The effects of oil and gas infrastructure noise on alarm communication in Savannah sparrows *(Passerculus sandwichensis)*

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ABSTRACT

Anthropogenic noise may interfere with avian acoustic communication, however some species alter the structure of vocalizations, to improve transmission in noise. Here, I conducted playback experiments to determine whether compressor stations, generator or grid-powered screw pump oil wells, and overall ambient noise levels affected responses of Savannah sparrows *(Passerculus sandwichensis)* to conspecific alarm calls at their nests. I also measured the structure of alarm calls, to determine whether Savannah sparrows altered vocalizations in noise. On control sites, Savannah sparrows responded to alarm calls by delaying provisioning visits. At compressor station sites, the loudest infrastructure treatment, they showed less of a delay. Close to compressor stations, Savannah sparrows lowered the frequency and increased the bandwidth of alarm calls. These findings suggest the compressor stations may interfere with anti-predator communication, but that Savannah sparrows can alter the structure of alarm calls at these sites, perhaps mitigating some effects of noise.

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CHAPTER 1: INTRODUCTION

1.1 Background

Grassland songbirds are declining at a faster rate than songbirds of any other ecosystem in North America (Herkert 1995; Sauer et al. 2012). In southern Alberta, increasing development from the oil and gas industry may negatively affect grassland songbird populations. One way that development may impact songbirds is if ambient noise produced by infrastructure prevents birds from detecting and responding to acoustic signals. Previous research has shown that anthropogenic noise has the potential to prevent female birds from detecting male songs (Habib et al. 2007), and nestlings from detecting parental feeding (Leonard and Horn 2012) and alarm signals (McIntyre et al. 2014). However, many species are also able to adapt to noise by shifting the frequency (Slabberkoon and Peet 2003), amplitude (Brumm 2004), rate (Brumm and Slater 2006), or tonality (Hanna et al. 2011) of vocalizations, so they can be detected over background interference.

Many birds respond to potential threats close to their nests by emitting alarm calls. These calls can function to solicit help in fending off a predator (Gill and Sealy 2003), warning others of approaching danger (Bernath-Plaisted and Yasukawa 2011), or signaling to predators that they have been detected (Bergstrom and Lachmann 2001). When nests are particularly exposed (e.g. cup nesting and ground nesting species) birds may respond to alarm calls close to their nests by delaying provisioning visits, so as to avoid revealing their nest's location to predators (Bernath-Plaisted and Yasukawa 2011). Responding appropriately to these calls may determine whether or not an individual or their nest survives, so if anthropogenic noise masks these signals (McIntyre et al. 2014), the fitness consequences for birds living in noisy areas could be significant. However, if birds are able to adapt to noise by altering the structure of alarm calls, so they can be

heard over background interference, anthropogenic noise may present less of a problem.

Despite the importance of anti-predator signaling to survival and reproductive success, much of the research on the effects of anthropogenic noise on acoustic communication has focused on territorial singing (e.g. Slabbekoorn and Peet 2003, Brumm 2004, Wood and Yezerinac 2006, Habib et al. 2007, Hanna et al. 2011, Lenske and La 2014, Gough et al. 2014) while the body of research on the effects of noise on alarm communication is comparatively much smaller (Lowry et al. 2012, McIntyre et al. 2014, Potvin et al. 2014).

This thesis aimed to determine whether ambient noise produced by gas compressor stations and grid-powered and generator-powered screw pump oil wells compromises the ability of Savannah sparrows (*Passerculus sandwichensis*), a common grassland generalist, to detect and respond to alarm calls, and to determine whether they are able to adapt to noise by changing the structure of vocalizations to improve transmission in noise. As a ground nesting bird, Savannah sparrows may be particularly dependent on effective anti-predator behaviours to adequately protect their nests from predators, so if anthropogenic noise interferes with anti-predator communication, the consequences for reproductive success could be significant. However, Savannah sparrows have also been shown to exhibit high levels of vocal adaptability (Williams et al. 2013) so may be able to alter calls to overcome interference.

1.2 Objectives

1. Determine whether oil infrastructure noise prevents adult Savannah sparrows from responding appropriately to alarm signals close to their nests

   a. Determine whether Savannah sparrows respond to alarm calls by delaying feeding visits

   b. Determine whether that delay is altered in the presence of oil and gas

infrastructure, or at increasing levels of overall (natural and artificial) ambient noise measured independently from infrastructure treatment

2. Determine whether Savannah sparrows adapt to noise by altering the structure of alarm calls to improve transmission in noise

    a. Determine whether Savannah sparrows alter the acoustic structure of alarm calls in proximity to oil and gas infrastructure, or with increasing levels of ambient noise measured independently from infrastructure treatment

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CHAPTER 2: LITERATURE REVIEW

2.1 Decline of grassland songbirds

Grassland songbirds are declining at a faster rate than songbirds of any other ecosystem in North America. Between 1966 and 2011, 16 out of 28 species of grassland bird encountered on Breeding Bird Survey routes had declined significantly, while only one species had shown a significant increase (Sauer et al. 2012). For some species, population declines are consistent throughout their breeding range, while for others, trends vary by region (Askins et al. 2007). In Southern Alberta, continuous tracts of mixed grass prairie provide one of the last refuges for grassland endemics such as Sprague's pipit (*Anthus spragueii*) and chestnut-collared longspurs (*Calcarius ornatus*), as well as more widespread grassland songbirds such as Savannah sparrows (*Passerculus sandwichensis*) (Sauer et al. 2012).

The decline of grassland songbirds has been linked to the loss, alteration, and fragmentation of native grassland habitats (Askins et al. 2007). Activities that increase disturbance in native grassland, such as agriculture, human settlement, and industrial development may reduce the abundance (Sliwinski and Koper 2012) or nesting success (Vander Haegen 2007) of grassland birds, by limiting appropriate nesting habitat, or changing predator communities. Nest failure due to predation is the most important determinant of reproductive success in grassland songbirds (Davis 2003), so activities that increase nest predation rates are of particular management concern.

2.2 Oil and gas development and grassland songbirds

In southern Alberta, increasing development from the oil and gas industry may negatively affect grassland songbirds. Several species avoid areas with oil or gas infrastructure (e.g. Francis

et al. 2009, Hamilton 2012). However, the mechanisms governing the effects of industrial development on birds are poorly understood. Oil and gas development may impact songbird populations by increasing fragmentation, disturbance from human and vehicle traffic, exotic vegetation, nest predators or ambient noise (Ludlow et al. 2015). There is growing concern that ambient noise produced by oil and gas infrastructure may prevent songbirds from detecting important signals used to communicate (e.g. Habib et al. 2007).

Two common types of oil and gas infrastructure found throughout southern Alberta are screw pump oil wells and gas compressor stations. Screw pumps are relatively small oil extraction structures, which rely on positive displacement to draw oil from the ground through one or more rotating screws (Koper et al. 2016). In remote areas, these structures are powered by large generators (generator-powered screw pumps), which produce noise at $79 \pm$ SD 3.5 dB(C) at 10 m. In areas containing transmission lines, screw pumps may be connected to the power-grid (grid-powered screw pumps). Grid-powered screw pumps also produce noise; however, they are quieter than generator-powered screw pumps (59 ± 2.0 dB(C) at 10 m). Gas compressor stations are facilities designed to pressurize natural gas for distribution through pipelines, usually consisting of one or more large motor-powered turbines. These structures are significantly louder than both types of screw pump (82 ± 3.1 dB(C) at 10 m). For all three infrastructure types, sound produced is broadband, but the majority of energy is concentrated within the lower frequency ranges. Compressor stations produce the greatest amplitudes at the lowest frequencies, followed by generator-powered screw pumps, then grid-powered screw pumps (Figure 2.1).
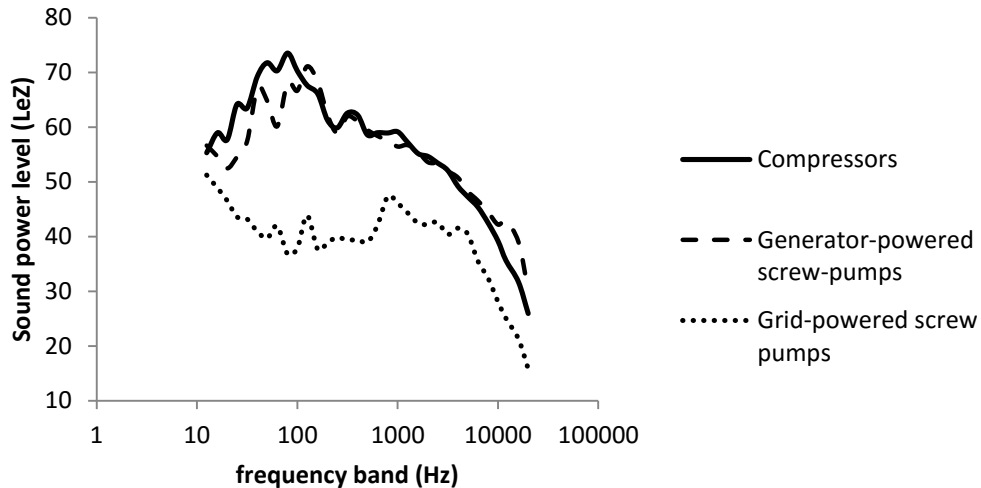
Figure 2.1. Sound profiles for ambient noise recorded 10 m from compressor stations ($n = 4$)

grid-powered screw pumps ($n = 5$) and generator-powered screw pumps ($n = 5$). Measurements

were made between April – August of 2013 and 2014 at representative infrastructure sites

located within the mixed-grass prairie surrounding Brooks, Alberta (50.5642° N, 111.898° W).

Measurements were taken at each 1/3 octave frequency band using a Bruel and Kjaer 2250 SPL

meter and frequency analyzer (dB(Z)), and averaged across all replicates for each infrastructure

type.

2.3 Anthropogenic noise and songbird communication

Many bird species rely on acoustic signals to attract mates (e.g. Wasserman 1977),

defend territories (Norwicki and Searcy 1998), solicit food from parents (e.g. Leonard and Horn

2001), and warn others of approaching predators (e.g. Bernath-Plaisted and Yasukawa 2011).

Given the importance of accurately relaying information within these signals, species have

evolved signal characteristics that transmit information in the presence of natural noise sources

such as wind, water, birds and insects (Wiley and Richards 1978). Similarly, signal receivers

have evolved the ability to detect and discriminate important information under these conditions

(Guilford and Dawkins 1991). However, anthropogenic noise from urbanization and industrial development may have different characteristics from natural noise sources that species have evolved with (Barber et al. 2010), and thus may prevent individuals from detecting or discriminating acoustic signals (e.g. Habib et al. 2007; Schroeder et al. 2012).

Anthropogenic noise may prevent birds from responding appropriately to acoustic signals. Nestling tree swallows (*Tachycineta bicolor*) failed to beg in response to the sound of adults arriving at the nest (Leonard and Horn 2012), and failed to respond to parent alarm calls (McIntyre et al. 2014a) more frequently, when exposed to elevated levels of ambient noise. Female house sparrows (*Passer domesticus*) living in noisy environments decrease provisioning rates, suggesting that noise either prevents females from detecting begging signals that nestlings use to communicate hunger, or that noise prevents nestlings from detecting and responding to parents arriving at the nest by begging (Schroeder et al. 2012). Male ovenbirds (*Seiurus aurocapilla*) that set up territories close to noisy compressor stations had lower pairing success than males that set up territories close to quieter well pads, suggesting that females were either less likely to detect males in noisy areas, or perceived them to be lower quality due to distortions caused by the noise (Habib et al. 2007). Anthropogenic noise has the strongest potential to mask songs that overlap in frequency with background noise. Because anthropogenic noise is generally loudest at low frequencies, birds with lower frequency songs may be disproportionally affected by noise pollution (Francis et al. 2012). Anthropogenic noise may also benefit some species, as elevated noise levels can increase nesting success by deterring nest predators from infrastructure sites or impairing their ability to find nests using auditory cues (Francis et al. 2009).

A number of species adapt to anthropogenic noise by altering the structure of vocalizations. Several species have been shown to increase the frequency (e.g. great tits (*Parus*

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major), Slabbekoorn & Peet 2003; song sparrows (*Melospiza melodia*), Wood and Yezerinac

2003) of songs, to avoid interference from low frequency background noise. When frequency

overlap between background noise and vocalizations is minimal, birds may also lower the

frequency of vocalizations, as lower frequency sounds transmit farther than higher frequency

sounds (Marten and Marler 1977, Potvin et al. 2014). Other species may increase the amplitude

of vocalizations (e.g. nightingales (*Luscinia megarhynchos*), Brumm 2004) to improve the signal

to noise ratio, increase the rate or duration of vocalizing to increase the chances conspecifics will

hear them through signal redundancy (Brumm and Slater 2006), or reduce the entropy or

bandwidth of vocalizations, as tonal signals transmit better than broadband signals (Hanna et al.

