size = 1.29, SE = 0.26,  $p = 0.0001$ ; Figure 4.6). When we included the effect of the recording method (manual, ARU) in the model, manual recordings had on average lower singing rates than ARUs (effect size = -0.79, SE = 0.31,  $p = 0.01$ ), and the effect of noise remained (effect size = 1.66, SE = 0.28,  $p < 0.0001$ ). Lastly, the number of song types in quiet places was higher (range = 2-4 song types) than in noisy places (range 1-2 song types) ( $X^2 = 50.885$ ,  $df = 1$ ,  $p < 0.001$ ) (effect size = 1.4, SE = 0.203,  $p < 0.0001$ ).

### ***Song attenuation test***

Distance and the additive effect of distance and height influenced the Signal to Noise Ratio of Lincoln's Sparrow song. As the distance increased, the signal to noise ratio decreased (LMM:  $\text{Chisq} = 375$ ,  $df = 1$ ,  $p < 0.001$ ) (Figure 4.7, Supplementary materials 2). The model that included distance and height influenced the signal to noise ratio of the song (LMM:  $X^2$  distance = 384.42,  $df = 1$ ,  $p < 0.001$ ;  $X^2$  height = 5.33,  $df = 3$ ,  $p = 0.1487$ ). When the speaker and recorders were both at a height of 1.5 m, there was a higher signal to noise ratio than when they were at 3.5 m or at the combination of 3.5 m for the speaker and 1.5 m for the recorder. The height of 2.5 m had a marginal negative effect in comparison to the other heights (Figure 4.8). There was no interaction effect between distance and height (LMM:  $X^2$  distance = 373.50,  $df = 1$ ,  $p < 0.001$ ;  $X^2$  height = 5.18,  $df = 3$ ,  $p = 0.15$ ;  $X^2$  distance:height = 0.44,  $df = 3$ ,  $p = 0.93$ ). Comparing the control area with the noisy area (site treatment = noisy, control), we found evidence that the

signal to noise ratio of the song attenuated more as distance increased in the noisy area than in the control area (LMMcontrolvsnoise:  $X^2$  distance = 198.03,  $df = 1$ ,  $p < 0.001$ ;  $X^2$  site = 38.69,  $df = 1$ ,  $p < 0.001$ ) (effect size = -0.11, SE = 0.01; effect size = -4.18, SE = 0.67; Figure 4.9).

Regarding the trills and the low frequency syllable of the Lincoln's Sparrow song, we found that distance was the only variable that had an effect on transmission (Figure 7, Table 2). There was no interaction between distance and height on Signal to Noise Ratio for the trill or the low frequency syllable (Table 2).

## **Discussion**

Anthropogenic noise sources (e.g. intermittent or chronic) create a particular context for animals to respond, avoiding the noisy area or adapting to the new acoustic conditions. Chronic noise might pose a stronger selection pressure for songbirds to adapt their vocalizations. In this study, we tested whether chronic noise had an effect on vocal features of Lincoln's Sparrow songs in sites with noise generated by compressor stations relative to quiet areas. Males breeding in noisy areas sang songs similar in the minimum frequency, maximum frequency part of the song, bandwidth, and peak frequency. We observed low variation in the high frequency part of the song and bandwidth in males singing close to compressor stations. Songs tended to have a more consistent bandwidth and high frequencies in noisy areas. Wider bandwidth songs have been associated with higher vocal performance, and with the production of more complex song structures in songbirds (Podos 1997, Phillips and Derryberry 2017). A recent study found that urban white-crowned sparrows (*Zonotrichia leucophrys*) increased the bandwidth to values similar to rural populations after a decrease in urban noise levels (Derryberry et al. 2020).

Preference for consistency in acoustic features in the Lincoln's Sparrow songs could also be due to birds singing a single song type that was more effectively transmitted in noisy environments. We found birds in quiet areas sang up to 4 song types in 3 min recordings whereas individuals in noisy areas usually sang 1 or a maximum 2 song types in the same period.

We evaluated the amplitude of the songs between the two treatments using the relative amplitude levels recorded in the song files at each treatment. The relative amplitude levels of Lincoln's Sparrow songs were higher in noisy areas. We recorded the male songs in both sites (noisy and quiet areas) at a distance of 10 m (handheld recorder with fixed gain) and the autonomous recorders were deployed on the singing perch or at 3 m maximum from the singing perch; thus, we were confident that distance to the recording device was not a major source of bias. Consequently, we provided evidence that Lincoln's Sparrow might sing louder to overcome chronic industrial noise similarly to other songbird species (Brumm 2004).

We also observed higher singing rates close to compressor stations. This behaviour reflects an adaptation observed in other birds singing in noisy environments to improve communication. Singing more songs per unit of time may increase the probability that the proper message is received (Díaz et al. 2011). This phenomenon is known as signal redundancy and it is in line with the idea of trying to improve song transmission when ambient noise increases (Wiley 1994). In the context of responses to ambient noise, singing more songs is a behaviour performed by chaffinches (*Fringilla coelebs*) in naturally noisy conditions (Brumm and Slater 2006). Experimentally, song sparrows (*Melospiza melodia*) increased song rates when exposed to simulated noise road for a short period of time (Proppe and Finch 2017). Similarly, we found that Lincoln's Sparrows in noisy conditions of high noise levels showed a higher singing rate, potentially to increase the likelihood of being heard in areas with chronic industrial noise.

An alternative explanation for the differences found in singing rates is that birds change their singing rate as a function of breeding status (Moller 1991, Gil et al. 1999). In natural conditions, unpaired Song Sparrows had a higher singing rate than paired males, and paired males sang more when the female was incubating (Foote and Barber 2009). If males in the study had lower pairing success in noisy areas, as was previously reported for Ovenbirds (*Seiurus aurocapilla*) (Habibet al. 2007), this may have contributed to the higher singing rates we observed in the noisy areas.

Testing the transmission of a Lincoln's Sparrow song with the playback experiments at different distances and heights in an area influenced by chronic industrial noise (compressor station) revealed a strong decrease of the signal to noise ratio when the distance increased, as expected. However, there was no effect of height on song transmission, suggesting that intervening vegetation does not impede song audibility. Song transmission increases at higher perching locations above 4 m (Barker and Mennill 2009, Sprau et al. 2012, Chitnis et al. 2020), higher than the ones we considered in our test. Interestingly, we observed individuals singing in higher perches in noisy areas, that could reduce predation risk (Beck & George 2000; Krams 2001) or enhance their ability to visually find and heard conspecifics (Dabelsteen 2005). These ideas have not being tested in the context of chronic industrial noise.