2011). Alterations to call structure are not limited to adult birds. Nestling tree swallows increase

the amplitude of begging vocalizations when exposed to noise in the short term (Leonard and

Horn 2005), and increase the minimum frequency and reduce the bandwidth of begging calls

when exposed to noise over the long term, even after noise is removed (Leonard and Horn 2008).

2.4 Alarm communication

Many birds rely on alarm calling to solicit help from conspecifics (Templeton et al. 2005)

and hetero-specifics (Hurd 1996), warn mates (Bernath-Plaisted and Yasukawa 2011) or

offspring (McIntyre et al. 2014b) of an approaching threat, or to signal to predators that they

have been detected (Bergstrom and Lachmann 2001). Higher rates of alarm calling were

correlated with a greater likelihood of nest success in red-winged blackbirds (*Agelaius

phoeniceus*) (Knight and Temple 1988), and American goldfinches (*Spinus tristis*) (Knight and

Temple 1986) indicating that for many birds, effective alarm communication is an important

determinant of reproductive success. While at least one urban-adapted bird species, the noisy

miner, was able to respond to noise by increasing the amplitude of alarm calls (Lowry 2012),

alarm calls designed primarily to warn others of a threat tend to be higher frequency (Marler 1955) and lower amplitude (Klump and Shalter 1984) than other vocalizations, which increases attenuation and therefore may make them particularly prone to masking. Further, alarm calls are typically less complex than songs (Potvin et al. 2014), so they may not be flexible enough to adapt to a changing acoustic environment. However, the fitness consequences associated with predation risk are high, so species may be under selective pressure to ensure alarm calls can be relayed even under sub-par conditions.

2.5 Savannah sparrows

Savannah sparrows breed throughout all provinces and territories in Canada and much of the Northern US (Wheelwright and Rising 2008). Like many grassland songbirds, populations are in decline throughout their breeding range. While western populations in southern Alberta have increased since 1960, their increase has been less apparent since 1980 (Sauer et al. 2012). Savannah sparrows are a popular model species for studying avian ecology and evolution, due to their high breeding densities, wide-ranging geographical distribution, and well documented behaviour (Wheelwright and Rising 2008). Long-term studies of populations on Kent Island, NB and Sable Island, NS have provided considerable information on behaviour and ecology of Savannah sparrows in eastern North America (e.g. Wheelwright and Rising 2003, Stobo and McLaren 1975). However, western populations have received less attention.

2.5.1 Breeding behaviour

Savannah sparrows begin nesting in late April or early May, although this varies by population (Wheelwright and Rising 2008). In southern Alberta, Savannah sparrows prefer nesting in micro-environments with dense grass or thick vegetation, which provides concealment

from terrestrial predators. The female choses the nest site and builds the nest over the course of 2-3 days (Wheelwright and Rising 2008). Once the nest lining is finished, she lays one egg per day until the clutch of 4-5 eggs is complete. Male Savannah sparrows rarely incubate, but actively defend the nest and are attentive to their mates during this time (Wheelwright and Rising 2008).

Eggs hatch 14-16 days after a clutch is initiated, following at least 12 days of incubation. Nestlings are born naked and blind. Nestling begging calls become audible 5 days after hatching (Wheelwright and Rising 2008). Offspring leave the nest 10-12 days after hatching. However, they may be force-fledged at as young as 7 days old, if their nest is disturbed (Pietz et al. 2012).

2.5.2 Nest defense behaviour

Savannah sparrows rely heavily on alarm calling during nest defense, alarm calling continuously when a threat is detected close to their nest (Wheelwright and Rising 2008). Savannah sparrows increase the rate of alarm calls over the course of the nesting cycle, particularly after nestlings hatch (Weatherhead 1978). While there is no literature that I am aware of that specifically describes the response of Savannah sparrows to conspecific alarm calls close to their nest during the nestling period, most adult passerines respond to alarm calls close to their nests by returning to the nest area (Gill and Sealy 2003), delaying provisioning (Bernaith-Plaisted 2011), increasing vigilance behaviour, or changing vocal behaviour (Beletsky 1989).

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2016.

CHAPTER 3: DOES OIL AND GAS INFRASTRUCTURE NOISE AFFECT RESPONSES OF SAVANNAH SPARROWS *(PASSERCULUS SANDWICHENSIS)* TO CONSPECIFIC ALARM CALLS?

Abstract

Many birds rely on anti-predator communication to protect their nests from predators, however few studies have examined the effects of anthropogenic noise on responses to alarm calls. Anthropogenic noise may impair anti-predator behaviour by masking vocalizations, preventing birds from detecting or discriminating acoustic signals, or by creating an additional stimulus they most focus on, drawing attention away from other important tasks such as predator avoidance. Here, I conducted field-based playback experiments to determine whether Savannah sparrows (*Passerculus sandwichensis)* responded to conspecific alarm calls by delaying feeding visits, and to determine whether this response was impaired in the presence of gas compressor stations or generator-powered or grid-powered screw pump oil wells. I also assessed whether alarm responses were impaired by overall noise levels, including both natural and anthropogenic noise sources, to determine whether effects were different from those of infrastructure alone. I played conspecific alarm calls, and, as a control, western meadowlark songs, to Savannah sparrows as they approached their nest to feed, and measured feeding latency. On control sites, which lacked active infrastructure, Savannah sparrows responded to alarm calls by delaying feeding visits. At compressor station sites, but not at generator or grid-powered screw pump sites, Savannah sparrows showed less of a delay. As compressor stations are the loudest infrastructure type, this suggests that infrastructure noise may prevent Savannah sparrows from responding appropriately to alarm calls. When the effects of overall noise levels were independently assessed, I found that Savannah sparrows increased feeding latency following control playbacks of western

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meadowlark songs at louder ambient background noise levels, suggesting that noise may interfere with the ability of Savannah sparrows to discriminate non-adaptive sounds in their environment from biologically relevant acoustic signals, such as alarm calls. Given that the effects of infrastructure on anti-predator behaviour were different from the effects of overall ambient noise levels, this suggests the mechanisms by which anthropogenic noise can interfere with acoustic communication may be more complex than previously thought.

3.1 Introduction

Many animals rely on alarm calls to deter predators (Bergstrom and Lachmann 2001), solicit help from conspecifics (Templeton et al. 2005), and to warn neighbours (Wilson and Hare 2004), mates (Bernath-Plaisted and Yasukawa 2011) and offspring (McIntyre et al. 2014a) about impending dangers. Alarm calls are anti-predator signals that may encode complex information regarding urgency (Sloan et al. 2005), size (Templeton et al. 2005), the type of predator (Gill and Bierema 2013) or predator behaviour (Griesser 2008). Many species respond differently to different types of alarm calls (Templeton et al. 2005, Gill and Bierema 2013), so communicating anti-predator information accurately is necessary to elicit the appropriate response from conspecifics. Responding to a potential predator can have life or death consequences, so animals are under selective pressure to ensure they are able to detect and react quickly to alarm calls (Gill and Sealy 2003). Indeed, higher rates of alarm calling during nest defense have been linked to improved nest survival for both red-winged blackbirds (*Agelaius phoeniceus*) (Knight and Temple 1988) and American goldfinches (*Spinus tristis*) (Knight and Temple 1986), suggesting that for many bird species, effective anti-predator communication is an important determinant of reproductive success. However, several factors may impair the ability of animals to display appropriate anti-predator behaviour, including hunger (Leonard et al. 2005), distracting stimuli

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(Dukas and Kamil 2000), and the presence of ambient anthropogenic noise (McIntyre et al. 2014b).

As increasing urbanization and industrial development encroaches on natural areas, there is growing concern that anthropogenic noise may interfere with acoustic communication (Slabbekoorn and Ripmeester 2008, Barber et al. 2010). Impaired communication resulting from anthropogenic noise has been linked to lower lek attendance in greater sage-grouse (*Centrocercus urophasianus*) (Blickley et al. 2012), reduced pairings success in ovenbirds (*Seiurus aurocapilla*) (Habib et al. 2007), and impaired nestling development in house sparrows (*Passer domesticus*) (Schroeder et al. 2012), indicating that the impacts of noise on communication have the potential to interfere with reproductive processes. The effects of noise on acoustic communication in individual species may lead to wider-reaching impacts on ecological communities, such as declines in occupancy and abundance of boreal songbirds (Bayne et al. 2008), and changes in avian community composition and species interactions (Francis et al. 2009).

One mechanism by which noise can interfere with acoustic communication is through frequency masking. Masking occurs when background noise overlaps with acoustic signals, thereby lowering the signal-to-noise ratio (Lohr et al., 2003) and preventing animals from appropriately detecting or discriminating information within signals. Masking can have several consequences for communication. In extreme situations, masking may prevent animals from detecting signals. For example, nestling tree swallows (*Tachycineta bicolor*) failed to detect parents arriving at the nest to feed them (Leonard and Horn 2012), and failed to detect parental alarm cues (McIntyre et al. 2014b) more frequently when exposed to elevated levels of ambient noise. When vocalizations are partially masked, noise may also prevent animals from

discriminating more complex information encoded within signals (Lohr et al. 2003). For example, avian mate-attraction songs can include subtle information regarding male quality, which may be lost if songs are partially masked. Male ovenbirds that established territories close to natural gas compressor stations had lower mating success than those living in quieter areas, a finding that has been attributed to this phenomenon (Habib et al. 2007). Finally, animals exposed to noise may decrease their response threshold, leading to a heightened rate of "false alarms" (Wiley 2006), whereby animals inappropriately respond to biologically irrelevant sounds when it is not adaptive to do so (Leonard and Horn 2012).

An alternative mechanism by which noise may prevent animals from responding appropriately to acoustic signals is through distraction. According to the "distracted prey hypothesis" (Chan et al. 2010) anthropogenic noise can add an additional stimulus that animals must focus on, drawing attention away from other important tasks such as predator avoidance. Distraction acts differently from acoustic masking in that it does not prevent animals from actually perceiving acoustic signals, but it impairs their ability to focus attention on composing an appropriate response (North and Hargreaves 1999). For example, Caribbean hermit crabs (*Coenobita clypeatus*) were less responsive to a silent looming object when exposed to playbacks of motor boat noise than they were during silence, even though noise did not hinder their ability to see the object (Chan et al. 2010). Another important aspect of the distracted prey hypothesis is that as long as noise can be perceived by an animal, it has the potential to distract them (Chan et al. 2010). Therefore the degree to which anthropogenic noise distracts may not be directly correlated with the amplitude of noise, as long as it can be heard (Banbury et al. 2001).

Savannah sparrows (*Passerculus sandwichensis*) are common and widespread, breeding in open grassy habitats throughout Canada and the northern United states. Like other ground-

nesting birds, Savannah sparrow nests are extremely vulnerable (Wheelwright and Rising 2008), so they must rely on camouflage and behavioural mechanisms for protection. When a predator is detected, Savannah sparrows emit a continuous stream of high-pitched chipping alarm calls until the danger has passed (Wheelwright and Rising 2008). However, there are no studies that I am aware of that have experimentally tested how Savannah sparrows respond to alarm calls, or how alarm calls function in nest defense.

While numerous previous studies have demonstrated that several bird species are capable of altering the structure of vocalizations in noise (Slabbekoorn and Peet 2003, Brumm 2004, Wood and Yezerinac 2006, Hanna et al. 2011, Lowry et al. 2012, Potvin et al. 2014) few studies have directly tested whether anthropogenic noise prevents birds from responding appropriately to acoustic signals (though see McIntyre et al. 2014b). Establishing whether anthropogenic noise actually impairs communication is essential to determining the degree to which industrial noise may impact fitness.

Here, I investigated whether industrial noise from oil wells and gas compressor stations prevent Savannah sparrows from responding appropriately to conspecific alarm calls at nests. I first determined how Savannah sparrows respond to conspecific alarm calls under natural conditions. I broadcast recordings of conspecific alarm calls, and as a control, the songs of a western meadowlark (*Sturnella neglecta*) (another common grassland bird found throughout the region), to Savannah sparrows prior to provisioning visits. I predicted that Savannah sparrows would respond to alarm calls by delaying feeding visits, to avoid drawing the attention of predators to their nests. To determine whether oil and gas infrastructure noise interfered with responses to alarm calls, I conducted the same experimental protocol on sites containing active, noise producing infrastructure. I predicted that if infrastructure noise prevents Savannah

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sparrows from responding appropriately to alarm calls, Savannah sparrows would show less of a delay close to noisier infrastructure and in areas characterized by louder ambient noise.

3.2 Methods

3.2.1 Study area

Research took place in native mixed-grass prairies in a 200-km radius surrounding Brooks, Alberta (50.5642° N, 111.898° W) during May – July of 2013 and 2014. Increasing development from the oil and gas industry is prominent in this area, and oil and gas extraction structures such as screw pump oil wells and natural gas compressor stations are common throughout the region. Screw pumps are relatively small oil extraction structures that rely on positive displacement to draw oil from the ground through one or more rotating screws (Koper et al. 2015). The amplitude of noise produced by screw pumps is dependent on how they are powered. Screw pumps connected to the power grid (grid-powered screw pumps) are quieter (59 $\pm$ 2.0 dB(C) at 10 m) than those powered by generators (generator-powered screw pumps, 79 $\pm$ 3.5 dB(C) at 10 m). Compressor stations are larger structures that pressurize natural gas through a combination of motors and turbines, and produce louder noise than screw pumps (82 $\pm$ 3.1 dB(C) at 10 m). Energy is concentrated within the lower frequency ranges for all infrastructure treatments, with compressors producing their greatest amplitudes at the lowest frequencies, followed by generator, then grid-powered screw pumps (Figure 2.1). Research took place on control sites, which were 200 x 800 m plots of native mixed-grass prairie located > 800 m from all paved roads and noise-producing infrastructure (~52 dB(C), $n = 12$ sites), and infrastructure treatment sites, which were 200 x 800 m plots of native mixed-grass prairie centered around one of 3 infrastructure treatments: compressor stations ($n = 4$ sites), generator-powered screw pumps ($n = 4$ sites) and grid-powered screw pumps ($n = 5$ sites). On control sites, ambient noise came

from mostly natural sources such as wind, insects and birdsong, while ambient noise on oil and gas sites originated from infrastructure, in addition to natural noise sources.

3.2.2 Response to alarm calls under natural conditions

Before establishing whether noise interferes with alarm communication, it was necessary to establish how Savannah sparrows respond to alarm calls under natural conditions. To determine whether Savannah sparrows responded to alarm calls by delaying feeding visits, I conducted playback trials at 21 nests on control sites.

To control for changes in parental investment over the course of the nesting cycle, I conducted all playback experiments when nestlings were five days old. I placed a digital recorder (Zoom H4N Handy Portable Digital Recorder with built in microphone, ZOOM Corporation, Tokyo, Japan) 30 cm from the nest, and a speaker (PureAcoustics HipBox Portable Audio Speaker, PureAcoustics Inc., Brooklyn, NY, USA) 2 m from the nest. The speaker was attached by an extension cable to an mp3 player (Apple iPod shuffle A1373: 2012-09, Apple Inc. Cupertino, California, United States) containing one of six possible alarm exemplars (Figure 3.1), which I recorded from birds in the region, but not on neighbouring territories, and, as a control, one of four possible western meadowlark song bouts (Figure 3.2), which I also recorded from birds in the region but not on study sites. I operated the iPod from a blind positioned 17-20 m from the nest. The digital recorder was also attached by an extension cable to a set of headphones, so I could hear when nestlings were begging, or when a parent arrived at the nest.

After a 10-minute period to allow birds to acclimate to the presence of the blind and equipment, I documented feeding behaviour on four provisioning visits, recording all movements within a 15-m radius of the nest as parents approached to feed. On the fifth visit, when a parent

arrived at a perch within a 15-m radius of the nest with food, I broadcast the first playback recording for 2 minutes (either Savannah sparrow alarm calls or western meadowlark songs, alternated among nests), and measured the time it took the parent to travel to the nest to feed. I recorded behaviour on two more feeding visits, and then allowed a period of 5 minutes for the birds to return to baseline behaviour before repeating the same procedure with the second playback recording. The time required to return to baseline behaviour (regular feeding intervals, no alarm calling) was determined from pilot trials during June of 2013. It was not possible to distinguish between adult Savannah sparrows, and thus nest was treated as the unit of replication in this study.

I characterized responses of Savannah sparrows to stimuli by their feeding latency, the time (in seconds) it took sparrows to travel from a perch within a 15-m radius of the nest to the nest, following the onset of conspecific alarm call or western meadowlark song playbacks. While not all perch locations were exactly the same distance from the nest for al birds, most birds paused at the same perch location prior to each feeding visit, making this distance consistent within nests. Individuals that took longer than 10 minutes (600 seconds) to feed following the onset of playback recordings were assigned a feeding latency value of 600 seconds (occurred at seven out of 60 nests, four following alarm playbacks, three following western meadowlark song playbacks). Feeding latency following each playback type was compared to feeding latency on baseline feeding visits, when no stimuli were played. A baseline feeding visit was the visit immediately prior to one on which a playback was broadcast, and baseline feeding latency was calculated as the time it took Savannah sparrows to travel to the nest from the same perch distance as on playback feeding visits. Observations from baseline feeding visits prior to both alarm and western meadowlark playbacks were combined, as there was no difference in the time

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it took Savannah sparrows to travel to the nest between pre-alarm playback and pre-western

meadowlark song playback visits (β=0.1859 SE= 0.2840, Wald's X^2=0.43 p=0.5129).

I dictated all observations into an Olympus VN-702PC digital voice recorder. I also

recorded the date, time, site ID, nest ID and wind speed at the beginning of the experiment.
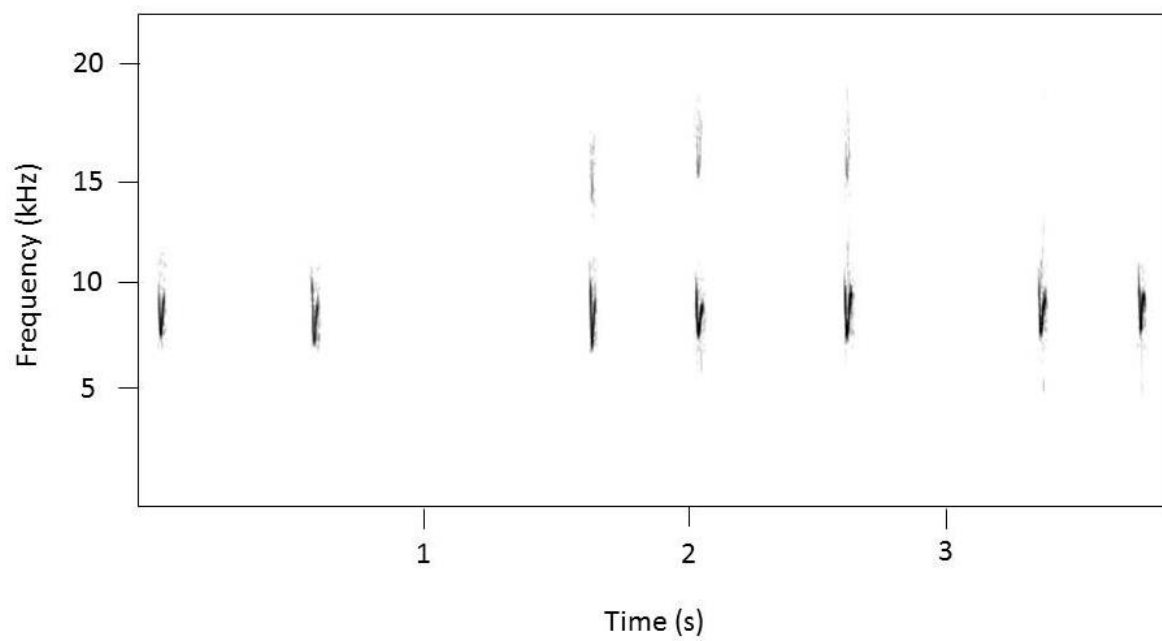
Figure 3.1. Excerpt from a representative Savannah sparrow (*Passerculus sandwichensis*) alarm

call playback. Recording was made from a field site within the vicinity of Brooks Alberta

(50.5642° N, 111.898° W) during June of 2013. The spectrogram was produced in RavenPro 1.4

using a Hann Window Function with a Fast Fourier transformation length of 512 samples, 3 dB

Bandwidth set at 135 Hz, and overlap of 50%.
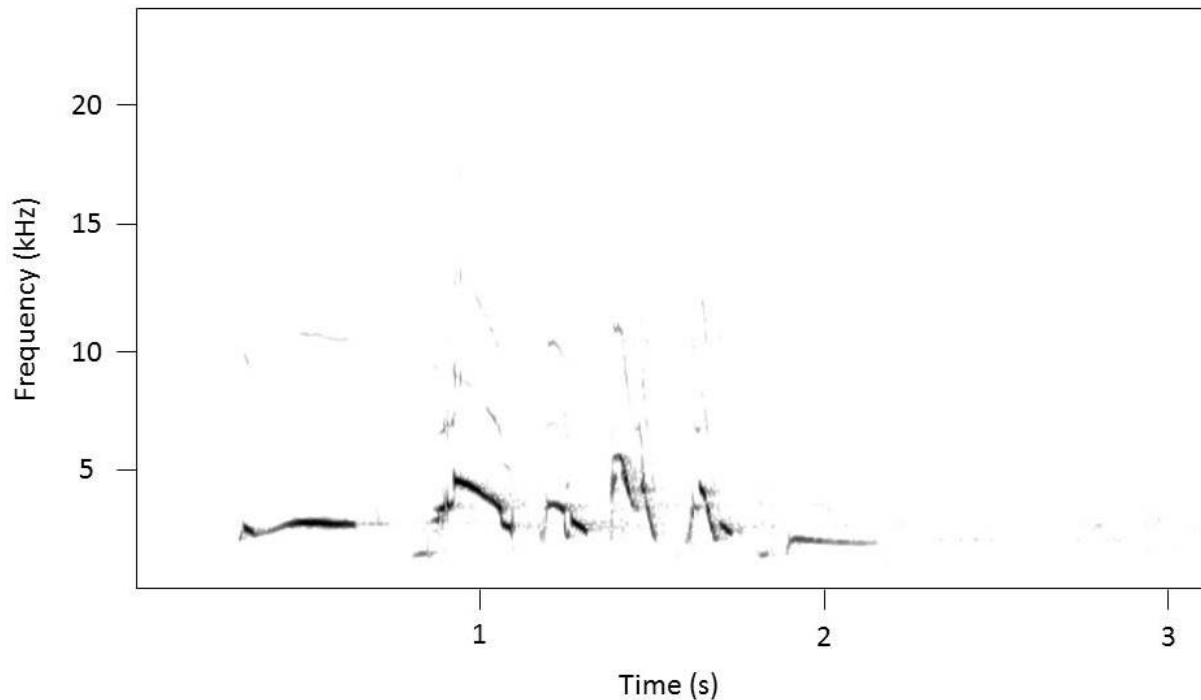
Figure 3.2. Excerpt from a representative Western meadowlark (*Sturnella neglecta*) song control playback. Recording was made from a field site within the vicinity of Brooks Alberta (50.5642° N, 111.898° W) during July of 2013. The spectrogram was produced in RavenPro 1.4 using a Hann Window Function with a Fast Fourier transformation length of 512 samples, 3 dB Bandwidth set at 135 Hz, and overlap of 50%.

3.2.3 Effects of oil and gas infrastructure on alarm responses

To determine whether infrastructure noise interferes with Savannah sparrow responses to alarm calls, meadowlark songs, or behaviour on baseline feeding visits, I conducted the same experimental protocol as above, at an additional 38 nests at sites containing active, noise-producing infrastructure (n compressor stations = 15 nests, n generator-powered screw pumps = 11 nests, n grid-powered screw pumps = 12 nests). I recorded the distance and direction to infrastructure for each

experimental nest, as well as the date, time, site ID, nest ID and wind speed at the beginning of the experiment, as on control sites.

3.2.4 Ambient noise

To quantify ambient noise levels during playback experiments, immediately following experimental trials I used a Zoom H4N digital recorder to record 30 seconds of ambient noise at a perch location within approximately 15 m of the nest, as part of the alarm call recording protocol described below in chapter 4. The microphone was oriented directly upwards for all recordings. Recording inputs were maintained constant at a sampling rate of 48kc/sec and 16-bit resolution, 100% recording volume, and 90° microphone configuration.

I uploaded recordings of ambient noise in RavenPro 1.5, using a Hann Window Function with a Fast Fourier transformation length of 512 samples, 3 dB Bandwidth set at 135 Hz, and overlap of 50%. The average power of ambient noise was measured by selecting all frequencies across the entire 30 s ambient noise recording, as well as two smaller frequency bands: 0-3000 Hz (the frequency range in which infrastructure noise is loudest) and 3000-12000 Hz (which includes the frequency range that overlaps with Savannah sparrow alarm calls). Average power was measured from power spectra. I calibrated noise levels by playing a recording of white noise of known sound pressure level, as determined using a Bruel and Kjaer 2250 SPL meter and frequency analyzer (C-weighting) 50 cm from the microphone, and digitizing the recording in Raven 1.5. I used the difference between the Raven reported sound pressure level and the actual sound pressure level of white noise to calculate the actual sound pressure level of ambient noise.

3.2.5 Statistical Analysis

Infrastructure

I used generalized linear mixed-effects models to assess the effects of infrastructure treatment on feeding latency following conspecific alarm calls, western meadowlark songs, and on baseline feeding visits when no stimuli were played. I treated playback type (conspecific alarm call, western meadowlark song, baseline), infrastructure treatment (gas compressor station, generator-powered screw pump, grid-powered screw pump, control), and their interactions as fixed effects, and nest ID as a random effect. To determine whether effects varied with distance from each infrastructure treatment, I modeled the effects of playback type, infrastructure treatment, distance from infrastructure, and their interactions on feeding latency. Where I found a significant effect of treatment or distance on baseline feeding visits, I re-ran models on each playback treatment separately, so that I could identify the effects of noise on stimuli independently as well as relative to baseline behaviour. To determine whether infrastructure treatment and distance from each infrastructure treatment altered relative responsiveness to conspecific alarm calls and western meadowlark songs, I compared feeding latency following conspecific alarm calls to feeding latency following western meadowlark songs.