Since distance was the stronger predictor on song transmission, Lincoln's Sparrow might be more reliant on close communication with conspecifics in noisy areas generated by compressor stations. In the control area, signal to noise ratio of the song was not as strongly affected by distance or height. Short distance communication can be useful in the context of sexual selection (Catchpole and Slater 2008) and within members of a pair (Gorissen and Eens

2004). Evidence in the zebra finch, *Taeniopygia guttata*, in laboratory conditions suggested changes in the short-range communication due to noise (Villain et al. 2016).

In conclusion, Lincoln's Sparrows appear to use two complementary behavioural adaptations to communicate in noisy conditions at compressor stations, singing louder songs and increasing the singing rate. Both behaviours are energetically costly, which can favor short distance communication. However, long distance communication is still required to maintain territories and attract females, therefore Lincoln's Sparrows in noisy areas may have to move more to encounter males and females. This, in turn, could lead to a higher exposure to predators and ultimately lower breeding success. Further investigation on these ideas would help to elucidate fitness consequences, such as low pairing success, and therefore potential effects on Lincoln's Sparrow populations living in areas with high levels of noise

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## Tables

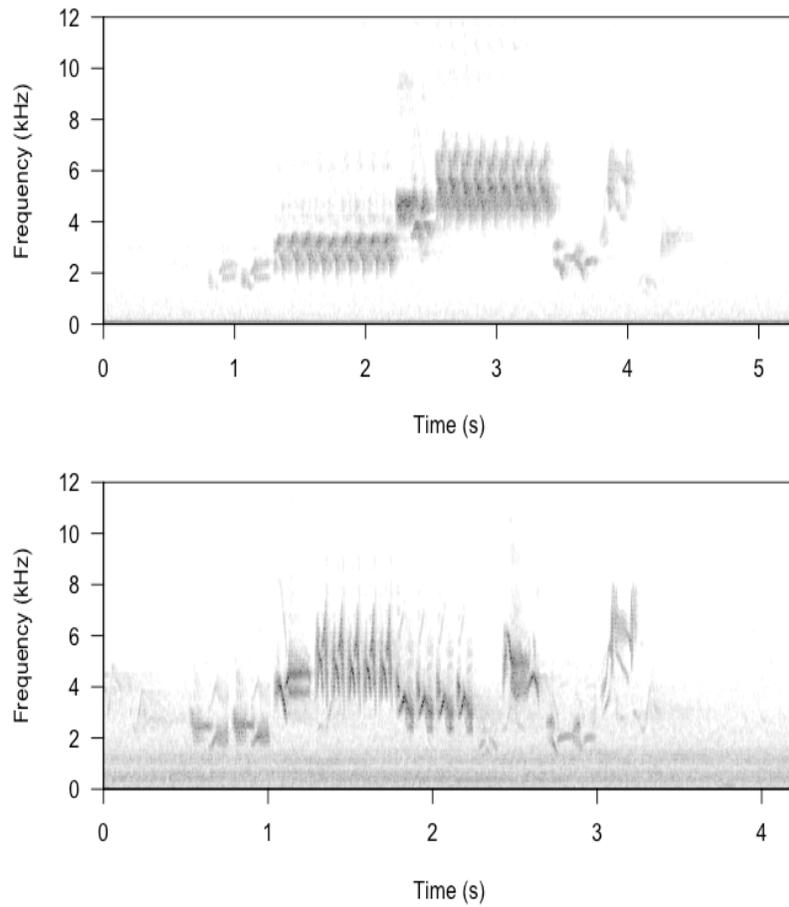
**Table 4.1.** Linear Mixed Effect models estimates and analysis of deviance testing the effect of quiet (control) versus noisy areas (compressor stations) on acoustic features of Lincoln's Sparrow songs.

<b>Model (Fixed effect)</b>	<b>Estimate</b>	<b>SD</b>	<b>Chisq</b>	<b>df</b>	<b>p-value</b>
Minimum frequency	50.4	56.5	0.7907	1	0.3739
Maximum frequency	191	119	1.8678	1	0.1717
Bandwidth	140	126	0.8567	1	0.3547
Peak frequency	24.3	230	0.2709	1	0.60

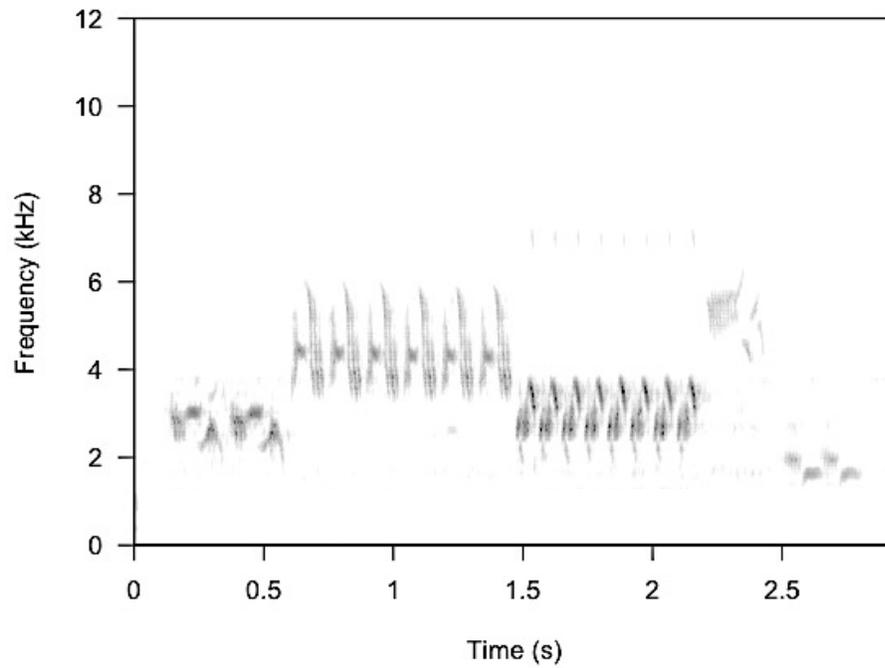
**Table 4.2.** Analysis of deviance of the Linear Mixed Effect models testing the effect of distance, height and the interaction between distance and height on the Lincoln’s Sparrow syllables (trill and low frequency syllable) transmission (Signal to Noise Ratio).