Ambient noise

I used generalized linear mixed-effects models to assess the effects of broadband (0-24000 Hz), low frequency (0-3000 Hz) and high frequency (3000-12000 Hz) noise on feeding latency following the playback of conspecific alarm calls, western meadowlark songs, and on baseline feeding visits when no stimuli were played. I treated playback type, sound pressure level, and their interactions as fixed effects, while I treated nest ID as a random effect. Where I

found a significant effect of noise on baseline feeding visits, I ran models on each playback treatment separately, as above. To determine whether noise altered relative responsiveness to conspecific alarm calls and western meadowlark songs, I repeated these analyses comparing feeding latency following conspecific alarm call playbacks to feeding latency following western meadowlark song playbacks.

Wind speed

As wind represents a significant source of natural ambient noise, I used generalized linear mixed-effects models to assess the effects of wind speed on feeding latency following conspecific alarm call and western meadowlark song playbacks and on baseline feeding visits, for all nests at infrastructure and control sites. I treated playback type, wind speed and their interactions as fixed effects, and nest ID as a random effect. To determine the effects of wind on relative responsiveness to stimuli, I repeated analyses comparing feeding latency following alarm call playbacks directly to feeding latency following western meadowlark song playbacks, as above.

All analyses were completed using SAS 9.1 Statistical software. I determined the distribution of response variable residuals using diagnostics graphs and deviance/*df* ratio. The variable "feeding latency" fit a negative binomial distribution for all models. Effects were considered significant at $\alpha = 0.05$.

3.3 Results

3.3.1 Response to alarm calls under natural conditions

On control sites, Savannah sparrows responded to both conspecific alarm calls and western meadowlark songs by delaying feeding visits. On average, Savannah sparrows took 5 times longer to return to the nest following the onset of conspecific alarm call playbacks than on baseline feeding visits when no stimuli were played (β=1.7138, *SE*= 0.2015, *df*= 153 *t*=8.51, *p*<0.0001), while they took 3 times longer to return to the nest following the onset of western meadowlark song playbacks (β=1.0431, *SE*=0.2067, *df*= 153, *t*=5.05, *p*<0.0001) than on baseline feeding visits (Figure 3.3).

While Savannah sparrows responded to both sets of stimuli by delaying feeding visits, this delay was more dramatic when conspecific alarm calls were played. On average, Savannah sparrows took more than twice as long to return to the nest following the playback of conspecific alarm calls as they did following the playback of western meadowlark songs (β=0.687, *SE*=0.2404, *df*=55, *t*=2.86, *p*=0.006, Figure 3.3).

3.3.2 Effects of oil and gas infrastructure

Savannah sparrows returned to the nest faster at compressor station sites following the playback of both conspecific alarm calls (β=-0.8612 *SE*=0.3175, *df*= 153, *t*=-2.71, *p*=0.0074) and western meadowlark songs (β=-0.8561, *SE*=0.3273, *df*=153, *t*=-2.62, *p*=0.0098), relative to baseline feeding visits, than they did on control sites. At grid-powered screw pump sites, Savannah sparrows also returned to the nest faster following conspecific alarm calls (β=-0.7504 *SE*=0.3396, *df*=153, *t*=-2.21, *p*=0.0286) relative to baseline feeding visits; however, this effect may have been driven in part by a trend in increased baseline feeding latency at these sites

(β=0.441, *SE*=0.2436, *df*=153, *t*=1.81 *p*=0.0722). There was no difference in feeding latency following either playback type between generator-powered screw pump sites and control sites. There were no significant effects of infrastructure treatment on baseline feeding latency (Figure 3.3).

While Savannah sparrows were less responsive to both sets of stimuli at compressor station sites, infrastructure treatment did not affect the qualitative responsiveness to stimuli: Savannah sparrows continued to take longer to return to the nest following the playback of conspecific alarm calls than they did following the playback of western meadowlark songs, at all infrastructure treatments (Figure 3.3).
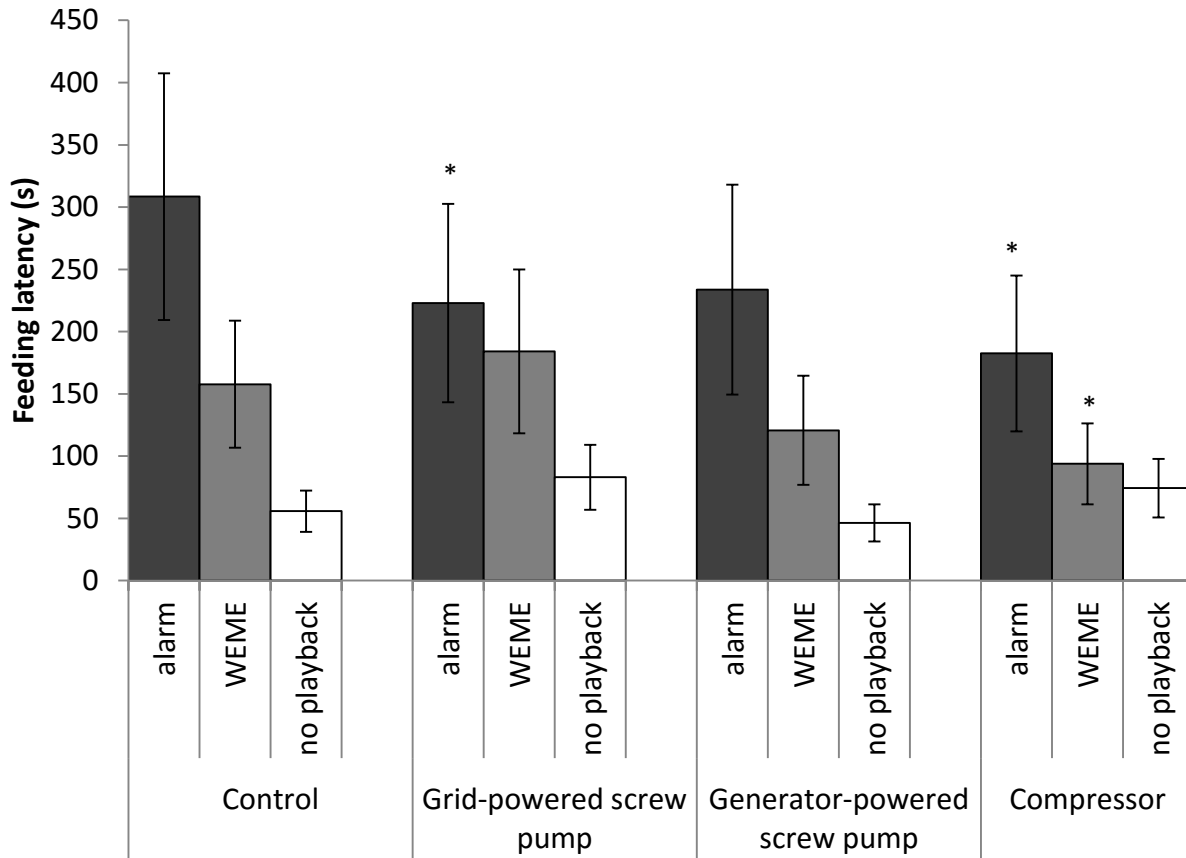
Figure 3.3. Average feeding latency (± SE) of Savannah sparrows (*Passerculus sandichensis)* in southern Alberta during May – July 2013 and 2014, following the playback of conspecific alarm calls (alarm), western meadowlark songs (WEME), and on baseline feeding visits when no stimuli were played (no playback), at control sites (*n=21*), compressor station sites (*n=15*), grid-powered screw pump site (*n=12*) and generator-powered screw pump sites (*n=11*). Asterisks indicate feeding latencies for each playback type that differ significantly from those on control sites.

Within compressor station sites, Savannah sparrows took less time to approach the nest on baseline feeding visits closer to the infrastructure than they did at the periphery of compressor

station sites (β=0.00582, *SE*=0.00228, *df*=144, *t*=2.55 *p*=0.0118, Figure 3.4). There was no effect of distance from infrastructure on feeding latency following either western meadowlark songs or conspecific alarm playbacks relative to baseline feeding visits. However, there was a trend towards a decrease in feeding latency between conspecific alarm calls and western meadowlark songs closer to compressor stations (β=0.004466, *SE*=0.002544, *df*= 51, *t*=1.76, *p*=0.0852). There was no effect of distance from generator or grid-powered screw pump sites on feeding latency on baseline feeding visits or following either playback type.
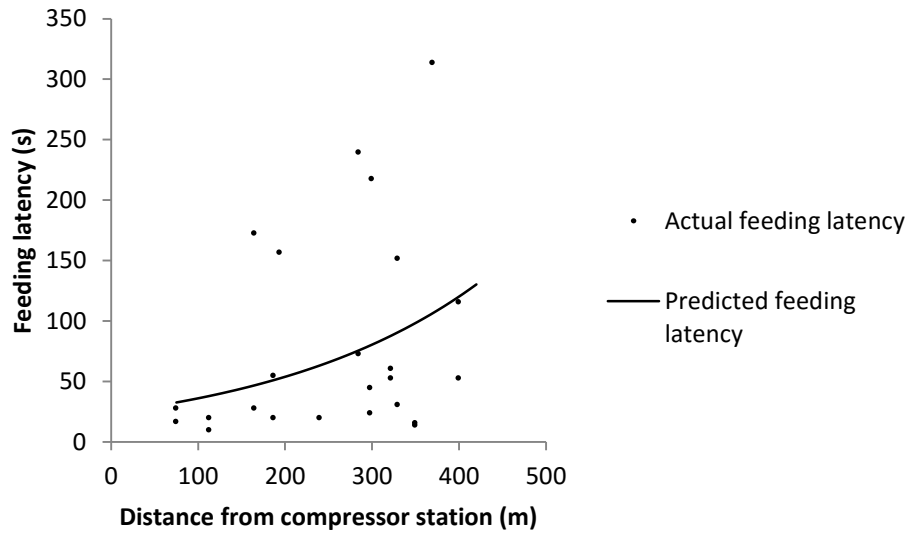
Figure 3.4. The effects of distance from compressor stations on feeding latency in Savannah sparrow (*Passerculus sandichensis)* in southern Alberta during May – July 2013 and 2014 during baseline feeding visits when no stimuli were played. *n*= 15 nests at compressor stations, 8 of which had 2 observations of baseline feeding latency, while 7 had only one observation.

3.2.3 Effects of ambient noise

Ambient noise recordings were only available for 41 out of the 60 nests at which experiments occurred, due to weather, technical difficulties and logistical constraints. Broadband noise ranged from $41 - 73$ dB(C) (mean=59 dB(C)), and was louder in the low frequency range $(50 - 82$ dB(C), mean=68 dB(C)) than the high frequency range $(21 - 48$ dB(C), mean= 30 dB(C)).

Savannah sparrows took longer to approach the nest following western meadowlark song playbacks, relative to baseline feeding visits, at increasing amplitudes of broadband (β=0.04149, SE=0.02133, df=99, t= 1.95, p=0.0546) and low-frequency noise (β=0.04135, SE=0.02127, df=99, t=1.94, p=0.0547), but not high frequency noise (Figure 3.5). There was no effect of noise level on feeding latency on baseline feeding visits or following the playback of conspecific alarm calls. There were no effects of ambient noise on the relative difference in feeding latency between conspecific alarm calls and western meadowlark songs.

a. b.
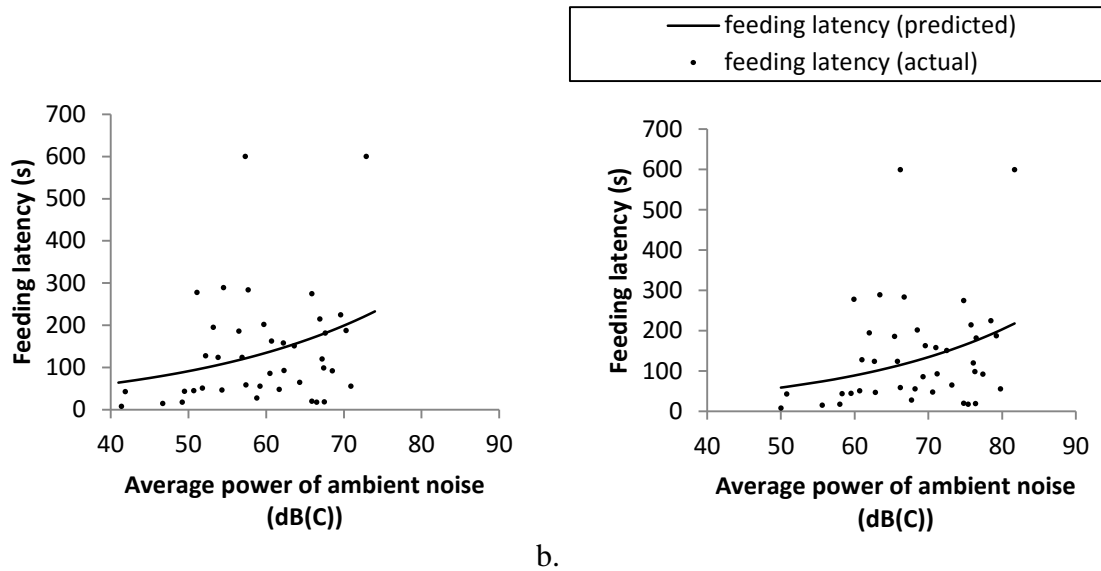
Figure 3.5 The effects of (a) broadband (0 – 24000 Hz) and (b) low frequency (0 – 3000 Hz) ambient noise on Savannah sparrow feeding latency following the playback of western meadowlark songs, n = 41 nests.