	<b>Fixed effect</b>	<b>Chisq</b>	<b>df</b>	<b>p-value</b>
<b>Trill</b>	Distance	457.11	5	<0.001
	Height	0.53	3	0.91
	Distance:Height	2.52	15	0.99
<b>Low syllable</b>	Distance	144.03	5	<0.001
	Height	1.55	3	0.67
	Distance:Height	9.57	15	0.84

## Figures

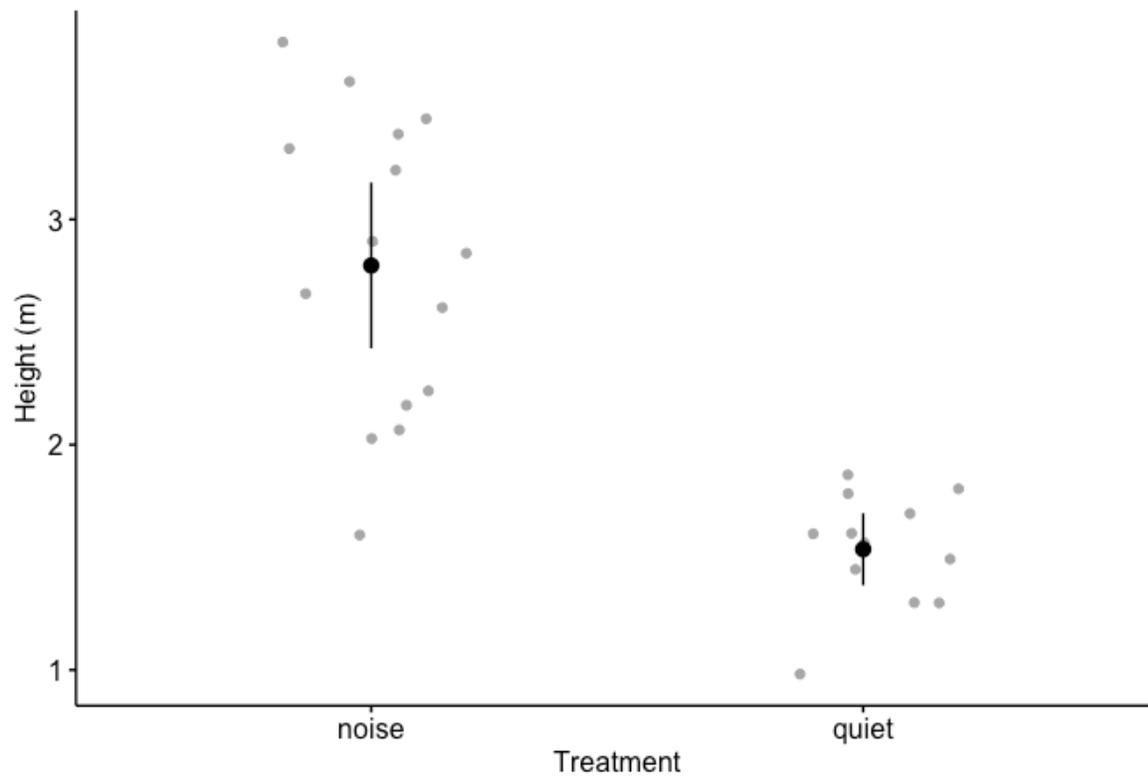


**Figure 4.1.** Spectrogram views of Lincoln’s Sparrow songs (two different males) in quiet and noisy areas. Notice the presence of low frequency syllables in both songs. Spectrograms generated with the R package “seewave”.

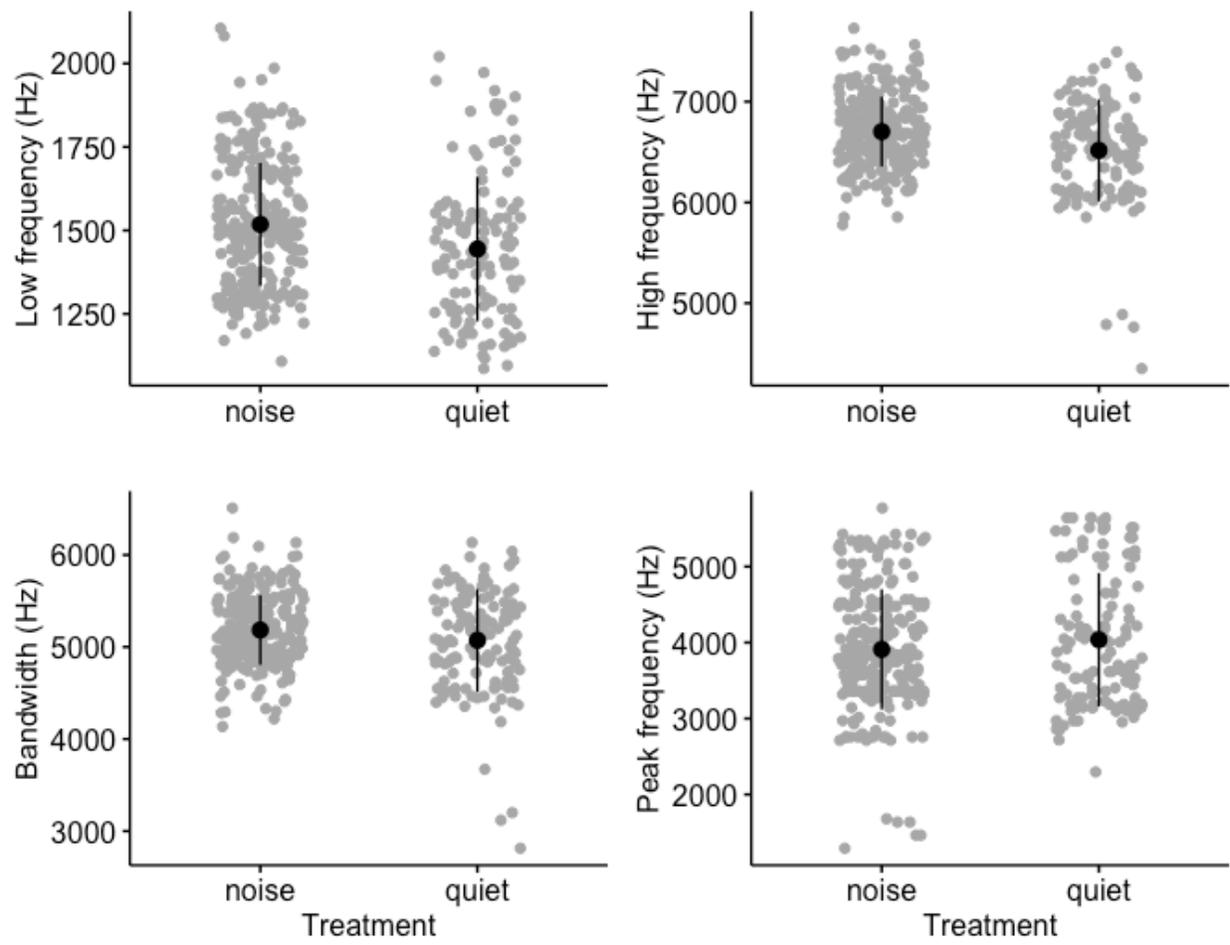


**Figure 4.2.** Spectrogram view of the Lincoln’s Sparrow song used in the playback experiment.

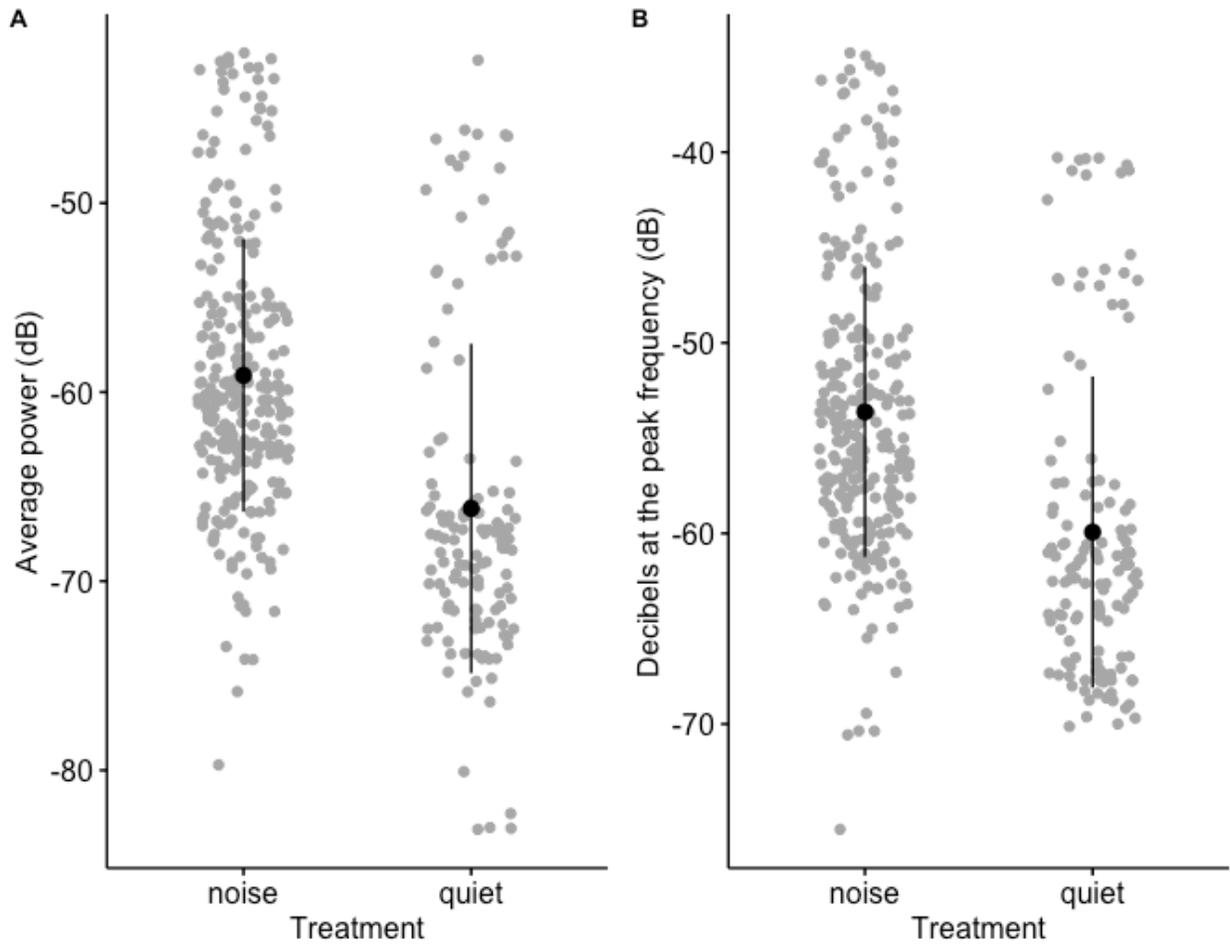
Lincoln’s Sparrow has a multisyllabic song. Syllables and trills can vary in frequency and amplitude within the song. Spectrogram generated with the R package “seewave”.



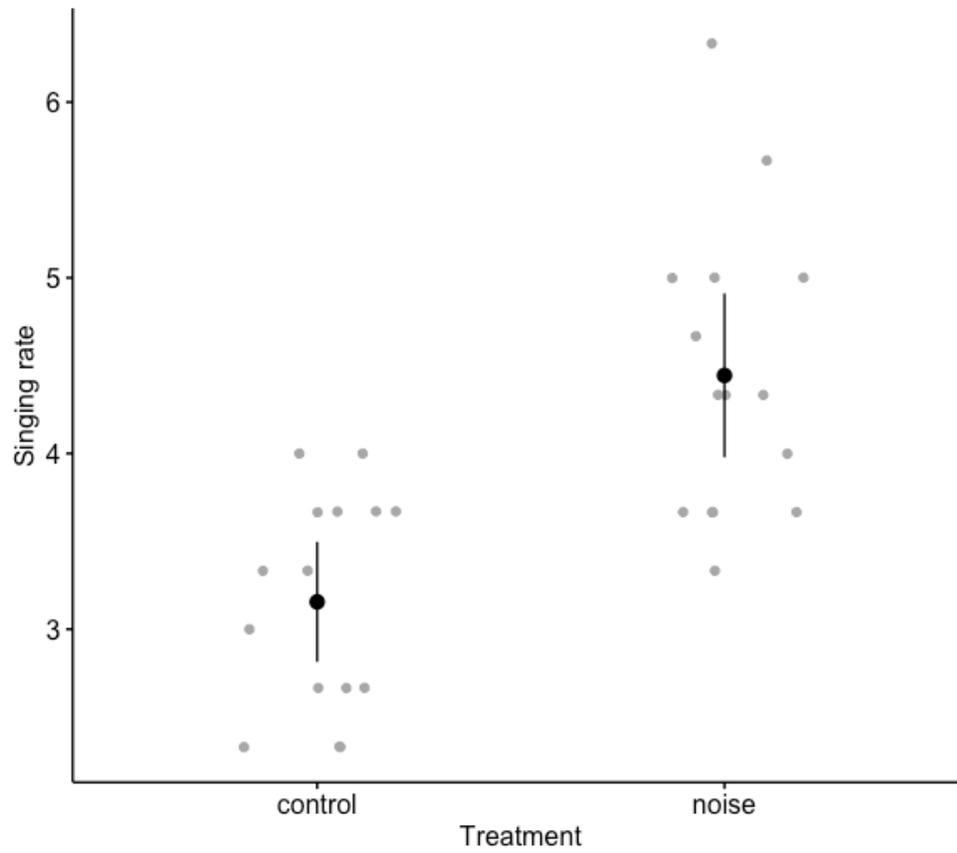
**Figure 4.3.** Singing perch height of Lincoln's Sparrows males in quiet and noisy areas (close to compressor stations). Error bars indicate 95% CI.