3.2.4 Effects of wind speed

Wind speed during experiments ranged from <1 – 15 km/hr (mean = 5.6 ±3.9). There was no effect of wind speed on feeding latency following either playback relative to baseline behaviour or on the relative difference in feeding latency between conspecific alarm call and western meadowlark song feeding visits (p >0.2).

3.4 Discussion

Overall, these findings support the hypothesis that Savannah sparrows respond to conspecific alarm calls by delaying feeding visits, and that this response is impaired by noise-producing infrastructure. Under natural conditions Savannah sparrows took longer to approach their nests following the playback of conspecific alarm calls than they did following control western meadowlark song playbacks and on baseline feeding visits when no stimuli were played, but at compressor station sites, Savannah sparrows approached their nests sooner than they did on control sites. This suggests that very loud infrastructure noise may prevent Savannah sparrows from responding appropriately to alarm calls, although moderate noise from oil wells may be insufficient to interfere with anti-predator communication. At louder ambient background noise levels, Savannah sparrows also increased feeding latency following playbacks of western meadowlark songs, suggesting that noise may interfere with the ability of Savannah sparrows to discriminate non-adaptive sounds in their environment from biologically relevant acoustic signals such as alarm calls (Wiley 2006, Leonard and Horn 2012).

3.4.1 Response to alarm calls under natural conditions

In the absence of anthropogenic ambient noise, Savannah sparrows responded to conspecific alarm calls by delaying feeding visits. This may be an effective anti-predator strategy for grassland breeding songbirds that build their nests directly on the ground (Wheelwright and Rising 2008), as their nests are especially vulnerable to predators. Indeed, nest predation is the leading cause for nest failure in grassland songbirds (Davis 2003), and thus these species must rely on well-camouflaged nests and cryptic behaviours to prevent their nests from being detected. Like some other bird species (e.g. the Siberian jay (*Perisoreus infaustus*), Eggers at al. 2005),

Savannah sparrows may be able to prevent their nests from being depredated by temporarily avoiding the area when a predator is in the vicinity to conceal their nest location, and thus awareness of predation risk is critical to protection of the nest. Because many grassland nest predators, such as rodents and snakes (Bernath-Plaisted 2015), are inconspicuous, parental alarm calls may function as a crucial warning system for mated pairs to signal to each other if a predator has been spotted. A similar response to alarm calls has been documented in female red-winged blackbirds (Bernath-Plaisted and Yasukawa 2011, Beletsky 1989), which delay feeding visits in response to male alarm calls. However, this is the first study that I am aware of to document this behaviour in Savannah sparrows.

Savannah sparrows also responded to the playback of western meadowlark songs by delaying feeding visits relative to baseline behaviour; however, they paused for less than half the time that they did following the playback of conspecific alarm calls. While any unexpected noise in the vicinity of their nests may be an indication of danger, birds must balance the pressure to protect their nests from potential predators with the need to provide sufficient food to their offspring (Eggers et al. 2006). Due to the extreme vulnerability of their nests (Wheelwright and Rising 2008, Davis 2003), Savannah sparrows may benefit from pausing to assess whether or not a danger is present after unexpectedly hearing any foreign noise close to their nest, but they also benefit from returning to feeding sooner than when they hear alarm calls, which are a reliable indicator of danger.

3.4.2 Effects of oil and gas infrastructure and ambient noise

Of all infrastructure treatments, compressor stations had the greatest effect on anti-predator behaviour during playback trials. At compressor station sites Savannah sparrows

approached their nests sooner following both conspecific alarm call and western meadowlark song playbacks, relative to baseline feeding visits than they did on control sites. Within compressor station sites, they also reduced feeding latency on baseline feeding visits close to the infrastructure, suggesting less caution in general during provisioning. Taken together, these findings suggest that Savannah sparrows may have been less vigilant when provisioning nestlings in the vicinity of compressor stations.

The less pronounced response to conspecific alarm call and western meadowlark song playbacks at compressor station sites could be explained by acoustic masking. Savannah sparrows still delayed feeding visits at compressor stations following playbacks, suggesting that they were able to detect the stimuli; however, this delay was far less pronounced than at control sites, suggesting that they may not have been able to discriminate information within signals regarding the level of danger. In other animals that rely heavily on acoustic cues to communicate predation risk, elements within alarm calls have been shown to encode information regarding the type of predator, or the amount of vigilance required. For example, when "chuck" elements are included in Richardson ground squirrel (*Urocitellus richardsonii*) alarm calls, conspecifics increase vigilance, and remain vigilant for longer than when these elements are not included in alarm call bouts (Sloan et al. 2005). Similarly, black-capped chickadees (*Poecile atricapillus*) produce more "d" notes when faced with smaller predators, which pose a greater threat to them, and respond to calls produced under these conditions with more aggressive mobbing behaviour (Templeton et al. 2005). Given that Savannah sparrows alarm call frequently during nest defense (Wheelwright and Rising 2008), and that acoustic elements of alarm calls vary considerably both within and between call bouts (see chapter 4), Savannah sparrow alarm calls may also encode more complex information about a predator besides the fact that it is present. If compressor

station noise prevented Savannah sparrows from discriminating such elements within conspecific alarm calls, they may have responded with less vigilance than they would under natural conditions.

However, there are some inconsistencies between the predicted effects of acoustic masking and the findings of this study. The potential for acoustic masking increases with the amplitude of ambient noise (Lohr et al. 2003, Brumm 2004) and the degree to which ambient noise overlaps in frequency with acoustic signals (Blickley and Patricelli 2012). However, I found no reduction in feeding latency with increases in ambient noise, including within the 3000 – 12000 Hz range, which overlaps in frequency with Savannah sparrow alarm calls. Furthermore, acoustic masking cannot explain why Savannah sparrows reduced feeding latency close to compressor stations during baseline feeding visits when no stimuli were played.

Lower feeding latency following playbacks at compressor station sites may be better explained by the distracting effects of anthropogenic noise than by masking. According to the distracted prey hypothesis, anthropogenic noise can reduce responsiveness to signals by adding an additional stimulus that animals must focus on (Chan et al. 2010). While it can be difficult to distinguish between masking and distraction, there are some differences in how these two mechanisms act on acoustic signals. While acoustic masking increases with the amplitude of ambient noise (Lohr et al. 2003, Brumm 2004) and the degree to which ambient noise overlaps in frequency with acoustic signals (Blickley and Patricelli 2012), distraction is independent of both these factors (Banbury et al. 2001, Smith 1989). Unlike the other infrastructure treatments, compressor stations can be heard by the human ear up to a kilometer away (personal observation), but the noise they produce may not contribute substantially to overall sound pressure level of noise throughout the compressor station sites when other natural noise sources

are present, such as wind, insects, and other birds. Distraction may also explain why Savannah sparrows reduced feeding latency during baseline feeding visits closer to compressor stations, as noise may distract Savannah sparrows from performing normal pre-provisioning anti-predator scanning (Dukas and Kamil 2000).

At grid-powered screw pump sites Savannah sparrows also had lower feeding latency following alarm calls relative to baseline feeding visits; however, this appeared to be driven primarily by a trend in increased feeding latency during baseline feeding visits. It is unlikely that this trend was caused by infrastructure noise, as grid-powered screw pumps were quieter than generator-powered screw pumps, which had no effect on anti-predator behaviour. One possibility is that Savannah sparrows were more vigilant during baseline feeding visits at grid-powered screw pump sites because of higher predator abundances. A study using the same sites and nests found that predation levels of Savannah sparrow nests were higher at grid-powered screw pump sites than on control sites or generator-powered well sites (Bernath-Plaisted 2015).

Surprisingly, increases in ambient noise were not linked to a decrease in feeding latency following either playback-type; on the contrary, Savannah sparrows increased feeding latency following western meadowlark song playbacks at higher amplitudes of ambient noise. Heightened responsiveness to inappropriate stimuli, such as western meadowlark songs, can be characterized as "false alarms", which occur when animals are not able to clearly discriminate acoustic information (Lohr et al. 2003), so increase their response threshold to all stimuli to ensure they continue to respond properly to biologically appropriate stimuli such as alarm calls (Wiley 2006). If ambient noise prevents Savannah sparrows from hearing all elements within western meadowlark songs, it may take longer for them to ascertain that these songs are not a reliable indicator of danger. However, false alarms come at a cost: if Savannah sparrows waste

too much time pausing to assess threats that are not real, they lose valuable time that could be spent provisioning nestlings (Eggers et al. 2005).

This elevated response to western meadowlark song playbacks with noise is better explained by acoustic masking than distraction. As predicted by masking (Lohr et al. 2003, Brumm 2004), post-playback feeding latency increased with the amplitude of ambient noise, and appeared to be driven primarily by low frequency noise (0 – 3000 Hz), which overlaps with the range occupied by western meadowlark songs (approx. 1500 Hz – 4700 Hz, Figure 3.2). Feeding latency following western meadowlark song playbacks did not increase at noisier infrastructure, suggesting that this effect may be driven primarily by natural noise sources in the environment, such as wind, insects and other birds (although there were no significant effects of wind speed alone on feeding latency). Given that these factors have been present throughout the evolutionary history and individual lives of Savannah sparrows, it seems unlikely that these natural noise sources would significantly affect their attentional abilities.

Taken together, these findings suggest that the effects of infrastructure on anti-predator behaviour may be different from the effects of overall ambient noise levels. These findings have significant conservation implications, as they suggest that noise reduction mechanisms may not be an effective means of reducing the impacts of oil and gas extraction structure on songbirds. The effects of distraction and masking are not mutually exclusive (Chan et al. 2010): while distraction may reduce feeding latency at compressor stations, and masking may increase post-meadowlark feeding latency with ambient noise, it is possible that both mechanisms can influence avian behaviour. Regardless of the mechanisms, the finding that Savannah sparrows are less responsive to anti-predator signals in the vicinity of compressor stations is of concern, and adds to a growing body of evidence that noisy anthropogenic structures have the potential to

negatively affect birds by interfering with acoustic communication (Habib et al. 2007, Blickley et al. 2012, Francis et al. 2012, Barber et al. 2010).

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CHAPTER 4: DO SAVANNAH SPARROWS ALTER THE STRUCTURE OF ALARM CALLS WHEN EXPOSED TO OIL AND GAS INFRASTRUCTURE NOISE?

Abstract

Many birds rely on alarm calls during nest defense to communicate about predation risk, and communicating these signals effectively is important to ensuring nestling survival. However, anthropogenic noise produced by oil and gas infrastructure has the potential to disrupt alarm communication by masking or distorting acoustic signals. Birds may overcome these effects by altering the structure of vocalizations to improve transmission in the presence of ambient noise. Here, I tested whether Savannah sparrows (*Passerculus sandwichensis*) altered the rate, duration, peak frequency, first quartile frequency, third quartile frequency, 90% bandwidth, or average power of alarm calls in the presence of gas compressor stations or grid-powered or generator-powered screw pump oil wells, and in relation to overall ambient noise levels (measured independently from infrastructure treatment). Savannah sparrows called at a lower peak frequency, first quartile frequency, and 3rd quartile frequency, and increased the bandwidth of alarm calls close to gas compressor stations, but did not alter call structure with proximity to screw pump oil wells, or in response to overall ambient noise levels. My results demonstrate that even unlearned, structurally simple avian vocalizations can be altered to mitigate effects of anthropogenic ambient noise.

4.1 Introduction

Birds rely on acoustic signaling for many aspects of their lives. Male birds sing to attract mates (e.g. Wasserman 1977) and defend territories (e.g. Nowick and Searcy 2004), nestlings beg to communicate hunger to parents (e.g. Leonard and Horn 2001), and birds of all ages and sexes rely on alarm signals to alert conspecifics to the presence of predators (e.g. Bernath-

Plaisted and Yasukawa 2011). Communicating these signals effectively can have important

consequences for pairing success, nestling development, and predator evasion, so birds are under

selective pressure to ensure vocalizations can be heard over natural background noise (Marler

1955). However, in areas with increasing levels of anthropogenic noise from urbanization and

industrial development, noise may be louder, or occupy different frequencies from natural

background noise (Barber et al. 2010). Accordingly, there is growing concern that anthropogenic

noise may mask or disrupt acoustic signaling (e.g. Habib et al. 2007; Schroeder et al. 2012,

McIntyre et al. 2014a).