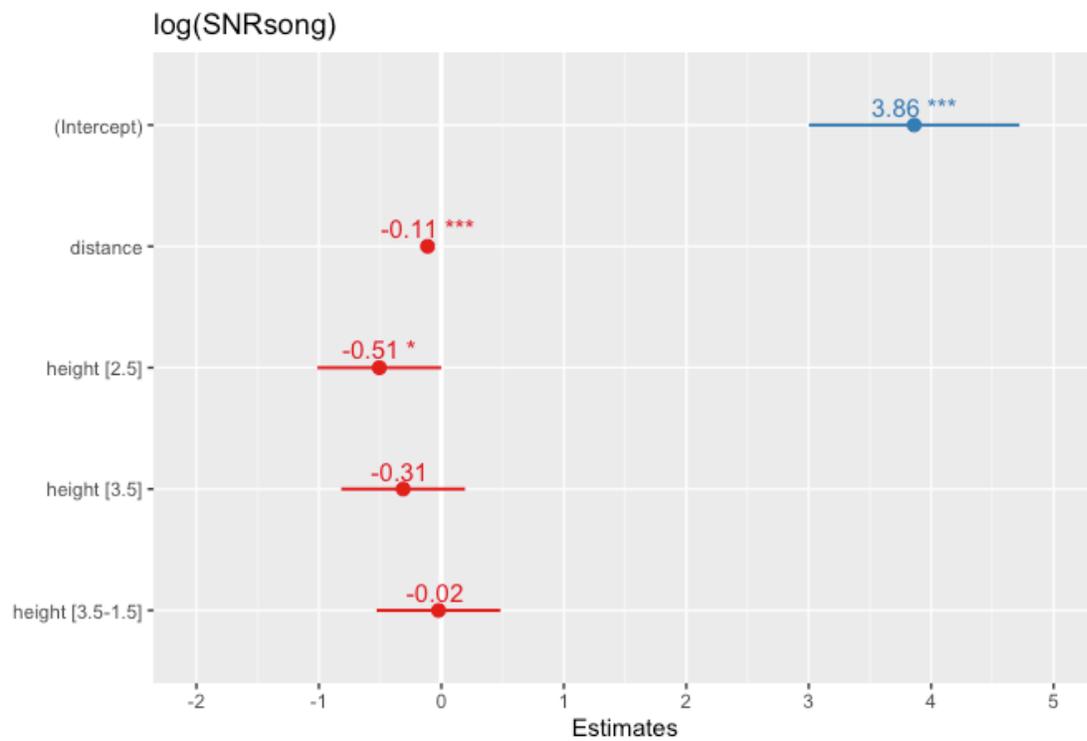
**Figure 4.4.** Comparison of Lincoln's Sparrow song features in noisy and quiet areas. Error bars indicate  $\pm$  SD.



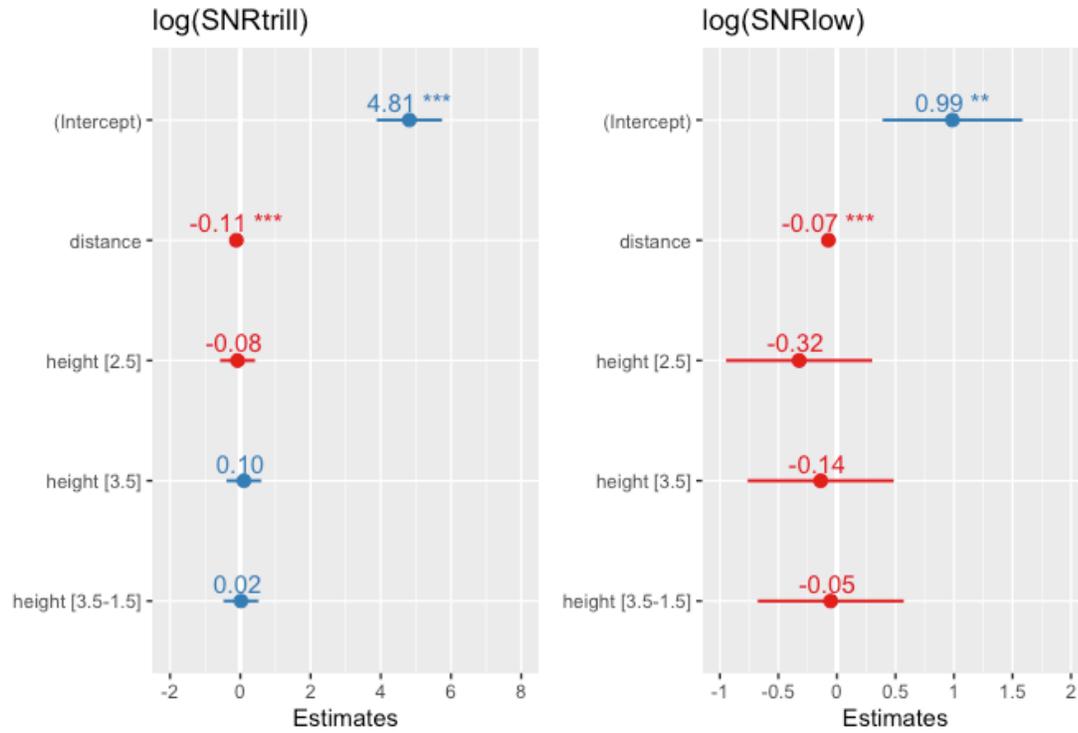
**Figure 4.5.** Differences in relative amplitude of Lincoln’s Sparrow songs singing in noisy and quiet areas (Error bars  $\pm$  SD).



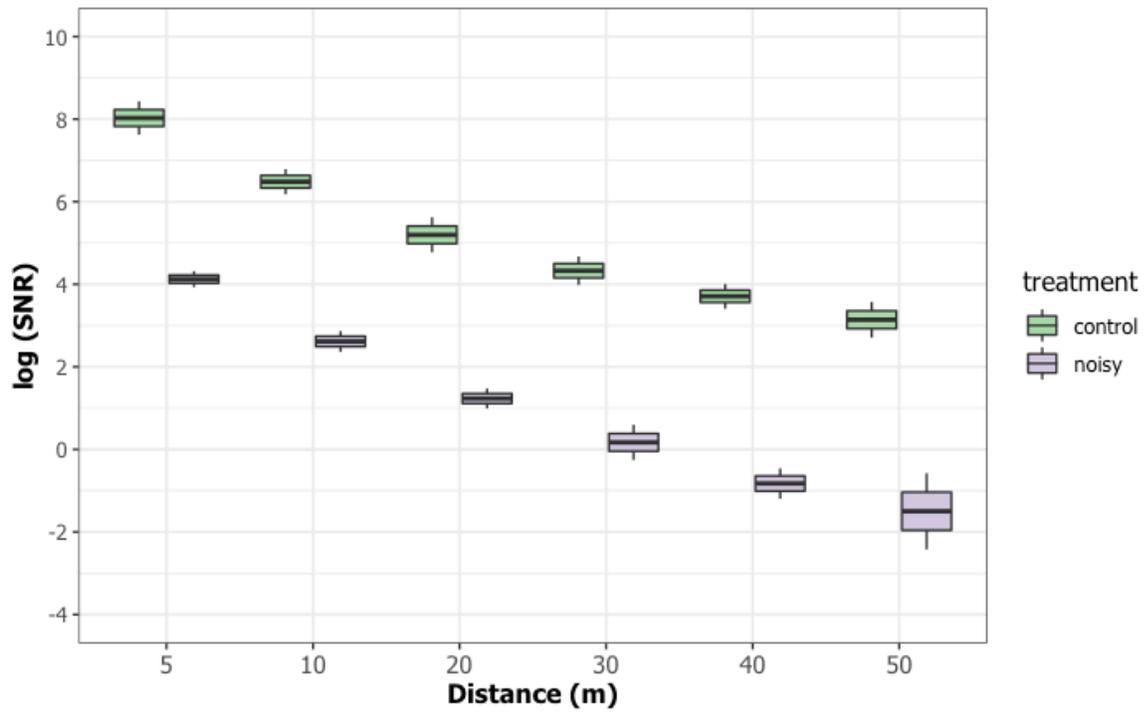
**Figure 4.6.** Singing rate in 3 min recordings of Lincoln's Sparrows males singing in quiet (control) and noisy areas (close to compressor stations). Error bars indicate 95% CI.



**Figure 4.7.** Estimates of the Linear Mixed Model with distance and height as predictors of sound attenuation of Lincoln’s Sparrow song. The symbol (\*\*\*) indicates a significant p-value.



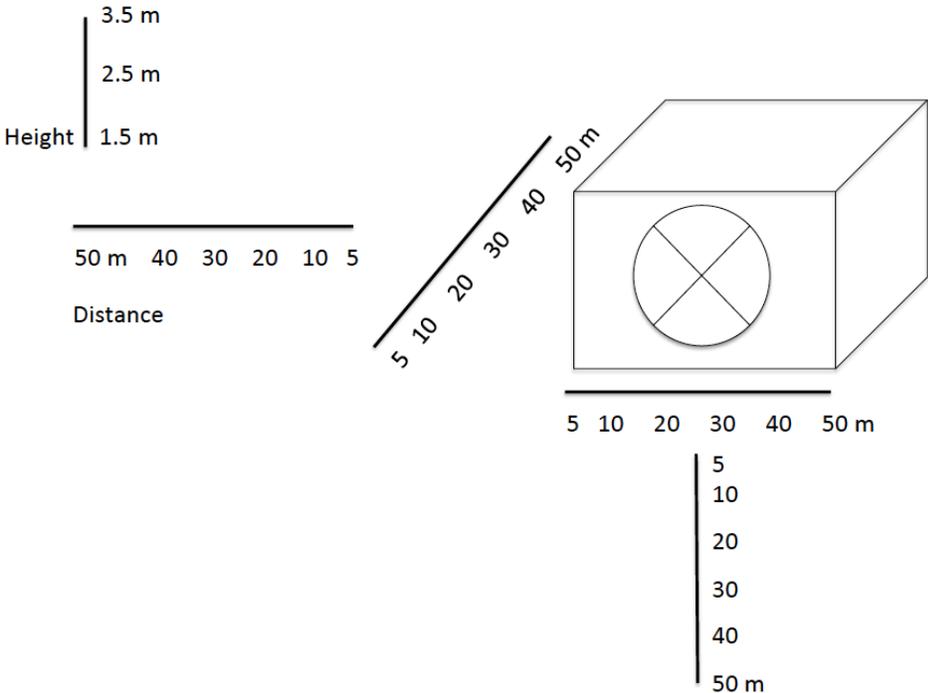
**Figure 4.8.** Estimates of the Linear Mixed Model with distance and height as predictors of trill (logSNRtrill) and low frequency syllable (logSNRlow) transmission of Lincoln’s Sparrow song. The symbol (\*\*\*) indicates a significant p-value.