Many birds use alarm calls during nest defense to solicit help from conspecifics in

fending off predators (Gill and Sealy 2003), signal to a predator that they have been spotted

(Bergstrom and Lachmann 2001) or distract the predator from the nest (Greig-Smith 1980), alert

mates of an approaching threat (Bernath-Plaisted and Yasukawa 2011), or to induce anti-predator

behavior in nestlings (McIntyre et al. 2014b). Communicating predation risk during nest defense

can have direct consequences for reproductive success: Both American goldfinches (*Spinus*

tristis) (Knight and Temple 1986), and red-winged blackbirds (*Agelaius phoeniceus*) (Knight and

Temple 1988) experienced greater nesting success when they alarm called at higher rates. Alarm

calls can encode valuable information about the nature of a threat, including the level of danger

(Sloan et al. 2005), the type of predator (Gill and Bierema 2013) or the predator's behaviour

(Greisser 2008). Alarm calls with different characteristics are designed to trigger different

behaviours in conspecifics (Templeton et al. 2005, Sloan et al. 2005), so it is important that these

characteristics be relayed effectively if conspecifics are to respond appropriately.

Anthropogenic noise has potential to interfere with acoustic communication by masking

or distorting avian vocalizations. The presence of industrial noise has been linked to lower

pairing success in ovenbirds (*Seiurus aurocapilla*) (Habib et al. 2007) and lower lek attendance in greater sage-grouse (*Centrocercus urophasianus*) (Blickley et al. 2012) suggesting that noise may prevent female birds from detecting or properly interpreting mate-attraction signals. Similarly, nestling tree swallows (*Tachycineta bicolor*) are less responsive to parental feeding cues (Leonard and Horn 2012) and alarm signals (McIntyre et al. 2014a) when exposed to elevated levels of ambient noise. The degree to which noise interferes with acoustic communication is thought to be frequency dependent, with the strongest masking effects occurring when vocalizations overlap in frequency with background noise (Blickley and Patricelli 2012). Because anthropogenic noise is generally loudest at low frequencies, birds with lower frequency vocalizations may be disproportionally affected by noise pollution (Francis et al. 2012). However, noise may also alter avian behavior (Naguib et al. 2013) and vocalization structure (Hanna et al. 2011) when there is no overlap in frequency between vocalizations and background noise.

Birds may alter the structure of vocalizations in several ways that help them to overcome acoustic interference. First, they may simply vocalize louder to increase the signal to noise ratio, a phenomenon known as the Lombard effect (Brumm 2004). This is one of the most effective ways for birds to improve signal transmission in noise (Nemeth and Brumm 2010) and has been documented in the songs of nightingales (*Luscinia megarhynchos*) (Brumm 2004) and the alarm calls of noisy miners (*Manorina melanocephala*) (Lowry et al. 2012). Second, birds may raise the frequency of vocalizations to avoid frequency masking from low-frequency anthropogenic (Slabbekoorn and Peet 2003, Wood and Yezerinac 2006) and natural (Lenske and La 2014) background noise. However, if masking is not a concern, birds may improve signal transmission by lowering the frequency of vocalizations (Potvin et al. 2014), as low-frequency sounds travel

farther than high frequency sounds (Marten and Marler 1977). Birds may also reduce the bandwidth or entropy of vocalizations, as tonal signals with a narrow bandwidth transmit better in noise (Hanna et al. 2011, Lohr et al. 2003). Finally, birds may increase the rate or duration of vocalizations, to increase the likelihood that conspecifics will detect vocalizations through signal redundancy (Brumm and Slater 2006).

While numerous studies have demonstrated that a variety of birds alter the structure of territorial and mate-attraction songs in the presence of ambient noise (Slabbekoorn and Peet 2003, Brumm 2004, Wood and Yezerinac 2006, Hanna et al. 2011), only a handful of recent studies have considered the effects of anthropogenic noise on alarm call structure (Lowry et al. 2012, Potvin et al. 2014, McIntyre et al. 2014a). While birds are under selective pressure to maximize the distance at which conspecifics can detect and locate territorial and mate attraction songs (Marler and Slabberkoon 2004), alarm calls intended to warn others of a threat benefit from being difficult to locate, and being only detectable at a short range, to avoid revealing the caller's location to predators (Marler, 1955, Klump and Shalter 1984). Alarm call structure is typically unlearned, and alarm calls usually consist of simple, single syllable notes designed to efficiently communicate danger, so they tend to be less complex and variable than songs (Marler and Slabbekoorn 2004). This has led some authors to question whether alarm calls are sufficiently flexible to be able to adapt to noise (Patricelli and Blickley 2006, Potvin et al. 2014). However, responding appropriately to alarm calls can have life or death consequences, so birds may be under especially high selective pressure to communicate these signals effectively even under sub-optimal conditions.

In the mixed-grass prairies of southern Alberta, increasing development from the oil and gas industry is altering the acoustic and physical landscape. In Western Canada, 11,102 and

11,226 new wells were drilled during 2013 and 2014, respectively, the years that this study took place (CAODC 2015). Oil and gas wells can impact grassland songbirds through increases in roads, traffic, habitat alteration, and noise produced by the infrastructure (Ludlow et al. 2015). However, the relative effects of these different factors are not well understood.

Savannah sparrows (*Passerculus sandwichensis*) are a common grassland generalist breeding throughout all provinces and territories in Canada and much of the Northern United States. Like other grassland songbirds, Savannah sparrows build their nests on the ground, making them especially vulnerable to predators (Wheelwright and Rising 2008). Parents respond to threats close to their nests by continuously emitting alarm calls, for up to 20 minutes or until the threat goes away (Wheelwright and Rising 2008). They react to these calls by delaying feeding visits, presumably to avoid revealing the location of their nest to predators (see chapter 3, above). The acoustic properties of Savannah sparrow alarm calls are similar to many other avian warning alarm calls, in that they consist of a series of simple, high frequency notes (approx. 7000 – 10 000 Hz, Figure 4.1) that are difficult to locate. These characteristics mean that Savannah sparrow alarm calls do not naturally transmit as far as songs, but also that they occupy a frequency range above which anthropogenic noise is generally loudest.

The purpose of this study was to determine whether Savannah sparrows respond to noise-producing oil and gas infrastructure by altering the structure of their alarm calls. The wider geographical distribution and broad range of habitats occupied by Savannah sparrows may make them more adaptable to disturbance than other grassland endemics. However, the simplicity of alarm call structure may mean that alarm calls are not flexible enough to be altered.
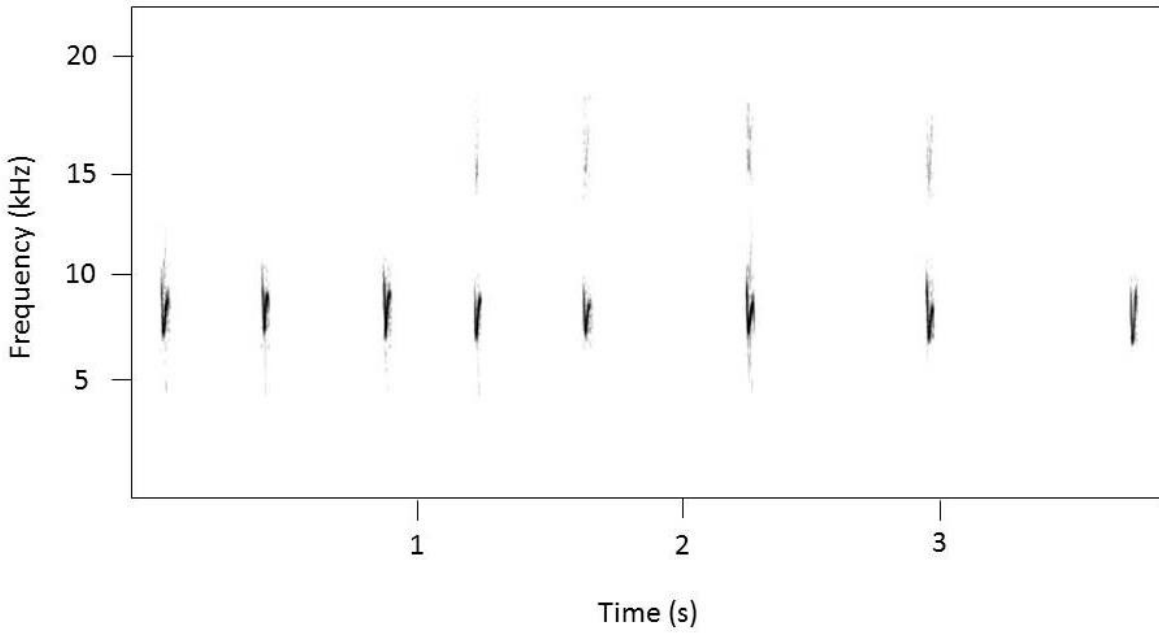
Figure 4.1. A representative sample of Savannah sparrow (*Passerculus sandwichensis*) alarm calls, recorded from a field site near Brooks Alberta (50.5642° N, 111.898° W) during June of 2013. The spectrogram was produced in RavenPro 1.4 Hann Window Function with a Fast Fourier transformation length of 512 samples, 3 dB Bandwidth set at 135 Hz, and overlap of 50%.

4.2 Methods

4.2.1 Study area

Research took place in native mixed-grass prairies in a 200-km radius surrounding Brooks Alberta (50.5642° N, 111.898° W) during May – July of 2013 and 2014. I recorded Savannah sparrow alarm calls at 800 x 200 m sites centered around one of three different types of infrastructure: gas compressor stations ($n = 4$ sites), generator-powered screw pumps ($n = 4$ sites), and grid-powered screw pumps ($n = 5$ sites). Gas compressor stations are facilities that pressurize natural gas for transport through pipelines, consisting of several noise producing turbines, motors and engines. These structures were the loudest of the three infrastructure treatments, producing noise at approximately 82 ± 3.1 dB(C) at 10 m. Screw pumps are a type of oil well that uses positive displacement to extract oil from the ground through one or more rotating screws. In remote areas, these structures may be powered by generators (generator-powered screw pumps), while in areas containing transmission lines they may be connected to the power-grid (grid-powered screw pumps). Generator-powered screw pumps produce noise at greater amplitudes (79 ± 3.5 dB(C) at 10 m) than grid-powered screw pumps (59 ± 2.0 dB(C) at 10 m). Most of the acoustic energy is located in the lower frequency ranges for all infrastructure treatments (Koper et al. 2015). Compressor stations produce their greatest amplitudes at the lowest frequencies, followed by generator-powered, then grid-powered screw pumps (Figure 2.1) I also recorded alarm calls on control sites, which were the same size as infrastructure sites, but were located >800 m from paved roads and noise-producing infrastructure (~52 dB(C) at 10 m, $n = 12$ sites).

4.2.2 Alarm call recordings

To determine whether Savannah sparrows responded to infrastructure noise by altering the structure of anti-predator vocalizations, I recorded alarm calls of 44 free-living adult Savannah sparrows between May and July of each year. I recorded alarm calls from 11 individuals at compressor stations, 8 individuals at generator-powered screw pumps, 10 individuals at grid-powered screw pumps, and 15 individuals at control sites.

I only recorded alarm calls from individuals with 5-day old nestlings, as Savannah sparrows may alter some call features, such as rate (Weatherhead 1978), as investment changes during the nesting cycle. An observer stood at the nest, immediately after conducting the alarm call playback experiment (described in chapter 3). When an adult approached within 10 – 15 m of the nest and commenced alarm calling, the observer used a Zoom H4N Handy Portable Digital Recorder with built in microphone (ZOOM Corporation, Tokyo, Japan), set in an XY stereo microphone configuration (90°) at the maximum recording volume, to record 10 seconds of alarm calls, pointing the microphone directly at the bird. Digital recordings were saved as uncompressed WAV files at a sample rate of 48 kHz with 16-bit resolution.

Once the recording was complete, a Garmin eTrex Legend H ® hand held GPS receiver (3 m precision) was used to measure the distance (in meters) to the perch location where the bird was calling, and 30 sec of ambient noise were recorded, with the microphone pointed straight up. The distance and direction from the microphone to the bird, and the bird's distance and direction to infrastructure, as well as the date, time, wind speed, and wind direction were also documented.

4.2.3 Acoustic Analysis

I uploaded recordings of vocalizations into RavenPro 1.5, using a Hann Window
Function with a Fast Fourier transformation length of 512 samples, 3 dB Bandwidth set at 135
Hz, and overlap of 50%. I selected vocalizations using the methods described by Podos (1997),
including only call features that fell within -24 dB of peak power, while everything else was
considered to be background noise. I extracted 7 call parameters that birds may adjust in order to
increase signal clarity in the presence of noise from all alarm calls recorded in the 10 second
period (15 ± 6 calls per bird) (Table 4.1). I used only robust parameters to assess the effects of
noise on call frequency, which vary little with the exact boundaries of the selection boxes
specified by Raven users, making them more objective (Charif et al. 2010). Average power of
each call was normalized to 1 m following Brumm (2004).