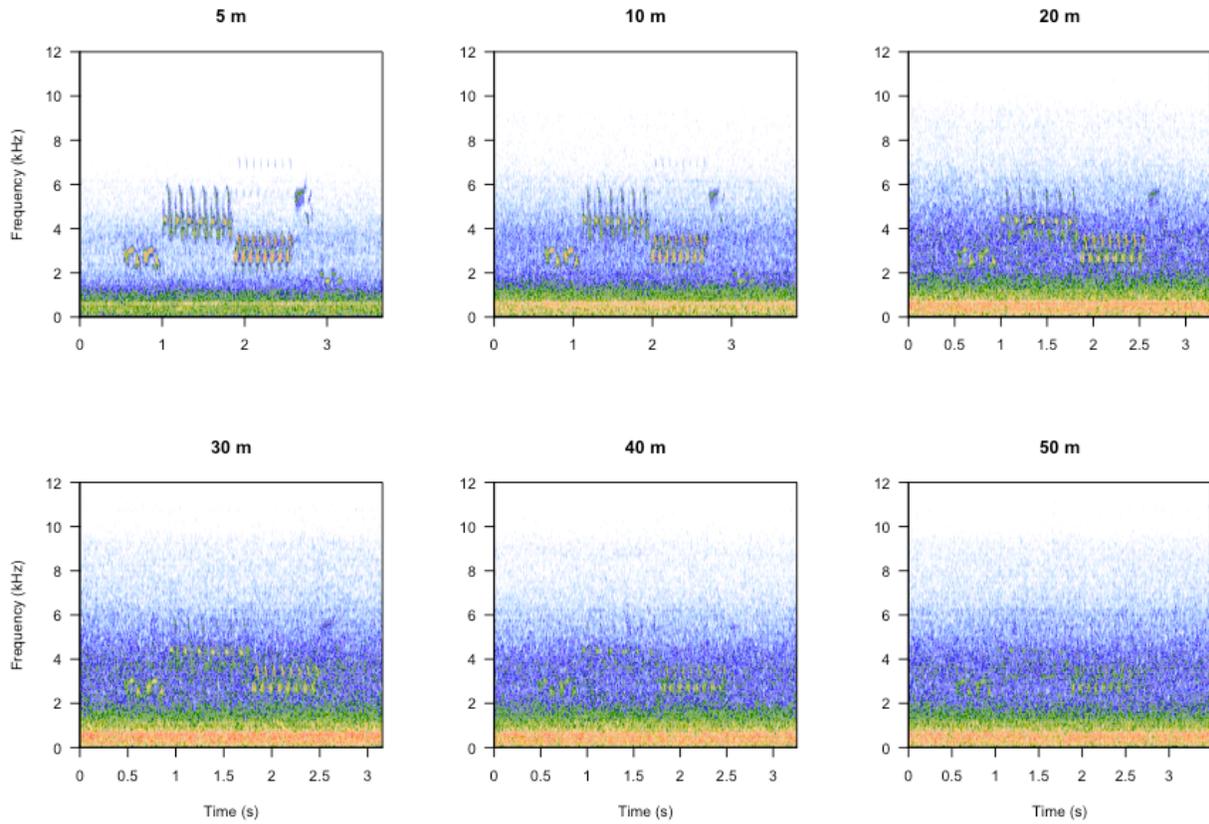
**Figure 4.9.** Graphical representation of the Signal to Noise Ratio (SNR) of the Lincoln's Sparrow song decreasing with distance in the control area and the noisy area (compressor station). Both test were performed at 1.5 m height.

**Supplementary materials**

**Supplementary materials 1.** Diagram of the location of the playback points relative to the sound source in the compressor station.



**Supplementary materials 2.** Spectrograms of the Lincoln’s Sparrow song played at different distances (speaker and recorder height = 1.5 m) located in a transect parallel to a compressor station. Spectrogram views generated with the R package “seewave”.



## Chapter 5. General discussion

The study of adaptations to new environmental conditions has become a topic of interest since negative effects on wildlife have been reported, including the effects of anthropogenic noise (Slabbekoorn and Ripmeester 2008, Barber et al. 2010, Blickley and Patricelli 2010, Gomez et al. 2016, Rosa and Koper 2018). Most of the studies on responses to anthropogenic noise by terrestrial animals come from comparisons between urban and rural areas, where noise is mainly produced by traffic (Reijnen et al. 1996, Forman et al. 2002, Perillo et al. 2017, Carral-Murrieta et al. 2020), leaving other noise sources and environments understudied (Jerem and Mathews 2021). The study of noise and especially chronic industrial noise in wildlands has been less studied than intermittent noise in cities (Bayne et al. 2008, Francis et al. 2009, Nenninger and Koper 2018). The focal species of both, urban and wild ecosystems are songbirds, since their communication relies mainly on acoustic signals (Francis et al. 2015, Shannon et al. 2016, Roca et al. 2016). The general response of some species is the avoidance of the areas influenced by noise, but others seem to tolerate this new acoustic condition. As previously stated in Chapter 3, whether some birds can tolerate high levels of chronic industrial noise remains an open area of investigation. In this dissertation, I provided insights in how the study of vocal responses of a songbird to chronic noise, the preference for disturbed areas with noise, and describing their songs in natural and less disturbed conditions, can contribute to better understand adaptations of a common species to chronic industrial noise.

In Chapter 2, I described for the first time the geographic variation of songs in Alberta, Canada, and measured the acoustic features of an understudied sparrow species, the Lincoln's Sparrow (*Melospiza lincolnii*). This sparrow is one of the most difficult sparrows species to

study because of its secretive habits. It breeds in remote boreal locations in dense shrubs close to water, such as meadows, bogs, and marshes surrounded by trees (Ammon 2020). Using autonomous recording units, it was possible to obtain recordings of multiple individuals during the breeding season, which allowed me to access acoustic data of this bird in different natural locations across Alberta. I found that Lincoln's Sparrows tended to use songs with wider bandwidths in deciduous forest (*Populus spp*); while in areas with conifers, the songs had shorter bandwidths. This suggests a potential flexibility to adjust their song according to the habitat where the birds live. Interestingly, I did not find geographic structure in their songs, unlike previous findings by Cicero and Benowitz-Fredericks (2000) in California, USA. One explanation for the lack of geographic structure could be that I was not able to record with confidence the entire repertoire of each male; alternatively, this pattern could also be explained by a potential high dispersion of juveniles that prevent the formation of dialects at this geographic scale. In terms of syllables, I found that unshared syllables (unique syllables) were lower in frequency than shared syllables in denser conifer forests. Both, the low frequency songs and unshared syllables in locations with conifers indicate a potential adaptation to increase transmission, which is in line with the acoustic adaptation hypothesis (Morton 1975, Wiley and Richards 1982). Finally, this chapter is a contribution of the use of autonomous recording units on the study of vocal features of songbirds. This type of study is usually performed with manual recorders and parabolas and/or shotgun microphones (Mennill 2011, Ehnes and Foote 2015, Shonfield and Bayne 2017). The challenge of the use of this technology is the small number of good quality recordings in comparison to masked song recordings (e.g., masked by other birds, insects, water, rain, wind, anthropogenic noise), and low amplitude recordings.

In Chapter 3, I tested the relative importance on Lincoln's Sparrow occupancy of vegetation type, which is known to be an important feature to explain habitat selection by birds (MacArthur et al. 1962, MacArthur 1964) and noise created by the oil and gas industry in Northern Alberta from facilities, compressor stations, active wells, and transportation. It was previously reported that Lincoln's Sparrow used open areas created by the energy sector, such as pipelines and well pads (Bayne et al. 2016), but these areas tend to have low levels of anthropogenic noise. Based on this, I constructed occupancy models to determine if noise predicted presence of Lincoln's Sparrow in disturbed areas. For this, I used a detection history of Lincoln's Sparrow on three consecutive days in three sites in a gradient of high, medium, and low industrial disturbances and noise. I developed an unbiased method to measure noise using un-calibrated recordings from autonomous recording units (ARUs). I found that occupancy of the species was influenced by total proportion of disturbances, vegetation, and noise, and, in lesser degree, by specific disturbances such as seismic lines, pipelines, or roads. Lincoln's Sparrow occupancy increased as natural open areas (grass and shrubs) increased, proportion of industrial settings increased, and noise levels decreased. These results can be interpreted as a preference for areas with regeneration of clearings surrounded by facilities and/or compressor stations, areas with fewer conifers, and a tolerance to moderate-high levels of noise. In light of the responses to noise by songbirds, this species seems to be tolerant of noise, which led me to ask what are the behaviours explaining the high probability of finding a Lincoln's Sparrow in a site with high levels of industrial noise?

In Chapter 4, I compared the vocal behaviours of Lincoln's Sparrow in areas near compressor stations (that had high levels of chronic industrial noise) with quiet areas. Others found that Savannah Sparrows adjusted their songs to areas with chronic industrial noise (Curry

et al. 2018) and that Song Sparrows adjusted their songs in urban areas with higher levels of anthropogenic noise (Wood and Yezerinac 2006.). Alternative responses to noise include increased amplitude and singing rates (Brumm 2004, Nemeth and Brumm 2010). Therefore, I hypothesized that Lincoln's Sparrow could 1) modified its frequency to overcome song masking by industrial noise, or 2) allocate more energy to increase the amplitude of the vocalizations and singing rates. I found support to the second hypothesis. Lincoln's Sparrows singing in areas influenced by chronic industrial noise had increased amplitude in their vocalizations and a higher singing rate than individuals in quiet areas. Increasing the amplitude as ambient noise increased is an expected response in animals known as the Lombard effect (Zollinger and Brumm, 2011). As amplitude increases, the frequency of a vocalization also tends to increase, which has resulted in confounding responses of frequency shifts in songbirds (Zollinger et al. 2012). I addressed this in two ways. First, I used the recommended threshold method (Podos 1997, Ríos-Chelén et al. 2017) to measure the acoustic features, specifically the low frequency part of the song with the power spectrum view instead the spectrogram view. Second, I used a handheld recording unit with a fixed level of gain maintained when I was recording the singing males. I also used ARUs that have fixed gain deployed on the singing perch. In addition, I provided evidence that the use of ARUs can be a useful tool to record the repertoire of Lincoln's Sparrow (Chapter 2) if it is deploy on the singing perch.

The other behaviour observed to improve communication in the context of chronic noise was the higher singing rate. This behaviour could be an adaptation to increase detection by conspecifics, but it could also be a signal of breeding status because unpaired males could sing more. Although I observed two paired males near compressor stations, and one of the females I captured had a brood patch, I was not able to observe the breeding status for all males. Further

investigation is needed to describe the singing behaviour of Lincoln's Sparrow in relation to its breeding status in natural conditions to have a more comprehensive understanding of their response in modified environments. It is possible that unpaired birds are establishing breeding territories in less suitable conditions, as previously reported for ovenbirds (Habib et al. 2007) and many other species (Reijnen et al. 1996, Reijnen and Foppen 2006), thereby impairing their breeding success.

An additional song attenuation test via playbacks revealed that Lincoln's Sparrow song was highly masked by chronic noise as the distance increased, but higher playback locations did not improve song transmission. I found this test highly valuable in providing evidence that long distance communication in these areas could be reduced, altering fundamental interactions such as territory maintenance and female attraction. This finding is in accordance with potential low pairing success for those males inhabiting areas with chronic noise.

### **Summary and final conclusions**

All the chapters of this dissertation included the use of acoustic data collected with ARUs. This new tool allowed me to study the songs of a sparrow species, the Lincoln's Sparrow, that has been overlooked in comparison to its sister species, the Song Sparrow (Harris and Lemon 1972, Marler and Peters 1982, Searcy et al. 1995, Peters et al. 2000) and the Swamp Sparrow (Searcy et al. 1982, Marler and Pickert 1984). I was also able to use detection data from a systematic design of ARUs deployed in the oil and gas industry in Northern Alberta, Canada, to understand occupancy patterns of the focal species across a range of disturbances, vegetation types, and noise that were not biased by roads or trails as occurs in some other occupancy studies

(e.g. Forman and Deblinger 2000, Brotons and Herrando 2001, Arévalo and Newhard 2011, Goodwin and Shriver 2011). The experimental design and the noise metrics developed in Chapter 3, can be used to answer similar questions on less common species, since ARUs are useful tools applied in monitoring programs of rare species and species of concern (Campos-Cerqueira and Aide 2016, Sugai et al. 2020). I contributed to the field of bioacoustics describing the geographic variation and acoustic characteristics of Lincoln's Sparrow. I describe that Lincoln's Sparrow can be tolerant to moderate and high levels of chronic industrial noise and which vocal strategies can explain this findings. I tested experimentally Lincoln's Sparrow song transmission using a playback technique in areas influenced by chronic industrial noise. This provided evidence for the nature of song transmission in chronic noise conditions in the field, but more importantly showed the impaired song transmission at very short distances, with potential effects in communication and fitness. I also reported a behavior of being more exposed in higher trees in noisy areas, which might increase communication, but at the same time could increase predation risk by flying predators (an ecological trap).

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