I calibrated average power of calls by playing a recording of white noise of known sound
pressure level, as determined using a Brüel and Kjær 2250 SPL meter and frequency analyzer
(C-weighting) (Brüel and Kjær, Nærum, Denmark) 50 cm from the microphone, and uploading
the recording into Raven 1.5. I used the difference between the Raven reported sound pressure
level and the actual sound pressure level of white noise to calculate the actual sound pressure
level of alarm calls.

Table 4.1. Call features that Savannah sparrows may alter to overcome acoustic interference

Call feature	Definition	Biological significance
Call rate (call/s)	The number of calls per second produced by savannah sparrows. Measured by counting the number of calls emitted over a 10 second period from the spectrogram in Raven 1.5, divided by 10.	Birds may increase call rate in noise to improve the chances of conspecifics hearing vocalizations through signal redundancy (Brumm and Slater 2006)
Duration (s)	The duration, in seconds of each individual alarm call. Measured from the selection spectrum in Raven 1.5.	Birds may increase call duration in noisy environments to improve the chances of conspecifics hearing vocalizations through signal redundancy (Brumm and Slater 2006)
Peak Frequency (Hz)	The frequency band (Hz) within a selected alarm call at which the highest power (peak power) is concentrated. Measured from the selection spectrum in Raven 1.5.	Birds may move the energy within alarm calls to higher frequencies in order to avoid acoustic interference from low frequency ambient noise (Slabbekoorn and Peet 2003, Wood and Yezerinac 2006, Lenske and La 2014) or move the energy within alarm calls to lower frequencies to increase transmission distance (Potvin et al. 2014, Marten and Marler 1977).
90% bandwidth (Hz)	The difference between the 5% frequency and the 95% frequency. Measured from the selection spectrum in Raven 1.5.	Birds may reduce the bandwidth of alarm calls as more tonal signals with a smaller bandwidth transmit better in noise (Hanna et al. 2011).
First quartile frequency (Hz)	The frequency that delineates interval within a selected alarm call that contains the bottom 25% of the energy within the selection. Measured from the selection spectrum in Raven 1.5.	Birds may raise or lower the bottom frequencies of alarm calls in noisy environments, if interference affects only lower frequencies.
Third quartile frequency (Hz)	The frequency that delineates interval within a selected alarm call that contains 75% of the energy within the selection. Measured from the selection spectrum in Raven 1.5.	Birds may raise or lower the upper frequencies of alarm calls in noisy environments, if interference affects only upper frequencies.
Aggregate entropy (u)	A measure of the energy distribution or disorder within a selected alarm call. Low entropy sounds are more tonal, with energy concentrated within one frequency band, whereas high entropy sounds have energy scattered across	Birds may decrease the entropy of vocalizations in noisy environments, as tonal signals transmit better than broadband signals (Hanna et al. 2011, Lohr et al. 2003).

	multiple frequency bands. Measured from the selection spectrum in Raven 1.5	
Average power (1 m) (dB (C))	A measure of loudness, average power was initially measured from the selection spectrum in Raven 1.5 as the spectral density averaged across a selected alarm call, then calibrated to dB(C) (McIntyre et al. 2014) and normalizing to 1 m (Brumm 2004).	Birds may vocalize louder in noisy environments to improve signal transmission by increasing the signal to noise ratio (Brumm 2004).

The average power of ambient noise at the bird's perch location was measured by selecting all frequencies across the entire 30-s ambient noise recording, as well as two smaller frequency bands: 0-3000 Hz (the frequency range in which infrastructure noise is loudest) and 3000-12000 Hz (which includes the frequency range that overlaps with Savannah sparrow alarm calls). Average power was measured from power spectra and calibrated with a white noise recording, as above.

To determine whether ambient noise measurements corresponded with predicted infrastructure noise levels, Leq, a time averaged value for Sound Pressure Level (SPL) in decibels (dB), was measured over a 30-s period at the noise source for each oil or gas structure using a Brüel and Kjær 2250 SPL meter and frequency analyzer. I measured the A-weighted Leq of broadband noise, and measured the Z-weighted Leq for individual 1/3 octave frequency bands. I then used the methods described in ISO protocol 9613-2 (ISO 9613-2, 1996) to predict the Leq of infrastructure noise at individual nests located within each infrastructure site, given the measured distance of each nest to the infrastructure and seasonal averages of climatic variables (barometric pressure, temperature, relative humidity) for the region. To determine whether low frequency and high frequency ambient noise corresponded with predicted

infrastructure noise levels, I averaged the sound pressure level of ambient noise at 1/3 octave frequency bands between 0-1000 Hz, and between 1000-10 000 Hz. This allowed me to separately assess the relationship between broadband, low frequency, and high frequency noise and predicted infrastructure noise levels.

4.2.4 Statistical Analysis

I used generalized linear mixed-effects models to assess whether Savannah sparrows altered alarm call structure in relation to distance from each infrastructure treatment and overall ambient noise (independent of infrastructure treatment). To determine whether changes in call structure were driven by any particular infrastructure type, I modeled effects of infrastructure treatment, (log) distance from the infrastructure, and the interaction between these two variables on each call parameter. To determine whether ambient noise level independently affected call parameters, I conducted 3 sets of analyses modelling the effects of broadband (0 – 24000 Hz), low frequency (0 – 3000 Hz), and high frequency (3000 – 12000 Hz) noise on each call parameter. As wind is an important natural source of noise, I also modeled the effects of wind speed on each call parameter.

I used generalized linear models to determine whether ambient noise in the environment at the time alarm calls were recorded corresponded with predicted sound pressure levels from infrastructure, and wind-generated noise. I conducted three separate analyses, modelling the effects of wind speed and predicted broadband (0-24000 Hz), low frequency (0-1000 Hz) and high frequency (1000 – 10 000 Hz) noise on the sound pressure level on ambient noise measurements in the corresponding broadband (0 -24000 Hz), low frequency (0 -3000 Hz) and high frequency (3000 – 12000 Hz) ranges.

Analyses were conducted using SAS 9.1 statistical software. I determined the distribution

of response variable residuals using diagnostics graphs and deviance/*df* ratio. In some cases,

variables were log-transformed to improve normality. I treated nest ID as a random effect for all

analyses performed. I used AIC to determine whether adding site as a random effect would

improve model fit. In all cases the AIC values for models including both random variables did

not improve model fit ($AIC_{site/nest} > AIC_{nest}$), so I did not include site in the analyses. All other

analyses were conducted following a frequentist approach (Mundry 2011). Effects were

considered significant at α= 0.05.

4.3 Results

4.3.1 Effects of oil and gas infrastructure

While there was no effect of distance from either grid-powered or generator-powered

screw pumps on any of the call parameters examined ($p > 0.1$), within compressor station sites,

closer to the infrastructure Savannah sparrows called at a lower peak frequency ($\beta = 0.2039$, *SE*

$= 0.07125$, *df* $= 636$, *t* $= 2.86$, *p* $= 0.0043$), first quartile frequency ($\beta = -0.4432$, *SE* $= 0.1763$, *df*

$= 636$, *t* $= -2.51$, *p* $= 0.0122$) and third quartile frequency $\beta = 0.1134$ *SE* $= 0.05937$, *df* $= 636$, *t* $=

1.91$, *p* $= 0.0566$), and alarm calls occupied a larger 90% bandwidth ($\beta = -1.0282$, *SE* $= 0.5293$

df $= 636$ *t* $= -1.94$, *p* $= 0.0525$) than on control sites. Farther from compressor stations, Savannah

sparrows raised the frequency and reduced the bandwidth of alarm calls to frequencies consistent

with those observed on control sites (Figure 4.2) There was no effect of distance from

compressor stations on other call structure parameters ($p > 0.1$).

4.3.2 Effects of ambient noise

Ambient noise ranged from 41 - 72 dB in the broadband frequency range (mean = 60 dB), and was louder in the low frequency range (mean = 68 dB, range: 50 - 81 dB) than in the high frequency range (mean: 30 dB, range: 21 – 48 dB). Both wind speed and predicted sound pressure level of infrastructure noise were positively correlated with broadband and low frequency noise levels. Neither wind speed nor predicted infrastructure noise levels contributed to high frequency ambient noise measurements (Table 4.2).

There was no effect of low frequency or broadband frequency ambient noise on any of the call parameters examined ($p > 0.1$). In the high frequency range, increases in ambient noise were linked with a trend in increased average power ($\beta = 0.1746$, $SE = 0.1055$, $df = 635$, $t = 1.66$, $p = 0.0984$) and 3rd quartile frequency of alarm calls ($\beta = 0.001799$, $SE = 0.001017$, $df = 635$, $t = 1.77$, $p = 0.0774$), but was not related to any of the other call parameters examined ($p > 0.1$).

Wind speed at the time of recordings ranged from < 1 km/hr to 16 km/hr. Wind speed had a marginally significant effect on the average power of alarm calls ($\beta = -0.3393$, $SE = 0.178$, $df = 636$, $t = -1.91$, $p = 0.0571$), with Savannah sparrows calling at a lower amplitude with increasing wind speeds. Wind speed had no effect on any of the other call parameters examined ($p > 0.3$).
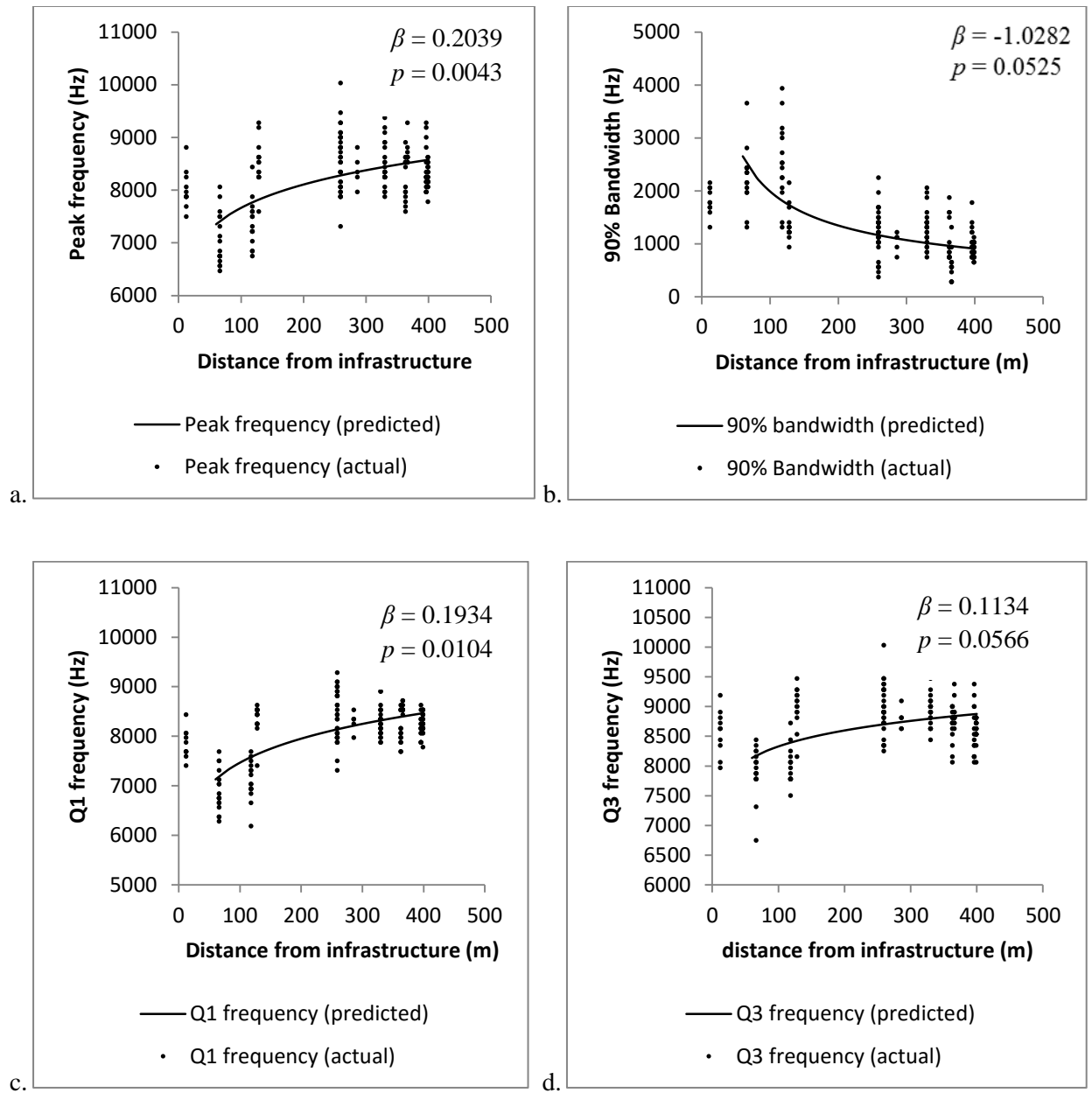
Figure 4.2 The effects of distance from compressor stations on a) peak frequency, b) 90% bandwidth, c) First quartile frequency and d) third quartile frequency of Savannah sparrow alarm calls. Recordings were made from 11 individuals at compressor station sites in southern Alberta during May – July of 2013 and 2014.

Table 4.2 The effects of predicted SPL (calculated using ISO protocol 9613-2, 1996) and wind speed on the ambient noise in the environment (extracted from calibrated recordings in Raven 1.5)

Frequency Range	Parameter	df	β	SE	Wald's X^2	p
Broadband noise (0 -24000 Hz)	**Intercept**	1	30.3628	11.6486	6.79	0.0091
	Predicted SPL	1	0.7145	0.3219	4.93	**0.0264**
	Wind speed	1	0.8162	0.2759	8.75	**0.0031**
Low frequency noise (0 -3000 Hz)	**Intercept**	1	24.7208	16.7168	2.19	0.1392
	Predicted SPL	1	1.1761	0.4887	5.79	**0.0161**
	Wind speed	1	0.8000	0.2720	8.65	**0.0033**
High frequency noise (3000 - 12000 Hz)	**Intercept**	1	3.3731	0.3489	93.44	<.0001
	Predicted SPL	1	0.0035	0.0164	0.05	0.8293
	Wind speed	1	-0.0084	0.0087	0.93	0.3340

4.4 Discussion

Savannah sparrows responded to natural gas compressor stations by shifting the energy within alarm calls to lower frequencies and increasing the bandwidth of alarm calls, but surprisingly, none of these changes in call structure occurred in relation to changes in ambient noise level measured independently from infrastructure treatment. This suggests that the effects of infrastructure on acoustic communication may not be driven by overall ambient noise levels, but by factors (acoustic and otherwise) specific to compressor stations.

One possible reason for the disproportionate effect of compressor stations on alarm call structure is that they were the loudest infrastructure treatment, so noise levels close to the infrastructure may be above a threshold at which Savannah sparrows can communicate effectively with unaltered alarm calls, while generator- and grid-powered screw pumps, producing only moderate levels of noise, may be sufficiently quiet not to cause interference. However, the types of changes in call structure observed close to compressor stations run contrary to numerous previous studies, which have found that birds raise, not lower, the pitch of songs when exposed to elevated levels of ambient noise (e.g. Slabbekorn and Peet 2003, Wood and Yezerinac 2006, Lenske and La 2014). In these instances, increasing the frequency of vocalizations is thought to improve signal transmission by reducing overlap with low-frequency masking noise (Slabbekoorn and Peet 2003). However, the songs examined in these studies were much lower in frequency than the alarm calls of Savannah sparrows. While the minimum frequency of Savannah sparrow alarm calls ranged from 4044 -9094 Hz, the minimum frequency of great tit (*Parus major*) songs range from 2820 – 3770 Hz (Slabbekoorn and Peet 2003), the minimum frequency of song sparrow (*Melospiza melodia*) songs range from 1200 – 2000 Hz (Wood and Yezerinac 2006) and the minimum frequency of white throated sparrow (*Zonotrichia*

albicollis) songs is approximately 2150 Hz (Lenske and La 2015). When the frequency of vocalizations overlaps with low frequency background noise, raising their pitch may be an effective way for many species to avoid acoustic interference. However, given that Savannah sparrow alarm calls fall well above the frequency range in which infrastructure noise is the loudest, they may derive little benefit from calling at a higher pitch.

Instead, lowering the frequency of alarm calls may improve signal transmission because low frequency sounds propagate farther than high frequency sounds (Marten and Marler 1977). Given that Savannah sparrow alarm calls are so high-pitched, they may be able to improve signal transmission by reducing the frequency of alarm calls, without risking increasing masking from low frequency anthropogenic noise. These results echo the finding of two recent studies which found red-winged blackbird trills to decrease in third quartile frequency when exposed to non-masking low frequency noise (Hanna et al. 2011), and silvereye (*Zosterops lateralis*) alarm calls to decrease in peak frequency, but increase in propagation distance, when exposed to urban noise (Potvin et al. 2014). These findings highlight the importance of considering the acoustic properties of vocalizations and ambient noise in understanding which vocal adjustments might be the most adaptive.

Another possible explanation for the disproportionate effect of compressor stations is that the higher concentration of physical structures associated with compressor stations may change the physical environment in ways that interfere with acoustic communication. In addition to being the loudest infrastructure treatment, compressor stations also have more physical disturbance associated with them than either of the other treatments, including more buildings, fans, fences and other structures. Warren et al. (2006) suggested that the higher density of reflective surfaces from buildings on city streets can cause reverberations that may mask or blend

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call features, thereby degrading the quality of acoustic signals. This effect could be expected to be similar to that observed in forested environments (Blummenrath and Dabelsteen 2004); however, concrete is less absorbent than vegetation, so the degrading effect of anthropogenic reflective surfaces is likely stronger than that of forests (Warren et al. 2006). These reflective surfaces may simultaneously act to amplify anthropogenic noise through a flutter-echo effect (Warren et al. 2006), further interfering with signal transmission. Accordingly, the elevated noise levels associated with compressor stations, combined with the higher density of reflective surfaces from buildings surrounding these structures, may create a particularly challenging environment for acoustic communication.

Lowering the frequency of alarm calls may not only improve signal transmission in noisy sites, but also in more structurally complex environments associated with compressor stations. Sounds that are lower in frequency propagate farther in structurally complex environments such as forests, as they are less susceptible to absorption, scattering and reverberations than higher frequency sounds (Marten and Marler 1977). Indeed, birds that live in forest habitats tend to sing at a lower frequency than those of open habitats (Boncoraglio and Saino 2007). Given that Savannah sparrows are grassland generalists and occupy a range of habitats, including lightly treed environments (Wheelwright and Rising 2008), they may be better equipped to adapt to more structurally complex acoustic environments than other grassland obligate species living in this area.

The increase in alarm call bandwidth close to compressor stations is surprising, as tonal signals with a smaller bandwidth transmit better in noise (Hanna et al. 2011) and in structurally complex environments (Warren et al. 2006) than those with more entropy and greater bandwidths. Accordingly, it does not seem likely that this change in call structure is adaptive, but

instead may be a side effect of lowering the energy of vocalizations to lower frequencies. Broadband vocalizations are also easier to locate than tonal signals with a narrow bandwidth (Klump and Shalter 1984) so this change in call structure may make Savannah sparrows with altered calls more susceptible to predation.

The sound pressure level of ambient noise was positively correlated with both wind speed and the predicted sound pressure level of infrastructure noise within the low and broadband frequency ranges, but not within the high frequency range. These results are not surprising, as infrastructure noise (Rosa et al. 2015) and wind-generated noise (Klump and Shalter 1984) are loudest within low frequency ranges, but taper off with increasing frequency. This suggests the sound pressure level of noise within the high-frequency range was influenced by factors other than wind or infrastructure, such as bird song and insect noise, which can occupy frequencies greater than 3000 Hz (personal observation). However, these factors were not directly measured in this study, so it is not possible to identify the source of this high frequency noise with great certainty.

Contrary to expectations, Savannah sparrows reduced call amplitude with increasing wind speeds. This finding was surprising, as wind represents a significant natural noise source, so it follows that Savannah sparrows should vocalize louder with increasing wind speeds. One possible explanation for this finding is technical rather than biological: Wind has the potential to affect propagation of signals by increasing refraction of sound waves (Embleton 1996). It is possible that greater wind speeds may have refracted alarm calls, reducing the amplitude of calls that reached the microphone.

Overall, the results from this study indicate that Savannah sparrows are capable of altering the structure of alarm calls in the presence of noise-producing oil and gas infrastructure. The ability to make these adjustments is dependent upon a number of factors including body size (Brumm 2004), the energy to produce louder vocalizations (Obweger and Goller 2001), and the behavioural flexibility required to detect acoustic interference and make appropriate changes to vocal features (Patricelli and Blickley 2006). This demonstrates that unlearned vocalizations such as alarm calls can be altered to enhance propogation (e.g. Patricelli and Blickley 2006, Potvin et al. 2014). Communicating alarm signals effectively is essential for Savannah sparrows to be able to adequately protect their nests from predation, so the selective pressures to be able to transmit these signals in a variety of acoustic conditions are likely considerable. These findings contribute to the growing evidence (Potvin et al. 2014, Lowry et al. 2014) that the simplicity of unlearned vocalizations such as alarm calls does not limit the ability of some birds, including Savannah sparrows, from modifying these calls to overcome acoustic interference.

While altering the structure of alarm calls may help Savannah sparrows communicate about predation risk in proximity to compressor stations, this does not necessarily mean that they are able to overcome the negative impacts of infrastructure noise. Birds that exercise vocal plasticity may suffer from increased energetic costs (Patricelli and Blickley 2006). It is also possible that these vocal adaptions are not enough to completely avoid the masking effects of infrastructure. Further work is needed to determine whether the alterations made to alarm calls are sufficient to overcome acoustic interference. While there is evidence that Savannah sparrows are less responsive to alarm calls produced under natural conditions at compressor station sites (Chapter 3) it is not clear whether they are equally unresponsive to altered calls. Future studies

might examine whether altered calls elicit a stronger response than unaltered calls from

Savannah sparrows nesting close to noise-producing infrastructure.

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CHAPTER 5: GENERAL DISCUSSION AND MANAGEMENT IMPLICATIONS

Overall, the findings of this thesis indicate that Savannah sparrows were less responsive to alarm calls in the presence of gas compressor stations, but that they altered the structure of alarm calls closer to this infrastructure. However, neither of these effects occurred at grid-powered or generator-powered screw pump sites, or increased with the amplitude of ambient noise in the environment. This suggests that both of these effects may be specific to the quality of noise produced by compressor stations, or physical factors associated with the infrastructure, such as the number or size of structures associated with these facilities.

In the introduction to this thesis, I postulated that if Savannah sparrows were able to alter the structure of alarm calls to overcome acoustic interference, anthropogenic noise may not present much of a barrier to communication. However, the degree to which altering calls may help Savannah sparrows to improve responsiveness to alarm calls depends on which mechanisms drive the effects of compressor stations on anti-predator behaviour. If reduced responsiveness to alarm calls at compressor station sites is driven by acoustic masking (Lohr et al. 2003), altering alarm calls may improve signal transmission. However, if effects are driven by distracting effects of infrastructure noise (Chan et al 2010), altering alarm calls may have little effect on the ability of Savannah sparrows to display appropriate anti-predator behaviour at these sites. Further work could address this question by determining whether Savannah sparrows are more responsive to altered calls than unaltered calls in the presence of gas compressor stations.

Under the Migratory Bird's Convention Act, oil and gas companies in Canada are required to avoid activities which cause direct mortality, loss of nests, or sensory disturbance to migratory birds such as Savannah sparrows (CEPA 2013). One approach that may be used to

reduce the impacts of noise pollution on people and wildlife is infrastructure noise reduction mechanisms. To reduce noise associated with screw-pump oil wells, efforts may focus on replacing generator-powered screw pumps with grid-powered screw pumps, as they are quieter. To reduce noise associated with compressor stations, fans may be equipped with sound-baffling structures, or hospital grade mufflers may be installed to reduce the amplitude of compressor station noise (communications with Cenovus Energy engineer, 2012).

The results of this thesis do not justify replacing generator-powered screw pumps with grid-powered screw pumps in order to reduce the impacts of oil well noise on songbirds. While generator-powered screw pumps are louder than grid-powered screw pumps, I found no difference in responses to alarm calls, or alarm call structure, between generator-powered screw pumps and control sites. Furthermore, Bernath-Plaisted (2015) found that nest success of Savannah sparrows and other grassland songbirds was significantly lower at grid-powered screw pump sites than at generator-powered screw pump sites, suggesting that factors other than noise associated with grid-powered screw pump sites such as transmission lines and roads may be detrimental to reproductive success of grassland songbirds (Bernath-Plaisted, 2015).

In contrast, there may be some benefits to adding noise reduction mechanisms to compressor stations. Savannah sparrows were less responsive to alarm calls, and altered the structure of calls at these sites, suggesting that compressor station noise may impact acoustic anti-predator communication. However, given the lack of clarity over whether these impacts were driven by the amplitude of noise, the quality of noise, or other physical structures associated with compressor stations, reducing the amplitude of compressor station noise may or may not improve anti-predator communication. Given the hefty price tag associated with these mechanisms (from discussions with Cenovus Energy engineer, 2012), it would be advisable to

determine the effectiveness of these structures on improving avian communication prior to widespread distribution.

While anthropogenic noise is one increasingly discussed impact associated with oil and gas development (Blickley and Patricelli 2010), other associated factors such as fragmentation and roads (Bi et al. 2011), exotic vegetation (Ludlow et al. 2015), human and vehicle traffic (Summers et al. 2011) and habitat alteration (Gilbert and Chalfoun 2011) may also impact songbirds. Bernath-Plaisted (2015) found that nest success was lower at all oil and gas infrastructure sites than at control sites; however, inactive (noise-free) infrastructure sites had equally reduced nest success, suggesting that factors other than noise impacted reproductive success. Thus, strategies to protect grassland songbirds in the face of increasing oil and gas development in southern Alberta must take into account factors other than just noise.

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